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# Geographic variability in the seasonality of euphausiid diel vertical migrations among three locations in coastal British Columbia, Canada

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Diel vertical migration (DVM) is a behaviour observed across zooplankton taxa in marine and limnetic systems worldwide. DVM influences biogeochemical cycling and carbon drawdown in oceanic systems and alters prey availability for zooplanktivorous species. DVM has been well studied among zooplankton, and many exogenous and endogenous triggers as well as adaptive significances have been hypothesized. However, second-order variability in DVM timing, the deviation of DVM times to respective dawn and dusk times throughout the year, is a less-studied phenomenon that can help identify the factors influencing migration timing as well as demonstrate the changes of DVM behaviours within and across systems. Here, we quantified seasonal trends in second-order variability of DVM timing of euphausiids at Brooks Peninsula, Clayoquot Canyon, and Saanich Inlet near Vancouver Island, British Columbia, Canada, over multiple years using upward-facing moored echosounders. We used generalized additive mixed models to characterize this seasonality. DVM timing relative to civil twilight times showed strong seasonality at all locations, with euphausiids remaining near the surface longer than expected in spring and summer, and shorter than expected in winter. Euphausiids spent less time near the surface at Brooks Peninsula and Clayoquot Canyon than at Saanich Inlet throughout the year. Increased primary productivity in Saanich Inlet, which reduced light penetration and hid euphausiids from visual predators, likely drove this difference. Our findings confirm that proper understanding of DVM behaviours must account for seasonal variability due to context-specific oceanographic and ecological parameters. This is particularly pertinent when attempting to model the biogeochemical or predator–prey interactions influenced by DVM behaviours.

**Keywords:** active acoustics, biological oceanography, diel vertical migration, euphausiids, predator–prey interactions, time series, zooplankton.

## Introduction

Euphausiids are a major component of the zooplankton community along the coast of British Columbia (BC) and a key trophic link between plankton and nekton (Robinson, 2000; Ware and Thomson, 2005). It is estimated that over a quarter of euphausiid production per year off the SW coast of Vancouver Island is consumed by Pacific hake *Merluccius productus* and Pacific herring *Clupea pallasii* (Robinson and Ware, 1994). These fish populations are thought to be limited by the available biomass of euphausiids (Ware and Thomson, 2005). In response, euphausiids in this region are known to perform diel vertical migration (DVM) as a mechanism to escape this predation pressure (Sato *et al.*, 2013).

DVM has been studied for over two centuries in zooplankton communities globally, in both marine and freshwater ecosystems (reviewed by Bandara *et al.*, 2021). It has been generally considered to be an anti-predator defence behaviour, whereby zooplankters hide from visual predators at depth during daylight hours, then migrate to the surface to feed at night, based on the widespread observation that most zooplankton perform vertical migrations around dawn and dusk, the transitions of civil twilight (Vuorinen, 1987; Pearre, 2003; Urmy and Benoit-Bird, 2021). However, debate has continued as to its evolutionary costs and benefits and the various endogenous and exogenous triggers of the behaviour (Kerr *et*

*al.*, 2015; Cisewski and Strass, 2016). Globally, it has been estimated that DVM by zooplankton results in a global export flux of 0.8 PgC year$^{-1}$ from the euphotic to the mesopelagic zone (Archibald *et al.*, 2019). The export estimates of these flux models are known to be sensitive to the ratio of time spent by zooplankton at depth but do not, however, account for variability of DVM timing beyond changes due to the timing of dawn and dusk.

As dawn and dusk times cycle over the course of a year, the timing of DVM events also changes with the twilight, a process known as first-order variability of DVM timing (Sato *et al.*, 2013). However, many other factors have also been found to influence these timings, including prey availability, predation risk at the surface vs. at depth, life history stage, turbidity, circadian clock mechanisms, among myriad others (Kerr *et al.*, 2015; Häfker *et al.*, 2017; Bandara *et al.*, 2021; Benoit-Bird and Moline, 2021). The effects of these factors can result in additional variability of DVM timings relative to dawn and dusk times, known as second-order variability. With so many factors influencing DVM behaviour, comparison among site-specific observations offers one means to parse the effects of individual forcing factors. To this end, modern active acoustic instruments have become invaluable for long-term and continuous observation of zooplankton DVM behaviour.
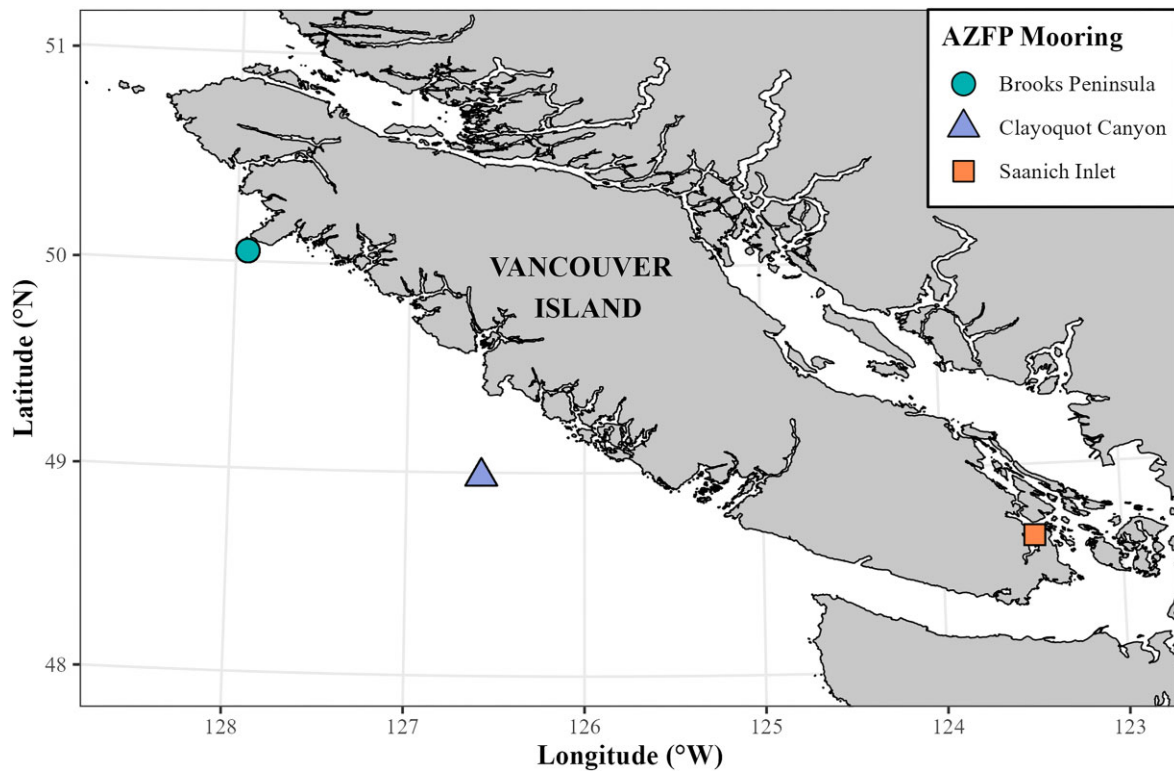
**Figure 1.** Locations of the three AZFP moorings used in this study.

Whereas traditional ship-board acoustic or plankton net monitoring of zooplankton location in the water column is limited by the availability of ship time, autonomous acoustic moorings can provide continuous samples of backscatter, which can be used to assess zooplankton behaviour at a given location over longer time periods. Several studies have used acoustic time series of more than 1 year to gather data on seasonality in zooplankton DVM behaviour (Tarling, 2003; Sato *et al.*, 2013; Cisewski and Strass, 2016; Inoue *et al.*, 2016). These studies include either fine temporal resolution data, long time scales from multiple monitoring locations, and analyses of the second-order variability of DVM patterns. However, none have integrated all of these contributing factors in a single analysis. Here we attempt to fill some of these gaps with the integration of fine-scale, long-term acoustic time series from three locations: the exposed Brooks Peninsula and Clayoquot Canyon off the west coast of Vancouver Island, and the sheltered Saanich Inlet within the Strait of Georgia in BC, Canada (Figure 1).

These three sites provided a comparative study of euphausiid DVM behaviour at regions with different oceanographic regimes, but which were at most 360 km apart. Using data from moorings maintained by Fisheries and Oceans Canada at Brooks Peninsula and Clayoquot Canyon, and the Ocean Networks Canada (ONC) cabled observatory at Saanich Inlet, we were able to compare exposed populations of euphausiids in well mixed and predator-rich waters, to sheltered populations in the Inlet, which experience highly seasonal food availability and a well stratified water column. We hypothesized that given the different oceanographic conditions between the regions, there would be significant differences in the second-order variability in DVM timing of euphausiids.

As Saanich Inlet experienced more seasonal fluctuation, greater primary productivity, and supports generally fewer predators of euphausiids than Brooks Peninsula or Clayoquot Canyon, we hypothesized that euphausiids in Saanich Inlet would display greater seasonality in DVM timing, which would be evident as greater second-order variability (Mackas *et al.*, 1997; Timothy and Soon, 2001; Gargett *et al.*, 2003; Peña and Varela, 2007; Perry and Schweigert, 2008). By characterizing the local variability in DVM timing of an abundant and ecologically critical taxon, we hope to demonstrate the importance of understanding the variability in DVM timing beyond that due to changes in dawn and dusk time over the course of a year.

## Materials and methods

### Oceanographic description of sites

From August 2017 to September 2019, two Acoustic Zooplankton and Fish Profilers (AZFP) developed by ASL Environmental Inc. were deployed by Fisheries and Oceans Canada for two 1-year periods at the continental shelf break at Brooks Peninsula and Clayoquot Canyon. Brooks Peninsula is located along the northwestern shelf of Vancouver Island, BC, Canada, while Clayoquot Canyon is a submarine canyon that incises the shelf break along the centre of Vancouver Island (Figure 1). Both sites are completely exposed to the Pacific Ocean and lie at the northern edge of the California Current upwelling zone, experiencing deep mixing due to the combination of strong waves and seasonal upwelling (Ware and McFarlane, 1989; McFarlane *et al.*, 1997). Many species of pelagic and demersal fish occur along the shelf break, including Pacific hake *Merluccius productus*, sablefish *Anoplopoma*

*fimbria*, Pacific herring *Clupea pallasii*, and Pacific salmon (*Oncorhynchus* spp.) (Robinson and Ware, 1994; Buckley and Livingston, 1997; McFarlane *et al.*, 1997; Robinson, 2000). Some of these species are resident year-round, while others transit through the area as part of their life cycle. These fish gather along the shelf break due to the large population of prey species that congregate in the upwelling zone along the shelf (Mackas *et al.*, 1997; Lu *et al.*, 2003). Brooks Peninsula and Clayoquot Canyon are therefore representative in many ways of the productive yet turbulent offshore environment along the shelf-break off the west coast of Vancouver Island.

Saanich Inlet, in contrast, is a reverse estuarine fjord that is highly sheltered, very productive, and which experiences little deep mixing (Herlinveaux, 1962; Gargett *et al.*, 2003). Saanich Inlet is well studied for its unique oceanographic conditions, as it receives nutrient-rich water from the nearby Fraser River plume, which strongly stratifies the upper 80 m of the water column in the inlet due to a shallow sill at the mouth (Anderson and Devol, 1973). This, in conjunction with the lack of fetch in the inlet (i.e. relative to prevailing wind) causes little mixing to occur, and thus an anoxic zone forms below 100 m within the inlet. Due to the high nutrient load and stratification, Saanich Inlet is highly productive and experiences strong spring phytoplankton blooms (Takahashi *et al.*, 1977; Gargett *et al.*, 2003). Blooms are seasonal, occurring in the spring/summer and somewhat in the fall, and the constituent phytoplankton is consumed by numerous zooplankters, including euphausiids. Pelagic fish, including Pacific herring (*Clupea pallasii*), exploit plankton blooms, and consume zooplankton; however, many demersal zooplanktivorous fish [e.g. Pacific hake (*Merluccius productus*) and rockfish species (*Sebastes* spp.)] are less abundant in the inlet due to anoxic conditions. Within Saanich Inlet, ONC operates the VENUS cabled undersea observatory, a powered oceanographic platform with a mounted AZFP instrument for continuous active acoustic monitoring of the water column (Owens *et al.*, 2022).

## Data collection

The AZFPs deployed along the exposed West coast of Vancouver Island at Brooks Peninsula and Clayoquot Canyon were deployed from September 2017 to August 2018 and again from August 2018 to August 2019. For the sheltered Saanich Inlet, AZFP data from the VENUS cabled observatory from October 2016 to December 2020 were used to accommodate for gaps in the time series due to maintenance of the mooring (Ocean Networks Canada Society, 2016, 2017, 2018, 2019a, 2019b, 2020a, 2020b). Each mooring was equipped with three transducer frequencies (67, 125, and 200 kHz at Brooks Peninsula and Clayoquot Canyon; 38, 125, and 200 kHz at Saanich Inlet), with ping rates of 12 s at Brooks Peninsula and Clayoquot Canyon, and 2 s at Saanich Inlet. Data from the 125 kHz transducers were used for the identification of the zooplankton migration. RBRduet pressure and temperature sensors (RBR Ltd) were mounted on the exposed moorings to calculate the mean mooring depth and determine true surface range. Full technical specifications of each mooring are provided in Supplementary Table A1.

Data collected from the exposed moorings were adjusted using CTD (conductivity, temperature, depth) sensor data collected from nearby sampling stations to determine the sound speed and absorption coefficient through the water column at each site (Supplementary Table A2) (Mackenzie, 1981; Francois and Garrison, 1982). Data collected from the Saanich Inlet mooring were calibrated and adjusted by ONC.

## Identification and enumeration of acoustic scatterers

To confirm that most of the acoustic scattering signal of the zooplankton was attributable to euphausiids, we compiled zooplankton biomass data from zooplankton tows conducted by Fisheries and Oceans Canada between 2016 and 2019 during daylight hours using bongo nets at stations within 37 km (i.e. 20 nautical miles) of each mooring. Only tows that sampled to at least 80 m were included for Saanich Inlet tows, and to at least 100 m for Brooks Peninsula and Clayoquot Canyon tows, as these depths should ensure that a representative sample of the zooplankton scattering layer during daytime was collected. We then determined the proportion of the total biomass and abundance of zooplankton greater than 5 mm in length to assess the main taxa that contributed to the acoustic signal. The acoustic signal of zooplankton was isolated from that of swimbladder-bearing fishes using a multi-frequency change in mean-value backscattering strength approach (De Robertis *et al.*, 2010).

## Determination of vertical migration times

We visually determined the vertical migration times of euphausiids in Echoview (Echoview Software Pty Ltd). To visually determine vertical migration times, we examined the 125 kHz echograms of $S_v$ (volume backscattering strength) data at a threshold of −80 dB each day and considered the migration timing as the time when the densest zooplankton scattering layer crossed the 20 m depth threshold line (Figure 2). For dusk migrations, this was when the first scatterers ascended above a depth of 20 m, while for dawn migrations this was when the last scatterers descended below 20 m.

To initially verify that these migration times followed civil twilight times, we fit the migration times for the dawn and dusk DVM events to linear models with the time of dawn or dusk, the location of the mooring, and the interaction between the two, as the predictors.

After determining the dawn and dusk DVM event times for each day, we calculated the deviation of each DVM event from civil twilight time as per:

$$Dev_{dawn} = DVM_{dawn} - t_{dawn}, \qquad (1)$$

$$Dev_{dusk} = DVM_{dusk} - t_{dusk}, \qquad (2)$$

where $Dev_{dawn}$ and $Dev_{dusk}$ are the deviations of the dawn and dusk DVM events from the actual dawn and dusk times in minutes, $DVM_{dawn}$ and $DVM_{dusk}$ are the times of the dawn and dusk DVM events, and $t_{dawn}$ and $t_{dusk}$ are the true dawn and dusk times for the given date and location. Using these definitions of deviation, dawn migration events with more positive $Dev_{dawn}$ values indicate that euphausiids are remaining at the surface longer than expected, while dawn migration events with more negative $Dev_{dawn}$ values indicate that euphausiids are remaining at depth longer than expected. The opposite is true for dusk migration $Dev_{dusk}$ values.
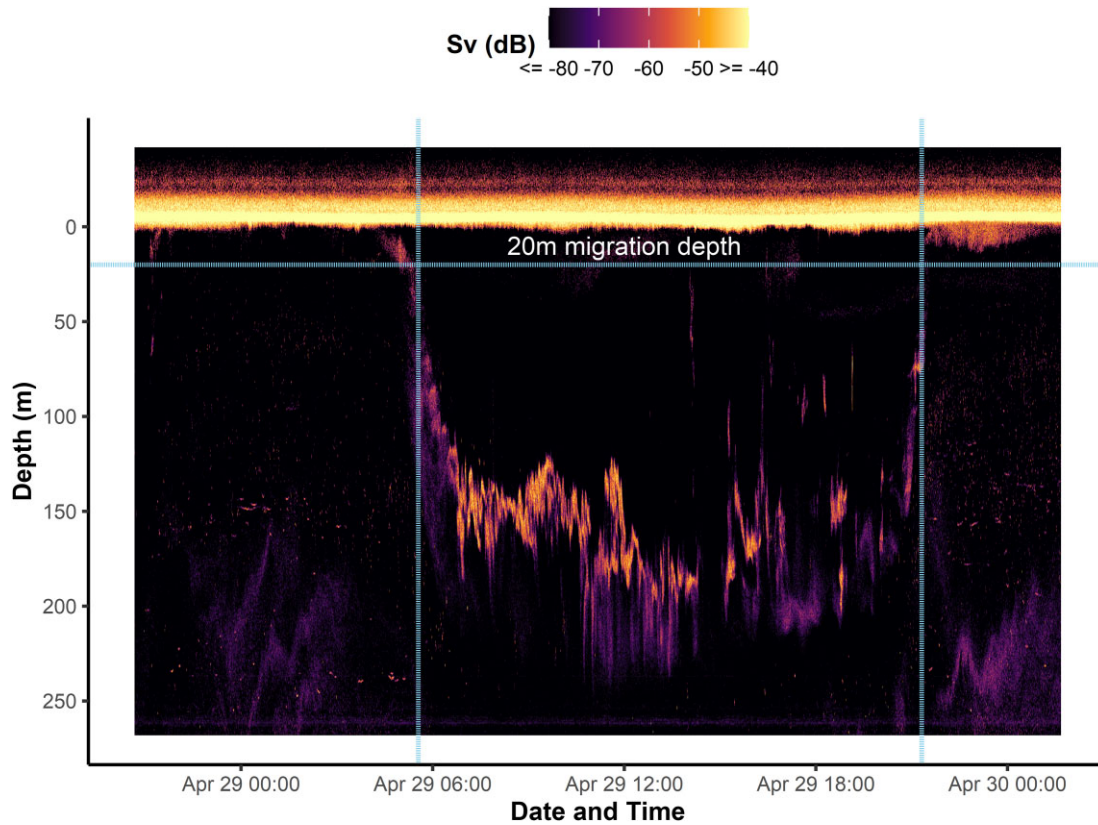
**Figure 2.** Example echogram of characteristic backscattering intensity ($S_v$, in decibels) at 125 kHz over a 24-h period on April 29, 2019, at Brooks Peninsula to demonstrate how migration timings were determined for each day. The horizontal line symbolizes the 20-m depth line used to define migration occurrence. The vertical lines indicate the identified migration times for this date. This example echogram represents a pre-classification phase of the analysis workflow, and thus includes backscattering from both zooplankton and fishes. The strong scattering visible below 100 m during daylight hours (around 0600–2100) is likely mainly comprised of euphausiid aggregations.

## Seasonal modelling of DVM deviation times using generalized additive mixed models with autoregressive terms

To test whether the deviations of DVM event times from dawn/dusk times changed seasonally at each location, we used corrected Akaike's information criterion (AICc) weights to compare two generalized additive mixed models with autoregressive terms (GAMMAR). By using GAMMARs, we were able to test whether seasonality (second-order variability) was significantly influencing DVM timing while accounting for temporal autocorrelation in the data. We compared two models; the seasonal model:

$$Dev_t = \beta_0 + s(day\ of\ year) + \varphi Dev_{t-1}, \qquad (3)$$

where $\beta_0$ is a constant intercept term, $Dev_t$ is the deviation of the DVM event from the civil twilight time for day $t$, $s$(day of year) is a seasonal smoothing term of the day of the year using cyclic cubic splines, and $\varphi Dev_{t-1}$ is an autoregressive order-1 term; and the null model:

$$Dev_t = \beta_0 + \varphi Dev_{t-1}, \qquad (4)$$

where the seasonal smoothing term has been removed. We fit both the seasonal and null models for each location-DVM event combination, resulting in six tests of seasonal and null models. We used an autoregressive order-1 term for each model as an autocorrelative function (ACF) of the deviations suggested a first order autocorrelative nature. The ACF of the

residuals of each model reveals that nearly all of the temporal autocorrelation is accounted for with the first order autoregressive term.

## Photosynthetically active radiation data collection

To quantify differences in light penetration at each site and as a proxy for phytoplankton density, we compiled photosynthetically active radiation (PAR) data from daytime CTD casts collected by Fisheries and Oceans Canada at oceanographic stations within 37 km (20 nmi) of each mooring location between May 2010 and September 2020. If similar cloud cover at each site is assumed, phytoplankton density should be inversely proportional to PAR at depth due to the attenuation of surface light. At Saanich Inlet terrestrial particles from the nearby Fraser and Cowichan rivers increase turbidity during winter months, whereas biogenic particles tend to dominate the water column during spring and summer (Sancetta, 1989). As the stations near Brooks Peninsula and Clayoquot Canyon were only sampled from May to August of each year, we only included data from these months at each mooring location. Using these data, we calculated the proportion of PAR at the surface ($\Leftarrow 5$ m depth) that penetrated to a depth of 20 m ($pPAR_{20}$) for each CTD cast. We compared the median $pPAR_{20}$ rather than the mean due to the distribution of $pPAR_{20}$ being highly positively skewed.
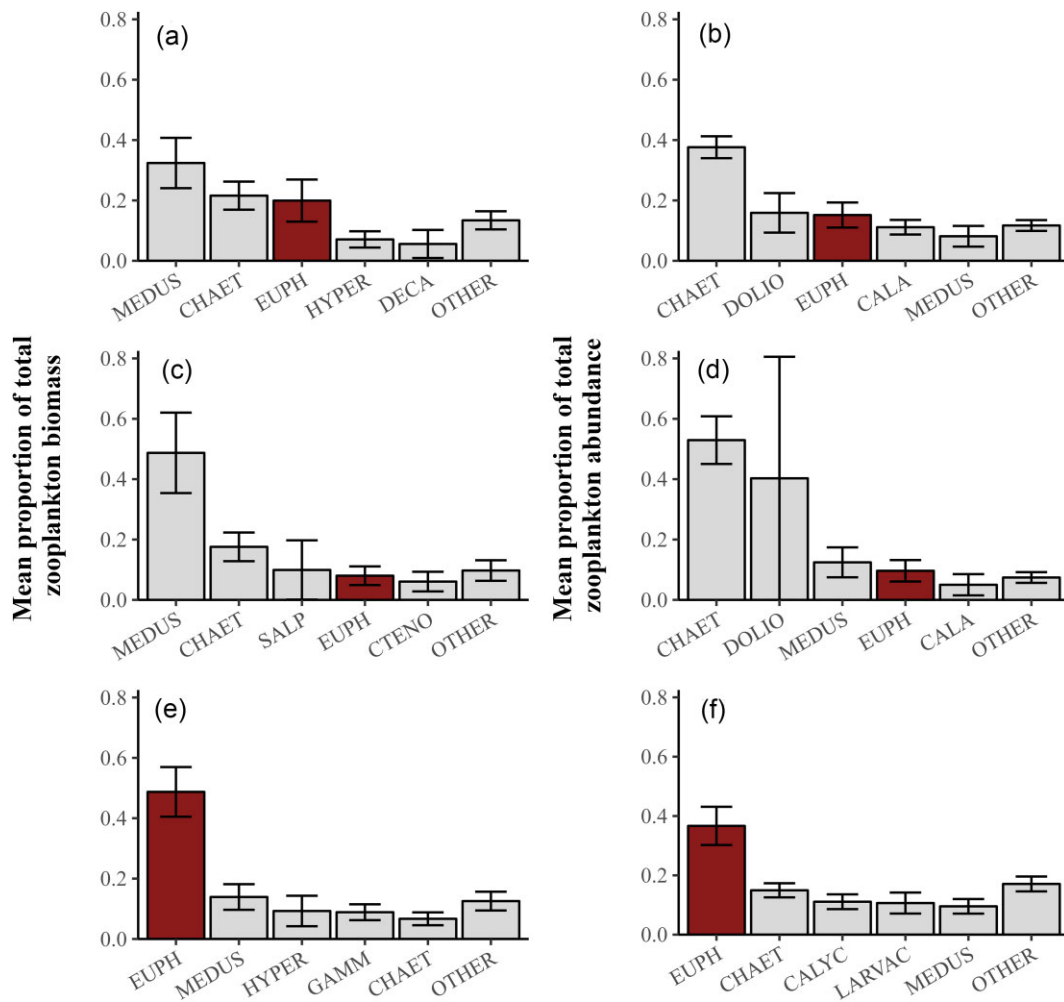
**Figure 3.** Mean proportion and standard error of total zooplankton abundance (a, c, and e) (ind. m$^{-3}$) and biomass (b, d, and f) (mg m$^{-3}$) from zooplankton tows at stations around Brooks Peninsula (a and b), Clayoquot Canyon (c and d), and Saanich Inlet (e and f). $n = 15$ at Brooks Peninsula, $n = 7$ at Clayoquot Canyon, and $n = 17$ at Saanich Inlet. MEDUS = Cnidarian medusae, CHAET = Chaetognatha, EUPH = Euphausiacea, HYPER = Hyperiidae, DECA = Decapoda, GAMM = Gammaridae, DOLIO = Doliolidae, CALA = Calanidae, CALYC = Calycophoridae, CTENO = Ctenophora, and Other = all other taxa contributing <0.05 of the total proportion.

## Results

### Zooplankton net tow results

Fifteen, seven, and seventeen zooplankton tows met our criteria for analysis at Brooks Peninsula, Clayoquot Canyon, and Saanich Inlet, respectively. Tows at Brooks Peninsula occurred only in May and September, while year-round sampling occurred at Clayoquot Canyon and Saanich Inlet. At Brooks Peninsula, euphausiids $\geq 5$ mm in length accounted for $19.94 \pm 6.98\%$ and $15.17 \pm 4.15\%$, respectively, of the total zooplankton biomass and abundance (highlighted bars in Figure 3, Supplementary Tables A3 and A4). At Clayoquot Canyon, euphausiids $\geq 5$ mm in length accounted for $8.01 \pm 3.09\%$ and $9.64 \pm 3.55\%$, respectively, of the total zooplankton biomass and abundance. Euphausiids $\geq 5$ mm in length accounted for $48.73 \pm 33.92\%$ and $36.67 \pm 26.58\%$, respectively, of the total zooplankton biomass and abundance in Saanich Inlet (highlighted bars in Figure 3, Supplementary Table A3 and A4). Euphausiids were among the most abundant and biomass-dominant zooplankton taxa at both sites, though less dominant at Brooks Peninsula and Clayoquot Canyon than in Saanich Inlet. Cnidarian medusae, chaetog-

naths, doliolids, and calanoid copepods were among the other most abundant and biomass-dominant taxa. These values are almost certainly considerable underestimates of actual euphausiid abundance and biomass; however, as the avoidance of nets by euphausiids is a well-documented phenomenon that can result in 10–20-fold underestimates of euphausiid abundance by net collection (Fleminger and Clutter, 1965; Sameoto *et al*., 1993). Previous studies within each region also confirmed that euphausiids are the dominant taxon within the zooplankton scattering layer (Lu *et al*., 2003; Sato *et al*., 2013).

### Confirmation of first-order variability in migration timing

Overall, 99.70% of the variance in dawn DVM times was explained by the time of dawn and mooring location, while 99.98% of the variance in dusk DVM times was explained by the time of dusk and mooring location (Figure 4). It must be noted that although these linear models captured much of the variability in first-order DVM timing, our analysis of second-order DVM variability was not based on the residuals of these
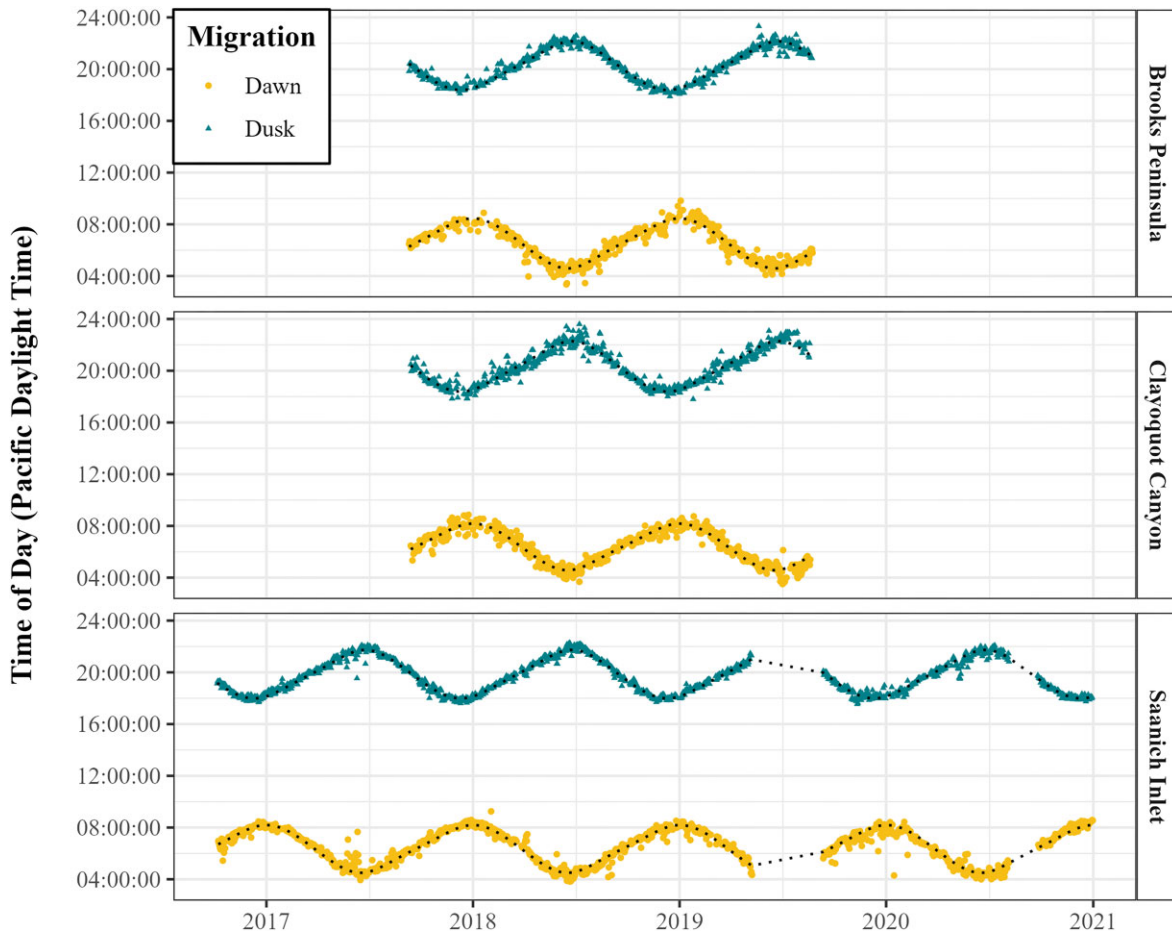
**Figure 4.** DVM times selected for the dawn (circles) and dusk (triangles) DVM events for each deployment day at Brooks Peninsula, Clayoquot Canyon, and Saanich Inlet. Dotted lines in each panel represent the linear models of DVM times as fit by dusk and dawn times, mooring location, and an interaction term between the two predictors. $R^2_{adj}$ = 0.99 for the dawn migrations and 0.99 for the dusk migrations.

models but, rather, directly from civil twilight times. This allowed us to identify seasonality, which would otherwise be masked by these simple linear models. This first-order variability is comparable to that reported in previous studies of DVM in this region (Sato *et al.*, 2013).

## Generalized additive mixed model (GAMMAR) results and residuals

GAMMAR models, which included a day-of-year smoothing term in predicting DVM deviation from civil twilight time received >99% of the AICc weight compared to the null model for each location-DVM event combination (Table 1). This indicates that the seasonal deviations of DVM events from civil twilight times for each location-DVM event combination were statistically significant. This finding is reinforced by the effective degree of freedom (edf) of the GAMMAR models, which was >2 for each location-DVM event combination, showing that the smoothing term was useful to the model in all DVM events at all locations (Table 2). ACF plots of the residuals of these models showed that the autoregressive order-1 term in each model captured the temporal autocorrelation between points in each time series, with $\varphi$ ranging from 0.2118 to 0.5046.

The modelled maxima and minima of dawn DVM deviations occurred consistently in late spring and early winter months, respectively, and vice versa for DVM deviations of

dusk migrations (Table 3 and Figure 5). The modelled maximum deviation of the dawn DVM event occurred around June 11th at Brooks Peninsula, May 19th at Clayoquot Canyon, and May 23rd at Saanich Inlet. The modelled minimum deviation of the dawn DVM event occurred around November 29th at Brooks Peninsula, December 19th at Clayoquot Canyon, and January 14th at Saanich Inlet. The modelled maximum deviation of the dusk DVM event occurred around December 13th at Brooks Peninsula, December 28th at Clayoquot Canyon, and January 3rd at Saanich Inlet. The modelled minimum deviation of the dusk DVM event occurred around June 29th at Brooks Peninsula, May 2nd at Clayoquot Canyon, and June 1st at Saanich Inlet.

Dawn DVM events occurred regularly before dawn at each location with the exception of Saanich Inlet, where dawn DVM events occurred after dawn for a brief period in late spring (Figure 5). The general seasonal trend of deviations from dawn timing was very similar at all three locations. Dawn DVM events occurred earlier before dawn for most days of the year at the exposed locations compared to the sheltered location; however, the exposed locations also showed a more notable local maximum of $Dev_{dawn}$ in fall than seen at Saanich Inlet, in addition to a late winter peak that occurred only at Brooks Peninsula. The earliest dawn DVM events relative to dawn times occurred at Clayoquot Canyon, while the latest occurred at Saanich Inlet.

**Table 1.** AICc and ∆AICc of the comparison of generalized additive mixed models with an autoregressive term fit to the deviation of dawn/dusk time for each location-DVM event.

| Location | DVM event | AICc | ∆AICc |
|---|---|---|---|
| Brooks Peninsula | Dawn | 5064.5 | − 24.7 |
| | Dusk | 5268.8 | − 87.6 |
| Clayoquot Canyon | Dawn | 5519.7 | − 30.0 |
| | Dusk | 5499.6 | − 37.6 |
| Saanich Inlet | Dawn | 10 974.3 | − 39.4 |
| | Dusk | 10 050.4 | − 99.0 |

Comparisons are between a GAMMAR with a smoothing term for day-of-year and a GAMMAR without this term. Models fit as per Equations (3) and (4). AICc weights were 1.00 for all comparisons and thus omitted from the table.

**Table 2.** Parameter estimates for the intercept ($\beta_0$) and autoregressive order 1 ($\varphi$) terms, edf, and $R^2_{adj}$ of the best-fit GAMMAR models for each location-DVM event.

| Location | DVM event | $\beta_0$ (SE) (minutes) | $\varphi$ | edf | $R^2_{adj}$ |
|---|---|---|---|---|---|
| Brooks Peninsula | Dawn | − 13.27 (1.29) | 0.3651 | 5.75 | 0.160 |
| | Dusk | − 5.32 (0.93) | 0.3713 | 4.98 | 0.367 |
| Clayoquot Canyon | Dawn | − 19.08 (1.05) | 0.2118 | 5.23 | 0.199 |
| | Dusk | 7.28 (1.24) | 0.3169 | 5.24 | 0.179 |
| Saanich Inlet | Dawn | − 10.98 (1.01) | 0.5020 | 4.904 | 0.129 |
| | Dusk | − 6.88 (0.66) | 0.5046 | 5.217 | 0.280 |

Models fit as per Equations (3) and (4).

**Table 3.** Minimum, maximum, and change in deviations of DVM event times from dawn/dusk times with standard errors, and Julian day of the year when the minimum and maximum deviations occur ($t_{min}/t_{max}$) based on the best-fit GAMMAR model for each location-DVM event combination.

| Location | DVM event | Minimum deviation (SE) (minutes) | $t_{min}$ | Maximum deviation (SE) (minutes) | $t_{max}$ | ∆Deviation (minutes) |
|---|---|---|---|---|---|---|
| Brooks | Dawn | − 33 (3) | 333 | − 1 (3) | 162 | 32 |
| Peninsula | Dusk | − 23 (2) | 180 | 14 (2) | 347 | 37 |
| Clayoquot | Dawn | − 39 (3) | 353 | − 4 (3) | 139 | 35 |
| Canyon | Dusk | − 12 (3) | 122 | 19 (3) | 362 | 31 |
| Saanich | Dawn | − 24 (2) | 14 | 2 (2) | 143 | 26 |
| Inlet | Dusk | − 23 (2) | 152 | 4 (2) | 3 | 27 |

Dusk DVM events occurred both before and after dusk at each location, though the seasonality of the shift varied widely between locations (Figure 5). The minimum $Dev_{dusk}$ occurred earliest in early May at Clayoquot Canyon, followed by a rapid rise to a local maximum in mid-July with $Dev_{dusk}$ values near the winter maximum, and a local minimum in early October. In contrast, dusk DVM events at Brooks Peninsula and Saanich Inlet showed only one minimum and maximum $Dev_{dusk}$, the minimum occurring later in Saanich Inlet and Brooks Peninsula than at Clayoquot Canyon (Figure 5). The maximum $Dev_{dusk}$ was at least 10 min greater at the exposed locations compared to Saanich Inlet, and the minimum was ~12 min greater at Clayoquot Canyon than at Brooks Peninsula or Saanich Inlet

### PAR results

Median PAR at 20 m depth ($PAR_{20}$) during summer months was higher at the exposed locations than at the Saanich Inlet (Table 4). The 25th and 75th quartiles of $PAR_{20}$ were 3 and 19 at Brooks Peninsula, 2 and 25 at Clayoquot Canyon, and 1 and 8 at Saanich Inlet. $PAR_{20}$ and median percent of PAR penetrating from 5 m depth to 20 m depth were significantly different between each of the exposed sites and Saanich Inlet ($p < 0.05$ for each pair through Pairwise Wilcoxon Rank-Sum test with Holm–Bonferroni $p$-value correction). The great-

est $pPAR_{20}$ was at Brooks Peninsula, followed by Clayoquot Canyon, and Saanich Inlet had the lowest median penetration of PAR to 20 m depth.

## Discussion

Despite having been studied for more than two centuries, our current understanding of DVM in ecologically dominant zooplankton such as euphausiids remains limited by the short temporal nature of most field observations (Sato *et al.*, 2013). Recent studies using state-of-the-art acoustic technologies have begun to change this view (Cisewski and Strass, 2016; Inoue *et al.*, 2016). That said, studies utilizing multiple years of acoustic data have generally focused on first-order DVM variability and do not consider how other latent ecosystem processes influence DVM timing relative to civil twilight times (Lorke *et al.*, 2004). To date, no studies of second-order variability of DVM timing have coupled long-term data from multiple geographic regions with sufficient temporal resolution to investigate spatial differences in DVM seasonality and their potential causes.

### First- and second-order DVM variability

As in prior studies, we found that DVM events at all three sites displayed high fidelity to civil twilight times (Tarling, 2003;
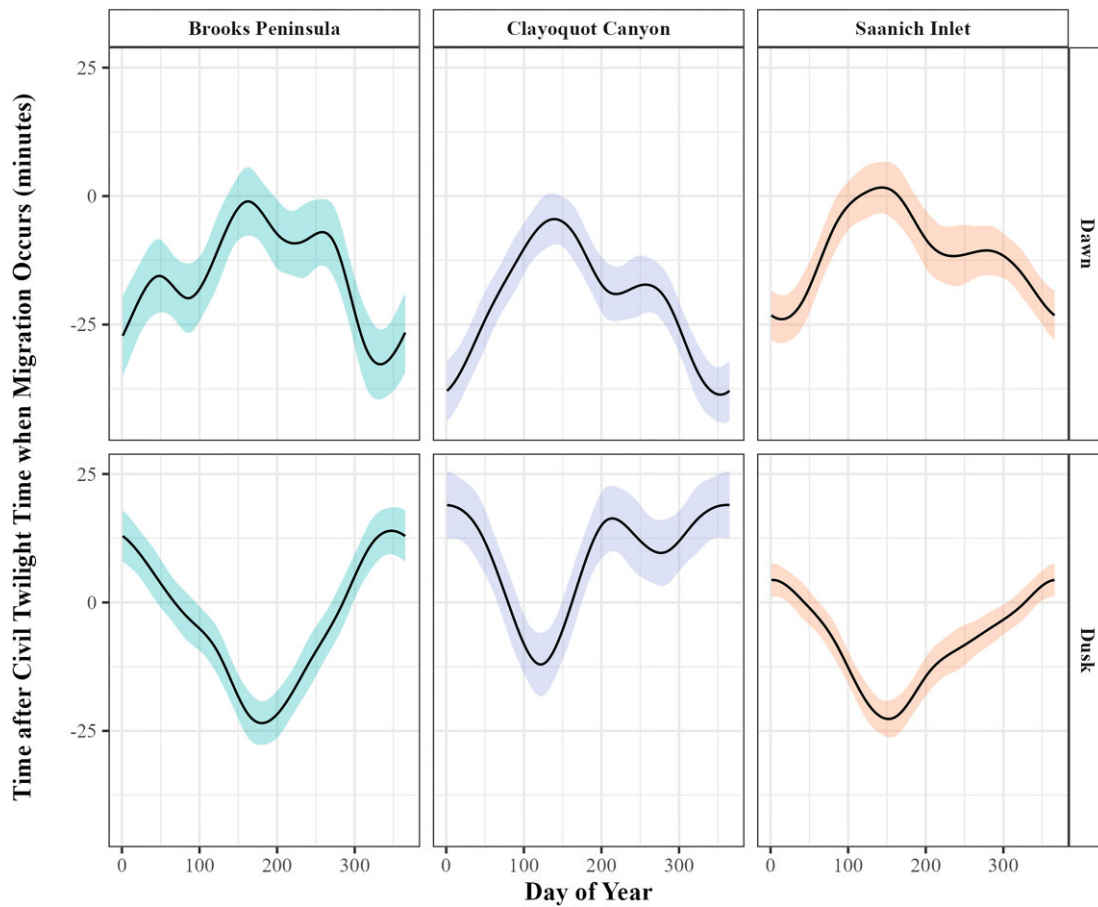
**Figure 5.** Deviations of DVM times in minutes from civil twilight times for each day of deployment at Brooks Peninsula, Clayoquot Canyon, and Saanich Inlet. Lines and coloured shading envelopes represent the best-fit generalized additive mixed models with autoregressive terms for each location-DVM event combination and 95% confidence intervals of each model.

**Table 4.** Median, 25th, and 75th quartiles of PAR ($\mu E\ m^{-2}\ s^{-1}$) at 20 m depth $PAR_{20}$ and percent of near-surface PAR at 20 m depth ($pPAR_{20}$) at each location.

| Location | Median $PAR_{20}$ ($\mu E\ m^{-2}$ $s^{-1}$), [q25, q75] | Median $pPAR_{20}$ [q25, q75] | $n$ |
|---|---|---|---|
| Brooks Peninsula | 8 [3, 19] | 6 [4, 12] | 79 |
| Clayoquot Canyon | 8 [2, 25] | 5 [2, 12] | 51 |
| Saanich Inlet | 2 [1, 8] | 2 [1, 3] | 33 |

Samples taken from CTD casts performed at daytime within 20 nmi of each location in the months of May to September from 2010 to 2020.

Lorke *et al.*, 2004; Sato *et al.*, 2013; Bianchi and Mislan, 2016; Inoue *et al.*, 2016). This reinforces the theory that the primary driver of seasonal change in DVM event timing is seasonality in civil twilight times. However, a considerable degree of second-order DVM variability also existed, which was not explained by this seasonality.

At each location-DVM event combination, we found significant seasonality in the deviation of DVM events from dawn/dusk times (Table 1 and Figure 5). These generally showed the same trends across sites—with euphausiids migrating downwards well before dawn in winter and closer to or just after dawn in spring and summer; and migrating upwards after dusk in winter and before dusk in spring and summer. These trends were as expected based on previous work (Sato *et al.*, 2013) and knowledge of local seasonal ecosystem processes affecting food availability. In addition to the gen-

eral similarities between locations, however, unique patterns of DVM timing deviations emerged from each location.

Euphausiids migrated downward closer to (and even after) dawn at Saanich Inlet, in contrast to the exposed sites (Figure 5). Euphausiids also tended to migrate downwards later at dawn at Saanich Inlet compared to the exposed sites. In general, euphausiids at Saanich Inlet remained near the surface longer relative to civil twilight times than those at the exposed sites, and euphausiids at Clayoquot Canyon spent the least time near the surface relative to civil twilight times. This suggests that euphausiids at Clayoquot Canyon experienced the least benefits and/or the greatest costs of remaining near the surface compared to those at Brooks Peninsula or Saanich Inlet, the latter of which seemed to experience the greatest benefits and/or the least costs of remaining near the surface.

## Possible benefits and costs

In terms of viewing DVM as an anti-predator behaviour, we can conclude that regional differences exist in the benefits (prey availability, turbidity, conspecific abundance, etc.) and costs (predator abundance) facing euphausiids in near-surface waters at these locations. Euphausiid populations at Saanich Inlet seem to have had the most benefits (or the fewest costs) among the three locations. Euphausiids at both the exposed locations (but particularly at Clayoquot Canyon) appear to have experienced the fewest benefits (or greatest costs) that favoured spending more time at depth. Several factors likely influenced variability in euphausiid DVM in this study: phytoplankton availability (and thereby shadowing), predator abundance, conspecific abundance, and ontogenetic seasonality.

### Phytoplankton abundance

Saanich Inlet is well known to be among the most productive regions off the coast of BC due to high nutrient loading and little surface mixing in the fjord (Herlinveaux, 1962; Parsons *et al.*, 1983; Timothy and Soon, 2001). In contrast, our offshore sites were located at the interface between the California upwelling zone and the Alaskan downwelling zone which, combined with the increased deep mixing via storm action, results in lower primary productivity in the region (Ware and McFarlane, 1989). Seasonal blooms of phytoplankton also correspond with increases of zooplankton biomass; thus, phytoplankton availability can act as a proxy for food availability for omnivorous euphausiids (Mackas, 1992; Nakagawa *et al.*, 2003, 2004; Cowlishaw, 2004).

While the functional advantage of the surface phase of DVM behaviour is assumed to allow access to near-surface feeding, conflicting evidence exists as to how phytoplankton abundance influences migration timing (reviewed in Pearre, 2003). The timing of the dusk-ascending DVM event has been noted to often be synchronous among individuals of a swarm, as all are presumably unsated (Kanaeva and Pavlov, 1976). However, the timing of the dawn descent DVM event can be asynchronous as individuals descend to digest after consuming their fill, which generally occurs earlier when food is abundant (Hardy and Gunther, 1935; Bohrer, 1980; Simmard *et al.*, 1986; Gibbons, 1993). We might therefore have expected that during the spring and fall, when phytoplankton abundance was greatest, euphausiids would have descended earlier relative to the dawn as they became quickly sated at the surface. However, we observed the opposite pattern, whereby euphausiids remained near the surface for the longest periods when phytoplankton abundance was theoretically highest (Figure 5). As we were unable to resolve individuals or small groups near the surface (95–281 m from the echosounder), it is possible that we only detected the final *en masse* migration of swarms from the surface near dawn. This descent was more likely influenced by ambient light levels than food abundance.

### Shadowing due to phytoplankton

Differences in phytoplankton density between the sites likely had a secondary effect on euphausiid behaviour, as phytoplankton attenuated incoming light in the near-surface layer, causing increased shadowing at depth (Lorenzen, 1972). Our PAR data showed that when primary productivity was highest, light penetration was lower in Saanich Inlet than at the exposed sites (Table 4). Thus, due to increased shadowing by phytoplankton, euphausiids at Saanich Inlet may have experienced lower predation risk in the surface waters than those at the exposed sites. This high turbidity at Saanich Inlet was expected based on previous work, and is due to high phytoplankton densities as well as terrestrial runoff from the Cowichan and Fraser rivers (Sancetta and Calvert, 1988; Sancetta, 1989). DVM has variously been postulated to be triggered by illumination via isolume preference, intensity thresholds, or changes in intensity over time (Russell, 1926; Cohen and Forward, 2009). Increased shadowing through phytoplankton attenuation would have resulted in both an earlier rise in shadowed isolume depth and triggering of minimal light threshold at dusk (and vice versa at dawn). However, this would not have changed the rate of change of light intensity at depth. Further, the general trends of migration deviations from twilight times that we observed did not correspond with the expected rates of change of light intensity during twilight, which would be maximized during the vernal and autumnal equinoxes (McFarland, 1986). Therefore, if the attenuation of light through increased phytoplankton abundance led to earlier dusk and later dawn migrations in euphausiids, the most likely trigger was not the rate of change of light intensity *per se*.

### Predation risk

Theoretically, the greatest potential cost for a euphausiid remaining in near-surface, food-rich waters is the risk of being detected and eaten by visual predators in the well-lit daylight hours (Zaret and Suffern, 1976; Robinson, 2000; Benoit-Bird and Moline, 2021). We would therefore expect euphausiids to remain at a depth proportional to the risk of predation (Loose and Dawidowicz, 1994). Similar visual predators, including Pacific Hake (*Merluccius productus*), Pacific Herring *(Clupea pallasii)*, and Pacific Salmon species (*Oncorhynchus* spp.), have been noted to be present at each site, though with differing abundances and seasonal trends (Mackas *et al.*, 1997; Robinson, 2000). It is possible that the differences in migration timing were due to increased predator abundance at the exposed sites; however further work will be required to determine the direct influence of predator abundance and predator community composition on second-order DVM timing.

### Conspecific abundance and ontogeny

The abundance, developmental timing, and proportion of zooplankton biomass comprised of euphausiids at each site are known to vary seasonally (Heath, 1977; Mackas *et al.*, 1997; Mackas *et al.*, 2013). As conspecific abundance increases, the probability of any individual within the swarm being consumed decreases, whereas the competition for food among conspecifics increases (Hamilton, 1971; Folt and Goldman, 1981; Foster and Treherne, 1981). Each factor alters euphausiid swarming behaviour, and may also incentivize swarms of euphausiids to remain near the surface longer relative to photoperiod to feed within the protection of the swarm (O'Brien, 1989; Kawaguchi *et al.*, 2010). *Euphausia pacifica*, the dominant euphausiid species at our sampling locations, spawns from May to September with adult biomass peaking in October (Mackas *et al.*, 1997; Mackas *et al.*, 2013). During this period, considerable energy is being allocated to gamete development and growth in the population, likely increasing the incentive to remain near the surface to feed. The summer peak in seasonal DVM deviation we observed at each location may thus have corresponded with a peak in the abundance of

euphausiids, which were feeding to accrue energy for this summer spawning event.

## A theoretical framework

The observed differences in DVM seasonality between stations likely resulted from differences in local oceanographic conditions. At the less productive exposed sites, euphausiids likely had fewer benefits to migrate to surface waters to feed during daylight hours (Robinson and Ware, 1994; Robinson, 2000) as well as greater costs from greater light penetration likely coinciding with the presence of visual predators (Zaret and Suffern, 1976). Thus, euphausiids tended to migrate to the surface well into the dark hours throughout the year. In the more productive waters of Saanich Inlet, euphausiids were likely influenced by strongly seasonal differences in prey availability and shading to risk staying in surface waters in the dimmed light for longer (Benoit-Bird and Moline, 2021). Therefore, euphausiids stay in the food-rich surface waters longer throughout the year at Saanich Inlet, but especially so in the spring and summer months, when massive food abundance makes surface feeding a more incentivized endeavour.

## Conclusion

This study provides novel insights into how local oceanographic conditions can contribute to significant behavioural shifts in euphausiid DVM, a behaviour that is traditionally assumed and modelled to vary little within a given geographic region for a given species. We demonstrate that DVM behaviours are variable even at local scales, and that this variability must be accounted for when considering the predator–prey dynamics, biogeochemical cycling, and environmental conditions which DVM behaviours elicit in an ecosystem. While this study quantifies spatial differences in seasonal DVM timing between locations, further analyses of these trends with environmental covariates must be conducted to examine key drivers behind this variability. Moored active acoustic systems paired with autonomous platforms for sampling *in situ* irradiance, fluorescence, environmental DNA, and near-surface conditions could provide these data. Further work should classify and enumerate seasonal trends in biomasses of euphausiids and their predators at each location to investigate the proximate influence each has on the timing of euphausiid migrations.

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## Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

The following supplementary material is available at ICESJMS online: the full specifications of the AZFP moorings used in this study (Supplementary Table A1), the sound speeds and absorption coefficients used in this study (Supplementary Table A2) as well as a description of their calculation, the abundances and biomasses of zooplankton taxa collected at each mooring location (Supplementary Tables A3 and A4), and a plot of the deviations of DVM timing from civil twilight timing for each mooring and migration (Supplementary Figure A1).

## Data availability

Data from Ocean Networks Canada are available publicly through the Oceans 3.0 Data Portal (https://data.oceannetworks.ca/home). Data from Fisheries and Oceans Canada are being collated for public availability and can be accessed by contacting the authors directly.

## Author contributions

NJE: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing. JFD: Conceptualization, Project administration, Supervision, Validation, Writing—review & editing. SG: Conceptualization, Funding acquisition, Methodology, Project administration, Software, Supervision, Validation, Writing—review & editing.

## Conflict of interest

The authors have no conflicts of interest to declare.

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