



# Swimming Activity as an Indicator of Seasonal Diapause in the Copepod *Calanus finmarchicus*

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Copepods dominate zooplankton biomass of the upper ocean, especially in the highly seasonal boreal and polar regions, for which specific life-cycle traits such as the accumulation of lipid reserves, migration into deep water and diapause are key adaptations. Understanding such traits is central to determining the energetic consequences of high latitude range shifts related to climate change and ultimately, biogeochemical models of carbon flow. Using the calanoid copepod *Calanus finmarchicus*, we explore a new indicator of diapause, swimming activity, and assess its relationship with respiration. Stage CV copepods were sampled in late summer from shallow (epipelagic) and deep (mesopelagic) water at both slope and basin locations within the Fram Strait at a time when the animals had entered diapause. Using high-throughput quantitative behaviour screening on *ex-situ* swimming activity, we found that irrespective of sampling station copepods from the mesopelagic show highly reduced activity ( $88.5 \pm 3.4\%$  reduction) when compared to those from the epipelagic with a clearly defined threshold between epi- and mesopelagic animals ( $\sim 5$  beam breaks  $30 \text{ min}^{-1}$ ). Mesopelagic individuals were also larger ( $12.4 \pm 8.8\%$ ) and had more lipid reserves ( $19.3 \pm 2.2\%$ ) than epipelagic individuals. On average, copepods from the basin station exhibited respiration rates similar to overwintering rates observed elsewhere ( $1.23 \pm 0.76 \mu\text{g C d}^{-1}$ ), while respiration rates of copepods from the shelf station were more consistent with active metabolism ( $2.46 \pm 1.02 \mu\text{g C d}^{-1}$ ). Nevertheless, active and diapausing rates were observed in individuals from both stations at both epi- and mesopelagic depths. We suggest that rapid screening of activity may provide an early indicator of diapause before it becomes fully apparent and consistent in other physiological indicators. Ultimately, swimming activity may provide a useful tool to assess the putative endogenous and exogenous factors involved in diapause onset, provide a handle on the energetics of diapause, and input to biogeochemical carbon models on *C. finmarchicus*.

**Keywords:** copepod, torpidity, metabolism, lipid, diapause, Fram Strait, Arctic Ocean

## INTRODUCTION

High-latitude seas are undergoing rapid climate-driven change, expected to affect the distribution and phenology of marine organisms, including the keystone zooplankton species *Calanus finmarchicus* (e.g., Wilson et al., 2016a, Wilson et al., 2016b). This copepod dominates zooplankton biomass in Atlantic-influenced seas (Auel et al., 2003), where it occupies a key trophic position as the main food source for commercially important fish like herring (Prokopchuk and Sentyabov, 2006) and endangered marine mammals such as North Atlantic right whales (Greene et al., 2003) and as a food source for many seabirds (Karnovsky et al., 2003; Kwaśniewski et al., 2012; Vogedes et al., 2014). By carrying out large-scale seasonal vertical migrations that often span hundreds of meters (e.g., Baumgartner and Tarrant, 2017) copepodite stages 4 and 5 (CIV-V), move carbon and lipids into deep-water layers in a process known as the lipid pump which has important implications for high-latitude carbon sequestration and pelagic-benthic coupling (Jónasdóttir et al., 2015; Visser et al., 2017).

To survive the food-depleted autumn and winter months at high latitudes, *C. finmarchicus* typically undergoes a period of dormancy in which CIV and CV copepodites form aggregations at depths below the permanent thermocline (Jónasdóttir et al., 2015). To meet the energetic reserves required to overwinter with subsequent molt and gonad development the following spring, large lipid reserves are accumulated (Hirche, 1996). To lower their metabolism, respiration rate is reduced to 10-20% of that recorded in shallower conspecifics (e.g., Hirche, 1983; Ingvarsdóttir, 1998; Ingvarsdóttir et al., 1999; Auel et al., 2003). Indeed, elevated metabolism impedes survival over the course of diapause, which may last 6 to 8 months (Baumgartner and Tarrant, 2017). Therefore, respiration measurements (as a proxy for metabolic rate) and collection depth, are typically used to distinguish diapausing copepods from those actively feeding and migrating.

Diapause is generally considered to be under endocrine control (e.g., Alldredge et al., 1984; Hirche, 1996; Baumgartner and Tarrant, 2017) and upstream expression of 'diapause associated' genes involved in antioxidative defense and lipid catabolism (Tarrant et al., 2008; Häfker et al., 2018a; Häfker et al., 2018b; Lenz et al., 2021; Payton et al., 2022). In addition, body size, lipid sac volume, and ambient temperature are all likely to affect metabolism at this time fueled by protein and lipid stores. These lipids are typically wax esters which undergo phase transitions at low temperatures and high pressure (e.g., Kirkesæter, 1977; Rey-Rassat et al., 2002; Tarling et al., 2022) and have been postulated as providing a means of buoyancy control (Pond and Tarling, 2011). For the copepodid stages CIV and CV, reaching optimal lipid sac fullness in spring has been suggested as a potential trigger for the onset of diapause (e.g., Pond and Tarling, 2011; Maps, 2014; Schmid et al., 2018). However, stored lipid energy reserves are only partially utilized at depth with most being used for re-ascent post diapause, molting, mate finding, and gamete production (Rey-Rassat et al., 2002). Hatching of offspring is then timed to coincide with favorable conditions associated with the spring phytoplankton bloom (Leu et al., 2011).

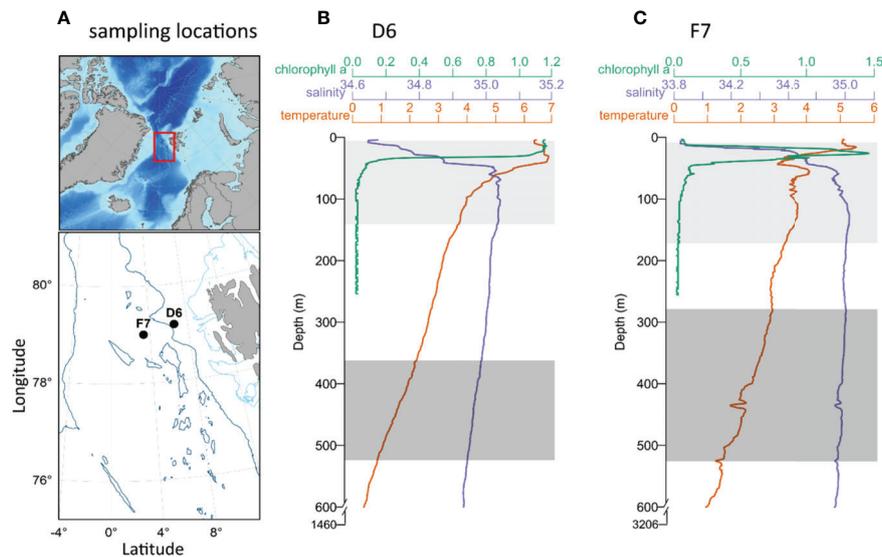
In addition to reduced respiration in diapause there are also many observational reports of reduced activity, often referred to as torpidity, in calanoid copepods from mid- and high- latitudes (e.g., Hirche, 1983; Alldredge et al., 1984; Hirche, 1987; Bathmann et al., 1990; Hirche, 1996; Auel et al., 2003; Hirche et al., 2006). Campbell (2003), citing Hirche (1983), described torpid *Calanus* copepods as having a distinctive "overwintering posture" in the laboratory, in which their first antennae is folded ventrally. Low intensity swimming is associated with low metabolic demand (Svetlichny and Hubareva, 2005) and is possibly adaptive in that it is less likely to attract tactile and visual predators than active swimming (e.g., Hirche, 1996; Hirche, 1998; Dale et al., 1999). However, these observations are not consistent with other studies reporting continued swimming and/or feeding during periods of metabolic reduction in boreal copepods such as *C. helgolandicus* (Corner et al., 1974; Williams and Conway, 1982; Williams and Conway, 1984) and *C. euxinus* (Svetlichny et al., 1998), as well as other high-latitude copepods (Norrbín, 1996). An "active diapause" that includes continued feeding, was previously reported in freshwater copepods (e.g., Wyngaard, 1988; Naess and Nilssen, 1991) and insects (e.g., Hodek, 2002).

Physiological indicators such as respiration rate, electron motor activity and clock gene expression can be useful detectors of diapause, but they are not immune to sampling and incubation artefacts, motivating studies to identify those indicators that most accurately simulate *in-situ* overwintering conditions (e.g., Båmstedt, 1980; Mayzaud, 1986; Campbell, 2003). It is likely that swimming activity integrates across such physiological and genetic processes and therefore an objective quantification of this may provide a novel indicator of diapause state. Our approach was to collect high-latitude *C. finmarchicus* from epipelagic and mesopelagic depths during late summer, with the aims of: i) comparing swimming activity to other metrics of physiological condition including mass-specific respiration rates, body size and lipid content, and in doing so; ii) better characterizing and distinguishing diapausing individuals of *C. finmarchicus*.

## MATERIALS AND METHODS

### Study Area and Stations

We sampled from the Fram Strait, northern Greenland Sea (Figure 1A), during August 2019 onboard RRS James Clark Ross. This region is a transition between southern boreal waters and northern polar waters and is a key area for pelagic production, where calanoid copepods comprise up to 70% of the zooplankton biomass (Smith, 1988; Hirche, 1991). Samples were collected at one slope station (D6; 79.2 °N, 6.6 °W; 20-22/08/19) and one basin station (F7; 78.9°N, 3.3°W; 13-14/08/19). In this region, *C. finmarchicus* are reported to enter dormancy in July and August (e.g., Hirche, 1987; Smith, 1988; Hirche, 1991) and D6 and F7 were considered to potentially represent differing overwintering habitats for *C. finmarchicus* in terms of both depth and temperature (e.g., Pepin et al., 2011; Jónasdóttir et al., 2019). Both stations were ice-free at the time of sampling.



**FIGURE 1 | (A)** Bathymetric map of the North Atlantic and Arctic Ocean. The area sampled within the Fram Strait (indicated by the red rectangle), shows the locations of slope station D6 and basin station F7 (black circles) west of Svalbard. Light and dark blue contours represent 200 m and 2000 m isobaths respectively. **(B, C)** Vertical profiles of temperature, salinity and chlorophyll A between the surface and 600 m (temperature and salinity) and 270 m (chlorophyll a), at D6 **(B)** and F7 **(C)** also showing total water depth. Light (epipelagic) and dark grey rectangles (mesopelagic) represent the integrated upper and lower depths respectively from which copepods were collected. Physical environment data were provided by Changing Arctic Ocean/Robyn Owen (British Oceanographic Data Centre).

## Physical and Biological Environment

Vertical profiles of temperature and salinity were measured at both stations to 600 m depth by a ship-board conductivity, temperature, and depth profiler (CTD; SBE911plus, SeaBird Electronics). An *in-situ* chlorophyll fluorometer (Aquatracka III fluorometer, Chelsea Technologies) on the CTD measured chlorophyll a concentration to a depth of 270 m. Niskin bottles collected seawater from 250 m at each station (salinity: ~35‰), which was subsequently filtered (0.2  $\mu\text{m}$ ) for use in the copepod swimming activity and respiration experiments.

## Zooplankton Sampling and Processing

Copepods were sampled using a Hydrobios<sup>®</sup> Mammoth MultiNet system, comprising nine individual nets (1  $\text{m}^2$  apertures, 300  $\mu\text{m}$  mesh) that were towed vertically at 10 – 20  $\text{m min}^{-1}$  (ascent speed). Two depth strata were targeted as part of a zooplankton sampling campaign, approximately 520 – 285 m and 170 – 5 m, hereafter referred to as mesopelagic and epipelagic, respectively. The upper and lower depths of the multinet system were set according to the vertical position of zooplankton at each station, as determined by an initial exploratory net deployment. *In situ* temperature ranges at mesopelagic depths were 0.9 – 1.9°C and 1.5 – 2.9°C in D6 and F7 respectively, and at epipelagic depths 3.8 – 6.9°C and 3.1 – 5.5°C at D6 and F7 respectively (**Figures 1B, C**).

During sampling and deck handling, zooplankton were shielded from changes in light intensity by covering the net cod-ends in dark material. Net contents were immediately transferred into filtered seawater and kept in lidded, light-excluding black buckets, within the onboard light and temperature-controlled room at 2°C. Stage CV *C. finmarchicus*

were manually selected from samples using a stereomicroscope (ZEISS Stemi 2000-C) under a dim red light in an onboard temperature-controlled room, taking care to avoid visibly damaged or dead animals. To distinguish *C. finmarchicus* from its closely related congener, *C. glacialis*, we used lack of redness of the antennae, shown to be a good indicator for *C. finmarchicus* (e.g., Nielsen et al., 2014; Daase et al., 2018). Subsequent molecular analysis of multinet samples collected concurrently at the same stations as described here confirmed that 99 – 100% of the identified sequences returned from both stations were *C. finmarchicus*. Unknowns comprised less than 5% of the total sequences returned (pers. comm.: Penelope Lindeque, Plymouth Marine Laboratory).

## Swimming Activity and Morphometrics

Across both stations, swimming activity was monitored for a total of 357 individual copepods (167 and 190 from meso- and epipelagic depths respectively). At each station, swimming activity was measured for 6 days using a high-throughput quantitative behavioural assay. Specifically, individual copepod activity was monitored using modified LAM10 activity monitors (Trikinetics<sup>®</sup>). These are infrared (IR) light beam arrays which detect the movement of an individual copepod in a test chamber (clear acrylic tubes of volume 5 ml, diameter 10 mm and length 64 mm, containing 0.2  $\mu\text{m}$  filtered seawater). IR beams were situated 5 mm above the bottom of each tube. Beam breaks were registered on a laptop computer using proprietary Trikinetics<sup>®</sup> software (filescan.exe). Six 32 channel LAM10 monitors were placed in constant darkness within an incubator at constant 4°C (D6) and 2.8°C (F7), consistent with the approximate water

temperatures at the base of the pycnocline at the respective stations. On culmination of the swimming experiments, all copepods (minus 27 and 17 from meso- and epipelagic depths respectively due to death/loss) were photographed laterally using a Carl ZEISS AxioCam MRc5 camera) to provide images used for measurements of body size (prosome areas) and lipid sac area (both in  $\text{mm}^2$ ). Length/area measurements were made by digitally tracing perimeters which allowed calculation of the lipid sac area/prosome area (LA/PA) ratios. Calibrated area measurements were made using the open-source software ImageJ (<https://imagej.net>). The mean number of beam breaks per 30 minute interval per individual were compared between depths (mesopelagic and epipelagic) and stations (slope and basin) using either a one-way ANOVA or Kruskal-Wallis rank sum, after testing for normality (Shapiro-Wilk test) and equal variance (Brown-Forsythe test). Statistical analyses were performed using R v 4.1.3., with an  $\alpha$  level of 0.05 for each test. Similar comparisons were performed with the morphometric data (prosome area and LA/PA).

## Respiration Analysis

For each station, oxygen consumption was measured in copepods collected from the same sampling events as those collected for the swimming activity experiment (described above). Ten *C. finmarchicus* CV were randomly sampled from each depth collection (meso- and epipelagic) and incubated for 2 days using a Loligo microplate respirometry system (1700  $\mu\text{l}$  well plates containing 0.2  $\mu\text{m}$  filtered seawater), calibrated to ambient collection temperatures. As with the swimming activity setup, respiration experiments were conducted in the dark within temperature-controlled incubators, at 4°C (D6) and 2.8°C (F7). Mass-specific respiration rates ( $\mu\text{g O}_2 \mu\text{gDW}^{-1} \text{h}^{-1}$ ) were calculated from oxygen consumption data during a 100-minute period after stabilisation using the respR aquatic respiratory analysis package (Harianto et al., 2019; Harianto et al., 2021) within the R computing environment (Development Core Team R, 2008). These rates were first determined per individual copepod ( $\mu\text{g O}_2 \text{h}^{-1}$ ) using oxygen concentrations between 80–90% air saturation to ensure independent respiration and adjusting for the background rate (0.2  $\mu\text{m}$  filtered seawater only). Respiration rates were then corrected for copepod mass using a prosome length (PL) to dry weight (DW) regression from *C. finmarchicus* in the Nansen Basin in summer ( $\text{DW} = 0.0095 \times \text{PL}^{3.3839}$ ; Hirche and Mumm, 1992). Mass-specific respiration rates were compared between depths and stations as described above.

## RESULTS

### Hydrography

Average temperatures within the sampled epipelagic and mesopelagic zones at D6 were  $5.16 \pm 1.17^\circ\text{C}$  and  $1.52 \pm 0.40^\circ\text{C}$ , respectively. Mean salinity values at D6 were  $34.96 \pm 0.13$  (epipelagic) and  $34.96 \pm 0.01$  (mesopelagic) (Figure 1B). At F7, average temperatures were  $3.78 \pm 0.53^\circ\text{C}$  in epipelagic and  $2.26 \pm$

$0.44^\circ\text{C}$  in mesopelagic zones, respectively. Mean salinities at F7 were  $34.85 \pm 0.30$  (epipelagic) and  $34.97 \pm 0.02$  (mesopelagic) (Figure 1C). Sea surface chlorophyll a concentrations were  $2.5 \pm 0.4 \text{ mg m}^{-3}$  at D6 (Figure 1B) and  $1.1 \pm 0.7 \text{ mg m}^{-3}$  at F7 (Figure 1C), and CTD profiles demonstrate that the water column of F7 was highly stratified with chlorophyll a maximum within the thermocline at 26 m (Figure 1B), while D6 had higher concentrations of chlorophyll a above its comparatively weaker thermocline (Figure 1C).

## Comparisons of Morphology, Respiration and Swimming Activity

Morphometric analysis revealed that copepods from the mesopelagic had larger bodies and greater lipid fullness (LA/PA ratios) compared to the epipelagic individuals (ANOVA,  $P < 0.05$ ). LA/PA ratios for both meso- and epipelagic copepods were higher on the slope than in the basin (Kruskal-Wallis ANOVA,  $P < 0.01$ , Table 1 and Figures 2, 3).

We found no significant difference in respiration rate between the meso- and epipelagic copepods at either station (One-Way ANOVA,  $P > 0.05$ , Table 1 and Figure 4). At D6 (4°C), average individual respiration rates were  $0.27 \pm 0.12 \mu\text{g O}_2 \text{h}^{-1}$  ( $0.0010 \pm 0.0006 \mu\text{g O}_2 \mu\text{gDW}^{-1} \text{h}^{-1}$ ) for mesopelagic copepods and  $0.34 \pm 0.12 \mu\text{g O}_2 \text{h}^{-1}$  ( $0.0014 \pm 0.0005 \mu\text{g O}_2 \mu\text{gDW}^{-1} \text{h}^{-1}$ ) for epipelagic copepods. At F7 (2.8°C), mesopelagic and epipelagic rates were  $0.14 \pm 0.08 \mu\text{g O}_2 \text{h}^{-1}$  ( $0.0005 \pm 0.0002 \mu\text{g O}_2 \mu\text{gDW}^{-1} \text{h}^{-1}$ ) and  $0.14 \pm 0.13 \mu\text{g O}_2 \text{h}^{-1}$  ( $0.0007 \pm 0.0006 \mu\text{g O}_2 \mu\text{gDW}^{-1} \text{h}^{-1}$ ) respectively. The mass-specific rates were significantly lower in the epipelagic copepods at the basin station when compared to the slope (Kruskal-Wallis ANOVA,  $P = 0.007$ ). Mass-specific rates were also lower in mesopelagic copepods from the basin than slope, but the large variability in the data meant that this difference was not statistically significant (Table 1 and Figure 4).

Comparing swimming activity in *C. finmarchicus* CV between depths, mesopelagic copepods were found to have a ~86% and ~91% reduction in mean number of beam breaks at D6 ( $1.12 \pm 2.86 \text{ 30 min}^{-1} \text{ ind.}^{-1}$ ) and F7 ( $2.11 \pm 3.63 \text{ 30 min}^{-1} \text{ ind.}^{-1}$ ) respectively when compared to those from the epipelagic ( $12.3 \pm 10.8 \text{ 30 min}^{-1} \text{ ind.}^{-1}$  and  $15.1 \pm 17.9 \text{ 30 min}^{-1} \text{ ind.}^{-1}$ , Kruskal-Wallis ANOVA,  $P < 0.001$ , Table 1 and Figure 5A). Epipelagic activity levels in individual animals did not differ significantly between stations (Kruskal-Wallis ANOVA,  $P = 0.91$ ) but mesopelagic activity levels were higher at F7 (Kruskal-Wallis ANOVA  $P = 0.014$ , Table 1 and Figure 5B). The cumulative distribution of light beam breaks recorded by each activity monitor was found to follow two different distributions (two sample Kolmogorov-Smirnov test,  $D = 0.97$ ,  $p < 0.001$ ) with ~5 beam breaks  $30 \text{ min}^{-1}$  marking the upper limit of mesopelagic activity and the lower limit of epipelagic activity recorded by each monitor (Figure 5C).

## DISCUSSION

### Overview

We used a high-throughput quantitative behavioural assay to investigate swimming activity in *C. finmarchicus* in relation to

**TABLE 1 |** Statistical comparison of each diapause indicator between stations (slope D6 and basin F7) and depths (epi- and meso-pelagic).

Dataset (test)	Comparison	n	Normality (P)	Equal variance (P)	F/H	P
Mass-specific respiration rates (ANOVA)	Slope-Depth	19	0.658	0.487	3.504	0.079
	Basin-Depth	15	0.155	0.159	0.531	0.479
	Mesopelagic-Station	16	0.185	0.116	3.917	0.068
	Epipelagic-Station	18	0.584	0.651	9.364	<b>0.007</b> slope
Prosome area (KW)	Slope-Depth	155	0.299	0.009	6.781	<b>0.009</b> meso
	Basin-Depth	158	0.014	<0.001	37.834	<b>&lt;0.001</b> meso
	Mesopelagic-Station	140	0.019	0.013	5.487	<b>0.019</b> basin
	Epipelagic-Station	173	0.011	0.032	3.645	0.056
LA/PA (KW)	Slope-Depth	155	0.291	<0.001	57.143	<b>&lt;0.001</b> meso
	Basin-Depth	158	<0.001	<0.001	18.441	<b>&lt;0.001</b> meso
	Mesopelagic-Station	140	0.0006	<0.001	30.119	<b>&lt;0.001</b> slope
	Epipelagic-Station	173	<0.001	<0.001	8.011	<b>0.005</b> slope
Swimming activity (KW)	Slope-Depth	192	<0.001	<0.001	79.552	<b>&lt;0.001</b> epi
	Basin-Depth	192	<0.001	<0.001	48.509	<b>&lt;0.001</b> epi
	Mesopelagic-station	192	<0.001	0.051	6.012	<b>0.014</b> basin
	Epipelagic-station	192	<0.001	0.187	0.011	0.914

The test used for each dataset (one-way or Kruskal-Wallis ANOVA) is noted, along with satisfaction ( $\alpha = 0.05$ ) or non-satisfaction of normality and equal variance. F or tie-adjusted H statistics and probability values are provided with statistically significant P values ( $P \leq 0.05$ ) highlighted in bold. <sup>slope</sup> = higher values at station D6, <sup>basin</sup> = higher values at station F7, <sup>meso</sup> = higher values in copepods from the mesopelagic, <sup>epi</sup> = higher values in copepods from the epipelagic. Significant comparisons shown in bold.

diapause, using samples collected in the Fram Strait in late summer. We found 88.5% reduction in the mean activity of larger, more lipid rich mesopelagic individuals relative to those sampled from the epipelagic, indicating that deeper living individuals had entered diapause during, or prior to, August. Here we discuss the significance of these findings in relation to the suite of other measured diapause indicators and highlight the utility of reductions in swimming activity (torpidity) as a novel indicator of diapause in high-latitude copepods.

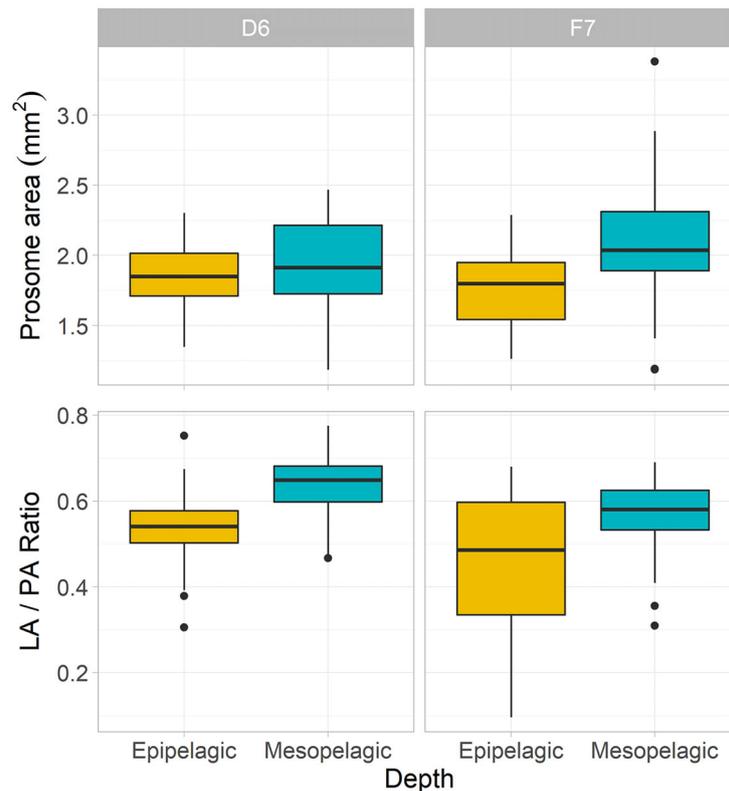
## Swimming Activity in the Context of Diapause

Previous observations of stage CV *C. finmarchicus* in diapause found them to remain motionless even when physically touched (e.g., Hirche, 1983; Hirche, 1987; Hirche et al., 2006) and illuminated (e.g., Alldredge et al., 1984). As well as being an adaptation for conserving energy, becoming torpid during diapause is considered to reduce the risk from tactile gelatinous and semi-gelatinous predators (e.g., Hirche, 1996; Dale et al., 1999). Nevertheless, a variety of terms have been used in earlier work to imply that diapause may be relatively “plastic”, with many qualitative terms used to describe this such as: active-diapause, pseudo-diapause, aleteo-diapause etc. (e.g., Naess and Nilssen, 1991; Hirche, 1996; Norrbin, 1996). This suggests that levels of torpidity may be variable within and between individuals over time. However, a conceptual model for the phases of diapause in *Calanus* developed by Hirche (1996) proposes that ‘deep torpor’ or ‘refractory phase diapause’ accompanying arrested development is only observed in autumn, after an initial ‘induction phase’ when some degree of metabolic reduction has already taken place. As copepods in the Greenland Sea and Fram Strait are reported to depart surface waters for overwintering territory in July (e.g., Hirche, 1987; Smith, 1988; Hirche, 1991), our finding of low swimming activity in late August (e.g.,  $\leq 5$  beam breaks  $30 \text{ min}^{-1}$ , **Figure 5C**) suggests that behavioural cessation occurs in the ‘induction

phase’ of the proposed model by Hirche (1996), at a time when other processes (reduced ingestion / digestive track and metabolism) are still ramping down. Thus, measurements of swimming activity, as shown here, may provide an additional indicator to the physiological states of diapause and a simple and reliable tool to readily distinguish animals not in diapause (e.g.,  $\geq 5$  beam breaks  $30 \text{ min}^{-1}$ ). Future work to compare these rates with individuals collected later in the season will help to rapidly, and potentially more reliably, distinguishing between ‘induction’, ‘refractory’ or ‘activation’ phases as described by Hirche (1996).

A key aim of this study was to compare measurements of swimming activity with other whole-animal diapause metrics including body size, lipid fullness and respiration. We show strong agreement between swimming activity and morphometric analyses in that animals with larger lipid reserves tend to be in deeper waters and less active. It has been shown that a certain degree of lipid storage is required in the congeners *C. glacialis* and *C. hyperboreus* before migration to diapause becomes an advantageous strategy (Schmid et al., 2018), a scenario likely to also hold true for *C. finmarchicus* at latitudes investigated here. Though LA/PA measurements are not widely available for *Calanus* copepods, our results from mesopelagic individuals are consistent with other measurements of lipid fullness in dormant *C. finmarchicus* (Pepin et al., 2011; Jónasdóttir et al., 2015; Schmid et al., 2018, **Figure 3**). It is therefore highly plausible that the mesopelagic individuals, which had accrued high LA/PA and less variable ratios than animals collected at epipelagic depths, had entered diapause, with a corresponding cessation of swimming activity.

Our results also indicate that mesopelagic individuals were larger in size than shallower counterparts. Differences in size can also be explained by variable feeding rates, quantity, or quality of food available to individuals (Pepin et al., 2011), or timing of development into the CV stage. Mechanistic models have found that individuals with better body condition (i.e., high fat/somatic



**FIGURE 2** | Morphometric characteristics of *C. finmarchicus* CV from epipelagic (yellow) and mesopelagic (blue-green) depths at slope station D6 and basin station F7. Boxplots of mean prosome area (PA) and lipid sac to prosome area (LA/PA) ratios per depth and station (box shows interquartile range around the median as the horizontal line, with black circles representing outliers).

body mass ratio) are able to afford the less risky option of entering diapause early to avoid predation (Fiksen and Carlotti, 1998). Moreover, in the same model, smaller and low body condition individuals were likely to remain at the surface in late summer, a behaviour that would be adaptive over starvation during the winter (Fiksen and Carlotti, 1998). Irrespective of the proximate factors involved, our data support that there are smaller copepods in the epipelagic and that these are more active than larger animals in the mesopelagic. This suggests that these smaller epipelagic copepods are actively foraging, presumably to increase lipid reserves with which to enter diapause successfully later in the summer or autumn (e.g., Smith, 1988).

Several studies have reported up to 70 – 90% reduction in respiration between active and dormant *Calanus* (Auel et al., 2003; Bailey, 2010 and references therein; Maps, 2014), yet the magnitude of metabolic reduction during the initiation phase of diapause remains under debate (Baumgartner and Tarrant, 2017). Intense metabolic reduction has been detected in the capital breeder *C. hyperboreus* sampled from ~2300 m in the Fram Strait (Auel et al., 2003; Hirche et al., 2006). Perhaps the shallower depths from which *C. finmarchicus* was sampled here (~500 m) explains the absence of consistent observations of

reduced respiration rates. *C. hyperboreus* in the Greenland Sea are reported to migrate to overwintering depths as early as April (Hirche, 1997). Jónasdóttir et al. (2019) compiled *C. finmarchicus* overwintering respiration data from numerous studies which together encompassed a wide range of habitats in the North Atlantic and sub-Arctic. Over this distributional range, the mean respiration rate was  $1.34 \mu\text{g C d}^{-1}$  (maximum:  $2.20 \mu\text{g C d}^{-1}$  and minimum  $0.65 \mu\text{g C d}^{-1}$ ). Comparing this with our data, we obtain average values within, or just above, this range. Similarly, Smith (1988) sampled *C. finmarchicus* (CV, AF) in the Fram Strait in June and July 1984, reporting mass-specific respiration rates of  $0.0006 - 0.0026 \mu\text{g O}_2 \mu\text{g DW}^{-1} \text{ h}^{-1}$ . This matches well with the distribution of weight specific rates we report in **Figure 4**, although we did observe several individuals with rates below  $0.0006 \mu\text{g O}_2 \mu\text{g DW}^{-1} \text{ h}^{-1}$  at F7, possibly since our study was carried out later in the year, when more animals would be in deep diapause.

Overall, respiration in *C. finmarchicus* CV show no clear difference between epi- and mesopelagic animals, but rates more closely resembled an overwintering metabolic state at basin station F7, and an active metabolic state at slope station D6. The high variability in respiration rates between individuals at both stations and depths reflect the likelihood of a mix of

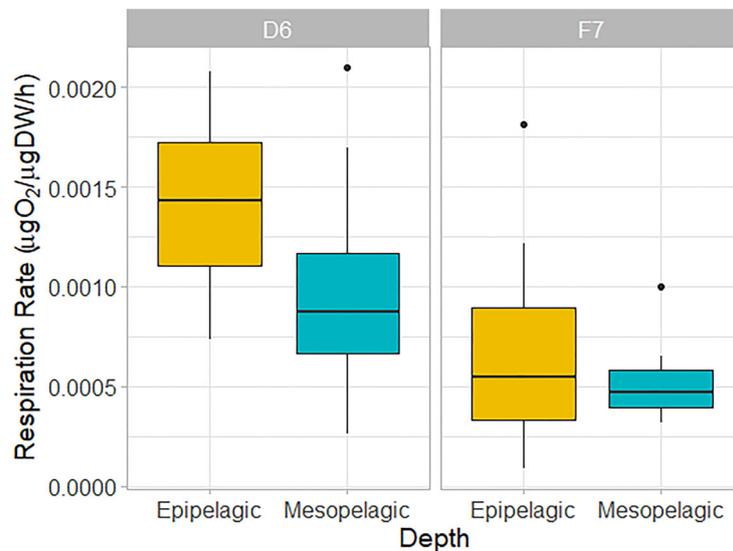


**FIGURE 3** | Representative images of *C. finmarchicus* CV from epi- (left) and mesopelagic depths (right) at slope station D6, showing larger body sizes and lipid sacs in deeper animals. Scale bar = 1mm.

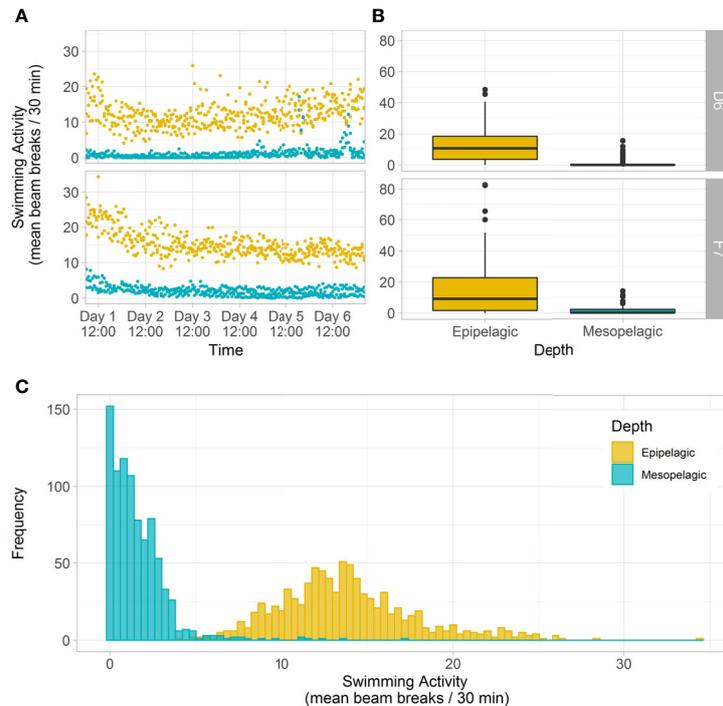
metabolic states present. This could be due to differences in the time since descent to mesopelagic depths, with late descenders ('stragglers'; Smith, 1988), still exhibiting higher respiration rates. We also note that swimming activity in mesopelagic individuals was, on the rare occasion, comparable to that of epipelagic animals (Figure 5C). We propose that further work should focus on the relationships between swimming activity and seasonal metabolic cycles using large sample numbers, as well as possible links with diel patterns of gene expression in early diapause (Tarrant et al., 2008; Häfker et al., 2018a; Häfker et al., 2018b; Lenz et al., 2021).

### A Comparison of Swimming Activity and Metabolic Rate

The relationship between respiration rate and swimming activity is not as apparent as with the other metrics measured. The observed reduction in swimming activity in mesopelagic animals without a large drop in respiration warrants further discussion. This could be due in part to our measurement of slope mesopelagic copepods at slightly warmer temperatures than they would experience *in situ* and that the marginal differences between depths at the slope station (D6) would likely be stronger if the mesopelagic copepods were



**FIGURE 4** | Weight-specific respiration rates of *C. finmarchicus* CV from epipelagic (yellow) and mesopelagic (blue-green) depths at slope station D6 and basin station F7. Box shows interquartile range around the median as the horizontal line, with black circles representing outliers.



**FIGURE 5** | Swimming activity (IR light beam breaks) of *C. finmarchicus* CV from epipelagic (yellow) and mesopelagic (blue-green) depths at slope station D6 and basin station F7, over 6 days in constant darkness. **(A)** Mean beam breaks recorded by each activity monitor ( $n=32$  animals) at 30-minute intervals across the 6-day monitoring period. **(B)** Box plots of mean beam breaks per individual CV copepod per depth and station, averaged over 6-days (showing interquartile range around the median as the horizontal line, with black circles representing outliers). **(C)** Histogram showing the frequency of mean beam breaks recorded by each activity monitor ( $n=32$  animals) at 30-minute intervals, pooled across both stations. There were slight differences in mesopelagic collection depths at the two stations: 375 – 500 m and 285 – 520 m at D6 and F7 respectively.

tested at a colder temperature. However, results from this and other studies suggest that reduced metabolism does not necessarily translate into reduced swimming or feeding activity (Corner et al., 1974; Williams and Conway, 1982; Williams and Conway, 1984; Norrbin, 1996; Svetlichny et al., 1998). This indicates that respiration measurements, by themselves, would not be able to distinguish ‘active’ diapause (Norrbin, 1996) from other diapause states. Interestingly, Båmstedt (1980) found that respiration rates of the copepod *Acartia tonsa* declined almost immediately after transfer to the lab, while the activity of the electron transport system took several days to change after collection. Other studies have noted unexpected relationships (or lack thereof) between oxygen consumption and weight in carbon (e.g., Ingvarsdóttir, 1998), or between seasonal oxygen consumption and life cycle events (e.g., Campbell, 2003 and references therein). It should be noted that in copepods, swimming typically contributes 30 – 40% to the total maintenance costs (Alcaraz and Strickler, 1988) and hence an active animal should have a much higher respiration rate than an inactive one. This is exemplified in *C. helgolandicus* in which a six-fold increase in respiration was observed at maximum activity when compared with being motionless (Svetlichny and Umanskaya, 1991). However, individual variability in respiration rate between active and inactive

animals has been reported (e.g., Båmstedt, 1980), hence demonstrating that measurements on individuals is important. The microrespirometry approach employed here is ideal for measuring low oxygen consumption rates in individual animals, but the small incubation chambers constrain nearly all activity. Subsequent studies should make activity and respiration measurements on the same individuals.

## Conclusion and Next Steps

Here we show that swimming activity, when combined with morphometric data and collection depth, provides an early, clear, and consistent indication of life history transitions in *C. finmarchicus*. The methodology we describe has potential applications in understanding the advantages, plasticity and energy budgets associated with diapause in this important group of copepods.

The finding that animals which remain in the epipelagic are active is perhaps not surprising. As was reviewed by Varpe (2012), there are trade-offs in remaining active and feeding at this time, with the optimal decision dependent on several exogenous (e.g., depth, temperature, predation pressure and latitude) and endogenous factors (e.g., lipid volume and storage capacity, reproduction strategy). For example, in Arctic fjords with few predators and rich organic food supply,

continued feeding during winter at depth, in combination with reduced metabolism, confers an advantage for lipid-poor individuals. This explanation may offer insights into similar observations in other habitats i.e., the ubiquity of high activity in Arctic fjords during the Polar Night as highlighted by Berge et al. (2015). The ‘decision’ to remain active will undoubtedly depend on food availability and the risk from predators dictated by local community structure. How this is scaled up to open ocean environments, where zooplankton populations are more partial to advection and where predators are more ephemeral, would need further investigation.

The insights gained from including swimming activity with a clearly defined threshold between epi- and mesopelagic animals (e.g., ~5 beam breaks 30 min<sup>-1</sup>, **Figure 5**) alongside more typical diapause indicators (depth of collection and body size) will help to interpret the duration of energy reserves for torpid and active animals. To do so requires linking individual variability in swimming activity with respiration within the population, thereby improving estimates of respired carbon released at depth during overwintering (Tarling et al., 2022). Such estimates would strengthen future attempts to calculate the magnitude of the *Calanus* lipid pump (Jónasdóttir et al., 2015; Visser et al., 2017).

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary materials. Further inquiries can be directed to the corresponding author.

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## AUTHOR CONTRIBUTIONS

All authors (JG, JF, GT, JC and KL) designed the study, contributed to data analysis, and drafted the manuscript. JG, JF and GT additionally collected field samples and carried out the lab work JG and JF contributed equally to this work. All authors contributed to the article and approved the submitted version.

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