

SHORT COMMUNICATION

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Interpreting vertical movement behavior with holistic examination of depth distribution: a novel method reveals cryptic diel activity patterns of Chinook salmon in the Salish Sea

M. C. Arostegui*, T. E. Essington and T. P. Quinn

Abstract

Aquatic organisms exhibit a variety of diel changes in vertical movement that are investigable through the use of biotelemetry. While certain species do not change their movements between day and night, others exhibit diel vertical migration (DVM) or a diverse range of diel activity patterns (DAPs). Consequently, day–night differences in depth distribution may be stark and easily detectable, or more subtle and difficult to identify. To augment the discovery and classification of cryptic diel vertical movement behavior, we developed and utilized a novel method that analyzed entire depth distributions while comparing diel period, season, and season/diel period models. This analysis revealed a seasonally variable DAP previously unreported in Chinook salmon (*Oncorhynchus tshawytscha*). In summer and fall, Chinook salmon in the Salish Sea juxtaposed shallow and confined daytime movements with nighttime bounce diving. This DAP was reversed in winter, when they occupied deeper sections of the water column during the day, resulting in a substantially overlapping, but more even depth distribution than at night. These results demonstrate the analytical utility of accompanying other metrics with holistic examination and visualization of the entire distribution of depth data. Additionally, we highlight the need to use a framework that answers all of the following questions: (1) does the target species exhibit seasonal variation in depth, (2) does it undergo DVM, (3) if it does not undergo DVM, does it follow a DAP, and (4) if it follows a DAP, what is the difference in vertical movement behavior between diel periods?

Keywords: Telemetry, Depth distribution, Diel activity pattern, Chinook salmon

Background

Biotelemetry is a powerful tool for investigating the movements of aquatic organisms that would otherwise be inaccessible to researchers. Transmitters and data loggers can provide data on the horizontal movements of animals, and also their depth distributions and vertical movements, yielding many insights into their behavior. Analysis of vertical movement data may reveal that a species' depth distribution is influenced by factors including temperature [1, 2], oxygen [3], the former two in concert [4], light level [5, 6], predation risk [7], prey movements

[8, 9], and foraging efficiency [10, 11]. Consequently, vertical distributions often vary with the seasons and diel periods [12, 13]. Thus, telemetry studies yield valuable information on the behavior and ecology of the target species in relation to its biotic and abiotic environment.

While certain organisms show no day–night differences in depth distribution, others exhibit behavior that can be categorized as diel vertical migration (DVM) or a diel activity pattern (DAP). DVM occurs when an organism occupies deeper water during the day and shallower water at night, or (less commonly) vice versa [8]. This behavior has been documented in numerous forage species, such as mesopelagic myctophid fish that reside at deeper depths (200–2000 m) during the day to avoid predation and migrate closer to the surface at night

*Correspondence: marosteg@uw.edu
School of Aquatic and Fishery Sciences, University of Washington,
Box 355020, Seattle, WA 98195, USA

(10–100 m) to forage when predation risk is reduced [14, 15]. Large predators including bluntnose sixgill [16] and bigeye thresher sharks [17] also undergo DVM, often foraging deeper during the day than at night. The diel separation of modal depths that defines DVM, where distributions are not significantly overlapping and are of a similar variance (see Fig. 2 of [16]), does not necessarily occur under a DAP. For example, blue marlin (*Makaira nigricans*) may repeatedly dive from the surface to waters 100 m deep or more and back during the day, whereas at night they stay almost exclusively at the surface (see Fig. 4 of [18]). In this case, the blue marlin nighttime distribution is a different shape than and entirely overlapped by the daytime distribution due to the stark difference in variance between diel periods. Such diving behavior differs from the disparate modal depths in day and night typical of DVM and therefore must be analyzed differently to be recognized as a DAP. It is important to note that DVM is a single specialized paradigm, whereas DAP represents a wide range of diel movement behaviors. This distinction is relevant because some authors, after finding no evidence of DVM and then not investigating further for any DAPs, may prematurely conclude that a species does not exhibit diel movement behavior.

A recent acoustic telemetry study employed a linear statistical model to assess seasonal and diel depth patterns of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, WA [13]. They found that Chinook salmon showed seasonal changes in depth distribution but did not exhibit DVM. However, because their model predicted average depths derived from hourly means of the depth detections per fish to explore diel movement patterns, they could not fully evaluate changes in variability in depths associated with DAPs.

Here, we illustrate the importance of holistic examination of diel depth distribution data applied to Puget Sound Chinook salmon data described above. We develop and apply a novel analytical method enabling researchers to assess whether the organisms exhibit seasonal changes in depth distribution, DVM, and DAPs. Utilizing acoustic telemetry data from Smith et al. [13] and more recently collected data, we demonstrate that subadult Chinook salmon in marine waters exhibit a seasonally variable DAP consisting of shallow, vertically confined movements during the day in summer/fall and at night in winter, and deeper, more variable movements during the night in summer/fall and day in winter. The novelty of this work is highlighted by the rarity of long-term acoustic telemetry studies on the vertical movements of immature anadromous salmonids in the marine environment [19, 20]. The method described in this paper provides both analytical flexibility and resolution by using the entire distribution of depth data, making it

applicable to other species with cryptic patterns of vertical movement.

Methods

Receiver deployment and fish tagging

Acoustic receivers were deployed in five regions of the Salish Sea in waters of the USA and Canada: the Strait of Juan de Fuca, the San Juan Islands, Whidbey Basin, Admiralty Inlet, and central Puget Sound (Fig. 1; see [13, 21] for more details). Immature (i.e., subadult) Chinook salmon ($n = 28$; Table 1) were captured and surgically implanted with depth recording acoustic tags (Vemco: Bedford, Nova Scotia, Canada) following the methods of Smith et al. [13] and Arostegui et al. [21]. The tags accurately recorded depths up to 110 m from the surface, but deeper detections had questionable precision and were subsequently classified solely as >110 m for analysis.

Data classification

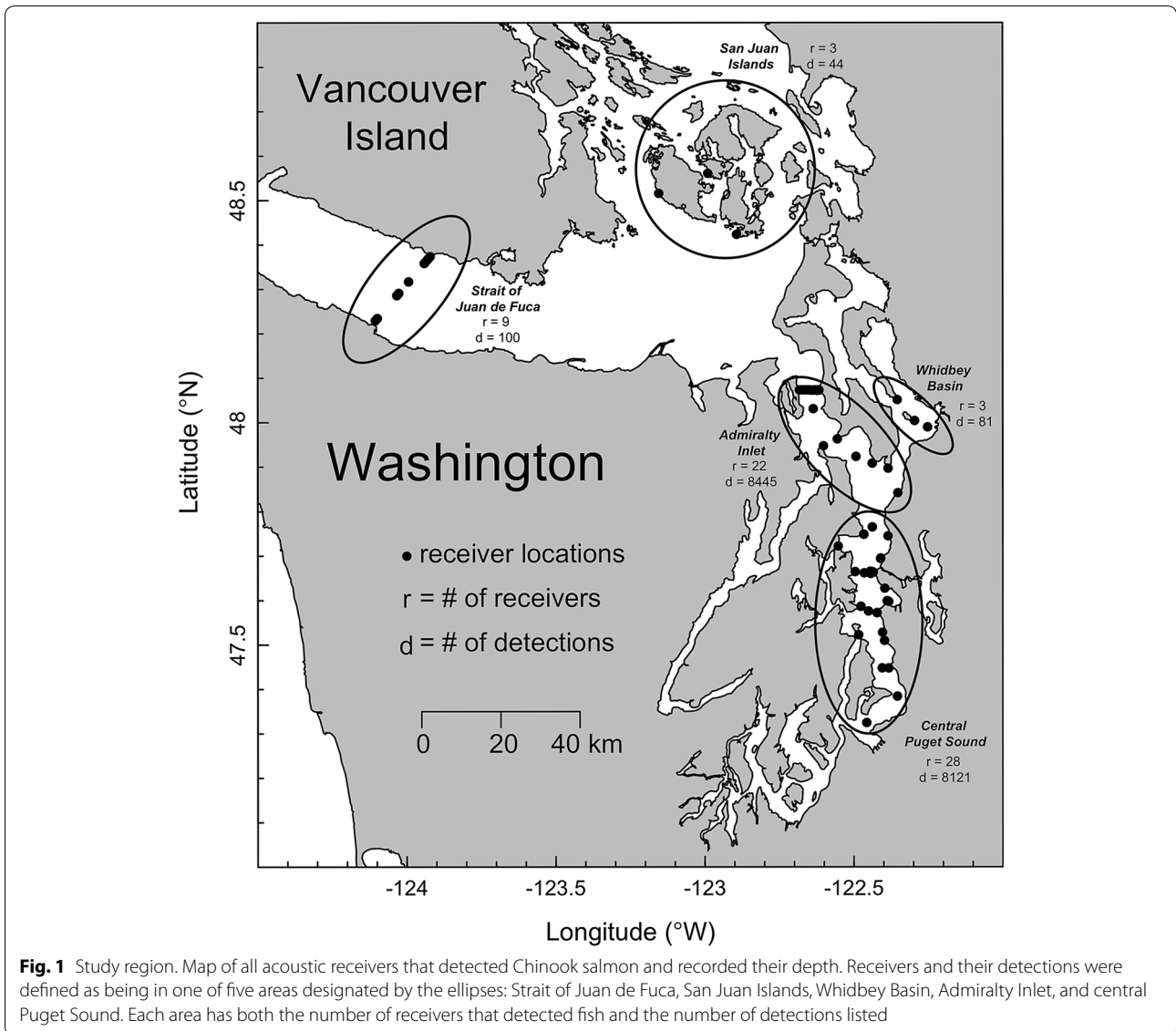
For each Chinook salmon, detections were classified by season, diel period, and depth bin. The seasons were defined as: summer (July–September), fall (October–December), winter (January–March), and spring (April–June). Day and night were defined as the time between sunrise and sunset, and sunset and sunrise, respectively, obtained from the Astronomical Applications Department of the US Naval Observatory [22] (http://aa.usno.navy.mil/data/docs/RS_OneYear.php, accessed October 2015). Ten-meter depth bins from 0 to 110 m were utilized plus one bin summing all detections >110 m, for a total of 12 bins.

Data selection

The four individual Chinook salmon with the most detections in a given season and diel period (i.e., summer day, summer night, fall day, etc.) were chosen to test the method (Table 2). The number of detections is equivalent to the amount of time a fish's depth was observed over a season within a specific diel period. This metric was utilized because fish that accumulate more detections are more likely to provide data that accurately represent the true depth distribution in a given season and diel period. The number of fish informing a specific estimated distribution was kept consistent to maintain the level of individual variability incorporated into each maximum likelihood estimated model.

Model data treatment

The data consist of proportions of detections in each depth bin for each fish, across day and night diel periods and seasons. A natural probability density function for these data is the Dirichlet. Here, the likelihood (L) for each vector of proportions (x_i) is:



$$L(x_i) = \frac{1}{B(\alpha)} \prod_{k=1}^K x_{k,i}^{\alpha_k - 1} \tag{1a}$$

$$\beta(\alpha) = \frac{\prod_{k=1}^K \Gamma(\alpha_k)}{\Gamma(\sum_{k=1}^K \alpha_k)} \tag{1b}$$

where x_i is the vector of proportions of time spent at K depth bins for fish i , α_k are the parameters of the Dirichlet distribution, so that the mean proportion in any bin equals $\frac{\alpha_k}{\sum_{k=1}^K \alpha_k}$.

We have four alternative models to test: The vector α_k is (1) the same for all diel periods and seasons; (2) different between diel periods but the same for seasons; (3) the

same for diel periods but different between seasons; (4) different between diel periods and seasons.

As we have 12 depth bins, there are 12 different values of α_k to be estimated. However, there are two related issues with parameter estimation of the vector α . The first is that our data consist of proportions in discretized depth bins that have a natural ordering to them (e.g., 1–10 and 10–20 m), so that a priori, we anticipate that the α_1 should be more similar to α_2 than it is to α_3 , and so on. Two, we wish to test different models that suppose different vectors α for diel periods and seasons. If the α_k are all estimated as free parameters, each distinct vector consists of 12 additional parameters that have to be estimated, which in model selection penalizes models that presume distributions are different across times or seasons.

Table 1 Tagged Chinook salmon information

| Serial # | Fork length (mm) | Tagging date | # of detections |
|----------------|------------------|--------------|-----------------|
| 3134 | 276 | 11/1/06 | 798 |
| 4996 | 330 | 6/7/07 | 1246 |
| 4997 | 370 | 6/7/07 | 3760 |
| 5033 | 401 | 11/2/06 | 3024 |
| 5035 | 296 | 11/1/06 | 567 |
| 6038 | 260 | 11/1/06 | 151 |
| 1040674 | 266 | 6/7/07 | 853 |
| 1040676 | 280 | 6/7/07 | 217 |
| 1040678 | 316 | 6/7/07 | 533 |
| 1055541 | 275 | 12/11/08 | 359 |
| 1082468 | 430 | 5/13/12 | 2058 |
| 1082477 | 425 | 4/12/12 | 1574 |
| 3130 | 342 | 6/7/07 | 81 |
| 3131 | 254 | 11/1/06 | 70 |
| 3133 | 369 | 6/7/07 | 354 |
| 4998 | 255 | 6/7/07 | 24 |
| 5034 | 505 | 11/1/06 | 23 |
| 1040675 | 346 | 6/8/07 | 354 |
| 1040677 | 330 | 6/7/07 | 18 |
| 1045449 | 260 | 12/12/07 | 29 |
| 1055537 | 273 | 12/11/08 | 64 |
| 1082469 | 400 | 6/24/12 | 401 |
| 1082470 | 400 | 6/24/12 | 14 |
| 1082471 | 450 | 5/13/12 | 10 |
| 1082472 | 400 | 6/24/12 | 162 |
| 1082473 | 425 | 5/13/12 | 2 |
| 1082474 | 430 | 4/22/12 | 35 |
| 1082476 | 440 | 4/5/12 | 1 |

Serial number, fork length (mm), tagging date, and total number of detections for the 28 subadult Chinook salmon tagged in this study. The 12 fish above the bold were utilized in the quantitative analyses and the 16 below were not

To address both of these problems, we fit a parametric function to describe how the estimated mean proportion of observation varies with depth. Specifically, we fit the following functional form:

$$\hat{p}(k) = \int_{y_{\min,k}}^{y_{\max,k}} f(y) dy \tag{2}$$

where $f(y)$ is a gamma probability density function with shape parameter θ and scale parameter k_g , y is depth, and $y_{\min,k}$ and $y_{\max,k}$ are the upper and lower bounds of the depth bin k . In other words, the estimated probability of being in depth bin k is the integral of a gamma probability density function over the depth range that bin k represents.

Given the vector $\hat{p}(k)$, and a multiplier α_{mult} , we can then obtain the vector α for the Dirichlet probability

density function and thereby calculate the likelihood for each observation:

$$\alpha_k = \hat{p}(k)\alpha_{\text{mult}}$$

Thus, the parametric model only required that we estimate three parameters, θ , k_g , and α_{mult} , rather than 12 distinct parameters in the vector α_k .

Occasionally, the $\hat{p}(k)$ would become too small, resulting in near-zero estimated probabilities so that some likelihoods could not be computed. To remedy this problem, we added a final variable, termed p_{floor} , which was the smallest value that $\hat{p}(k)$ could take. This was done by adding a constant small probability ε to Eq. 2 above and constraining $\hat{p}(k)$ such that the sum over all $k = 1$:

$$\varepsilon = \frac{p_{\text{floor}} - \min_k \left(\int_{y_{\min,k}}^{y_{\max,k}} f(y) dy \right)}{1 - K p_{\text{floor}}} \tag{3a}$$

$$\hat{p}(k) = \frac{\hat{p}(k) + \int_{y_{\min,k}}^{y_{\max,k}} f(y) dy + \varepsilon}{K\varepsilon + \sum_k \int_{y_{\min,k}}^{y_{\max,k}} f(y) dy} \tag{3b}$$

We set p_{floor} to 0.0001.

Depth distribution models

Four different models (null, diel period, season, and season/diel period) were fitted to test for their ability to describe the Chinook depth distribution proportions. The null model was fit to data consisting of 32 individual distributions from the four seasons and two diel periods (Table 2). The “diel period” model presumed that depth distributions varied by diel period only. The “season” model presumed that depth distributions varied by seasons only, and the “season/diel period” model presumed that depth distributions were different for each season and diel period. Thus, the null model estimated a single vector of parameters, the diel model estimated two vectors of parameters (for day and night), the season model estimated four vectors of parameters, and the season/diel period model estimated eight vectors of parameters (24 parameters total).

Parameter estimation and model comparison

Maximum likelihood estimates of the θ , k_g , and α_{mult} parameters were calculated with the “mle2” function of the “bbmle” package in R [23], using the L-BFGS-B method with bounded parameters [24]. We used a modified version of the “ddirichlet” function (modified to calculate log-likelihoods) of the “gtools” package in R [25]. All computation was conducted in R (version 3.2.2) [26], the code and data for which is provided [see Additional files 1, 2].

Table 2 Detection data

| Serial # | Season | Diel | Depth bin (m) | | | | | | | | | | | Total | |
|----------|--------|-------|---------------|-------|-------|-------|-------|-------|-------|-------|-------|--------|---------|-------|------|
| | | | 0–10 | 10–20 | 20–30 | 30–40 | 40–50 | 50–60 | 60–70 | 70–80 | 80–90 | 90–100 | 100–110 | | 110+ |
| 4996 | Summer | Day | 57 | 88 | 85 | 66 | 15 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 312 |
| 4997 | Summer | Day | 52 | 78 | 44 | 95 | 173 | 92 | 79 | 51 | 17 | 1 | 3 | 0 | 685 |
| 1082468 | Summer | Day | 73 | 135 | 198 | 261 | 111 | 74 | 34 | 29 | 21 | 18 | 16 | 68 | 1038 |
| 1082477 | Summer | Day | 12 | 19 | 63 | 83 | 99 | 68 | 48 | 48 | 27 | 37 | 51 | 222 | 777 |
| 4996 | Summer | Night | 4 | 24 | 11 | 14 | 7 | 4 | 1 | 4 | 10 | 17 | 23 | 192 | 311 |
| 4997 | Summer | Night | 44 | 84 | 66 | 57 | 127 | 93 | 49 | 38 | 21 | 1 | 1 | 0 | 581 |
| 1082468 | Summer | Night | 101 | 180 | 134 | 129 | 74 | 59 | 40 | 35 | 28 | 11 | 17 | 54 | 862 |
| 1082477 | Summer | Night | 11 | 17 | 41 | 38 | 37 | 48 | 47 | 36 | 58 | 67 | 91 | 265 | 756 |
| 3134 | Fall | Day | 0 | 63 | 80 | 55 | 43 | 19 | 21 | 17 | 2 | 0 | 0 | 16 | 316 |
| 4997 | Fall | Day | 4 | 1 | 18 | 29 | 58 | 111 | 85 | 95 | 74 | 12 | 1 | 1 | 489 |
| 5033 | Fall | Day | 13 | 104 | 359 | 124 | 66 | 10 | 2 | 0 | 0 | 0 | 0 | 0 | 678 |
| 5035 | Fall | Day | 7 | 41 | 33 | 6 | 9 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 104 |
| 3134 | Fall | Night | 10 | 145 | 145 | 63 | 52 | 10 | 11 | 37 | 15 | 0 | 2 | 2 | 492 |
| 4997 | Fall | Night | 1 | 16 | 71 | 106 | 119 | 220 | 206 | 189 | 110 | 29 | 13 | 84 | 1164 |
| 6038 | Fall | Night | 22 | 3 | 1 | 1 | 0 | 0 | 0 | 7 | 35 | 10 | 8 | 27 | 114 |
| 1040674 | Fall | Night | 1 | 7 | 0 | 5 | 7 | 40 | 0 | 1 | 1 | 0 | 8 | 27 | 97 |
| 4997 | Winter | Day | 0 | 1 | 0 | 5 | 11 | 61 | 37 | 37 | 37 | 40 | 0 | 14 | 243 |
| 5033 | Winter | Day | 25 | 146 | 315 | 408 | 404 | 168 | 27 | 16 | 2 | 0 | 1 | 0 | 1512 |
| 5035 | Winter | Day | 22 | 6 | 10 | 24 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 76 |
| 1055541 | Winter | Day | 4 | 6 | 3 | 3 | 1 | 4 | 12 | 10 | 0 | 0 | 0 | 0 | 43 |
| 4997 | Winter | Night | 1 | 3 | 10 | 4 | 41 | 102 | 87 | 40 | 20 | 10 | 2 | 55 | 375 |
| 5033 | Winter | Night | 99 | 163 | 193 | 134 | 87 | 38 | 16 | 18 | 5 | 7 | 2 | 0 | 762 |
| 5035 | Winter | Night | 33 | 164 | 102 | 19 | 12 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 333 |
| 1055541 | Winter | Night | 28 | 38 | 38 | 32 | 42 | 51 | 20 | 6 | 5 | 1 | 3 | 1 | 265 |
| 4997 | Spring | Day | 94 | 51 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 149 |
| 1040674 | Spring | Day | 56 | 118 | 46 | 1 | 0 | 2 | 2 | 2 | 0 | 1 | 0 | 0 | 228 |
| 4996 | Spring | Day | 339 | 176 | 55 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 576 |
| 1040678 | Spring | Day | 122 | 68 | 13 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 206 |
| 4997 | Spring | Night | 54 | 14 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 74 |
| 1040674 | Spring | Night | 13 | 71 | 5 | 2 | 0 | 1 | 8 | 4 | 1 | 0 | 0 | 0 | 105 |
| 1040676 | Spring | Night | 72 | 13 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 86 |
| 1082468 | Spring | Night | 18 | 13 | 0 | 0 | 4 | 1 | 5 | 2 | 6 | 7 | 11 | 64 | 131 |

Detections per depth bin by the four individual Chinook salmon with the most detections in each of eight season and diel period combinations. Note that the 32 observed distributions displayed here come from 12 different Chinook salmon

Results

The 28 Chinook salmon were detected 16,791 times at 65 different acoustic receivers from November 1, 2006, to December 23, 2012 (Table 1; Fig. 1). In a given season/diel period, individual fish were detected 0–1512 times. Among the 32 distributions from the top four individuals with the most detections in each of the eight season/diel periods, the mean number of total detections was 435.63 ± 363.56 (Table 2). The 32 season/diel period distributions came from 12 of the 28 Chinook salmon (Table 2). These 12 fish exhibited no significant difference in fork length (mm) from the 16 fish that did not

contribute to the models (Student's *t* test: $P = 0.1422$), indicating no size-related bias in the likelihood of detection.

The median of the individual mean depths of the four distributions in each season/diel period was greater at night than during the day in all seasons except winter (Fig. 2). The variation in depth tended to be greater at night than during the day in all four seasons; however, in the winter the interquartile ranges were fully overlapping (Fig. 3).

The season/diel period model had the lowest Akaike information criterion (Table 3). Independently, the diel

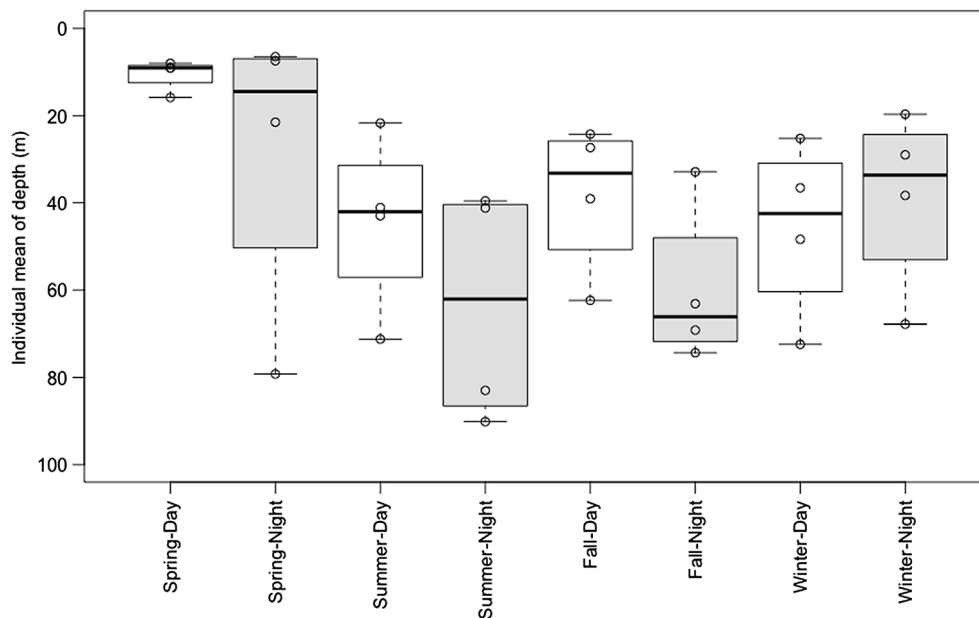


Fig. 2 Individual mean depth. Box plots of the individual mean depth for the Chinook salmon distributions ($n = 4$) in each season/diel period. These calculations are based off of all the raw depth detections for each individual fish in the corresponding season/diel period. Daytime and nighttime boxes are *white* and *gray*, respectively. Detections from >110 m were changed to exactly 110 m due to the depth limitation of the acoustic tags, making these calculations conservative

period and season significantly improved fitting to the Chinook depth data (compared to the null model), but season more substantially improved the model than diel period (Fig. 4). However, the interaction of season and diel period significantly improved the model more than either of the factors alone (Table 3). The season/diel period model output exhibited greater 50, 70, and 90% occupancy depths at night than during the day in all seasons except winter (Table 4). This represents a deeper and more variable depth distribution at night than day in summer, fall, and spring (Fig. 4).

The more even (i.e., variable) depth distributions in one diel period versus the other indicated DAPs (Table 4; Figs. 2, 3, 4). Daytime distributions with a shallow mode were fish confining their movements to a small depth range closer to the surface than the bottom (Figs. 4, 5). In contrast, nighttime distributions with more equal proportions across all depth bins represent bounce diving (repeated, brief vertical movements) by Chinook salmon (Figs. 4, 5). While the frequency and amplitude of these dives varied, both the preliminary analyses and the model indicated that this behavior primarily occurred at night (Figs. 3, 4). The juxtaposition of shallow and confined daytime movements with nighttime bounce diving, particularly in summer and fall (Fig. 4), revealed a DAP in the Chinook salmon depth distributions. In the model, this DAP was reversed in winter; during the

daytime, they occupied deeper sections of the water column, resulting in a more even distribution than at night (Fig. 4). The preliminary analysis exhibited a shallower median nighttime than daytime mean depth in the winter (Fig. 2); however, it did not detect a difference in depth variation between day and night (Fig. 3). Regardless, both methods demonstrated a reverse in the DAP during the winter; Chinook salmon shifted their depth distribution higher in the water column at night (Figs. 2, 4).

Discussion

The depth distribution of subadult Chinook salmon varied seasonally and revealed diel activity patterns. Conventional methods demonstrated that median mean and standard deviation of depth were higher at night in all seasons, except winter, and the Gamma-Dirichlet method linked the underlying cryptic differences in depth distributions to DAPs. The contrast of a more variable and deeper depth distribution at night strongly overlapping with a less variable and shallower depth distribution during the day, and the reverse in winter, shows that Chinook salmon do not exhibit classically defined DVM, confirming the conclusions of Smith et al. [13]. Consistent with our DAP findings, Candy and Quinn [27] found that during the summer in Johnstone Strait, British Columbia, Canada, Chinook salmon swam deeper and had greater rates of vertical movement during the night than day. The

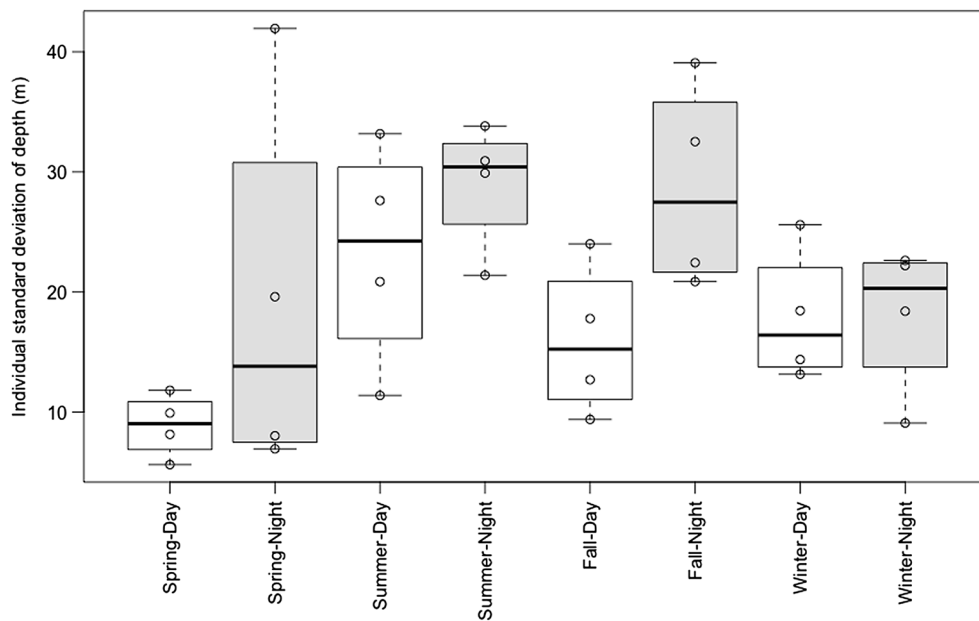


Fig. 3 Individual standard deviation in depth. Box plots of the individual standard deviation in depth for the Chinook salmon distributions ($n = 4$) in each season/diel period. These calculations are based off of all the raw depth detections for each individual fish in the corresponding season/diel period. Daytime and nighttime boxes are *white* and *gray*, respectively. Detections from >110 m were changed to exactly 110 m due to the depth limitation of the acoustic tags, making these calculations conservative

Table 3 Model comparison

| Model | AIC | # of parameters | Δ AIC |
|--------------------|----------|-----------------|--------------|
| Season/diel period | -6709.52 | 24 | 0.00 |
| Season | -6662.46 | 12 | 47.06 |
| Diel period | -6521.04 | 6 | 188.48 |
| Null | -6511.91 | 3 | 197.61 |

Akaike information criterion (AIC), number of parameters, and Δ AIC for each of the four models tested

notable nighttime bounce diving by Chinook salmon in summer and fall may result from them ascending to feed on prey that undergo nighttime DVM toward the surface [28, 29] and then descending to avoid marine mammal predators including harbor seals [30, 31] and southern resident killer whales [32, 33]. However, we did not test any behavioral hypotheses to explain the DAPs, and their ecological purpose requires further examination.

The Chinook salmon DAPs found in this study, conducted in interior marine areas, exhibit both similarities and differences to vertical movement patterns documented in earlier studies of Chinook salmon and other Pacific salmonids. Walker and Myers [34] observed an immature aged 1.2 (1 freshwater and 2 ocean winters) Chinook salmon rearing in the Bering Sea that similarly exhibited seasonally variable vertical movement behavior. In the summer, this fish was surface-oriented at night and

underwent vertical movements into deeper water during the day [34]. It then reversed its pattern in the winter by becoming surface-oriented during the day and undergoing deeper movement at night [34]. These intra-seasonal movement patterns in the Bering Sea are opposite of the DAPs we observed in Puget Sound in the summer and winter. However, both the fish in Walker and Myers' study [34] and the ones in this work reversed their movement pattern between these two seasons, suggesting that this inter-seasonal reversal in vertical movement behavior may be a characteristic trait of Chinook salmon. Steelhead, coho, pink, chum, and sockeye salmon in the North Pacific Ocean in spring and summer were surface-oriented at night and deeper during the day [35, 36], contrasting with the DAPs by subadult Chinook salmon we documented in those seasons. In interior marine waters between Vancouver Island and the British Columbia mainland, adult sockeye salmon homing to the Fraser River in summer were documented swimming in shallower water at night and deeper water during the day [37]. A subsequent study on sockeye salmon in that same area reported different diel patterns in the two study years [38], revealing the need to continue investigating the complexities of movement behavior. Further interspecific comparisons of seasonal and diel vertical movement patterns in the marine environment would be enabled by the collection of more long-term data on all of the Pacific salmonids [19, 20].

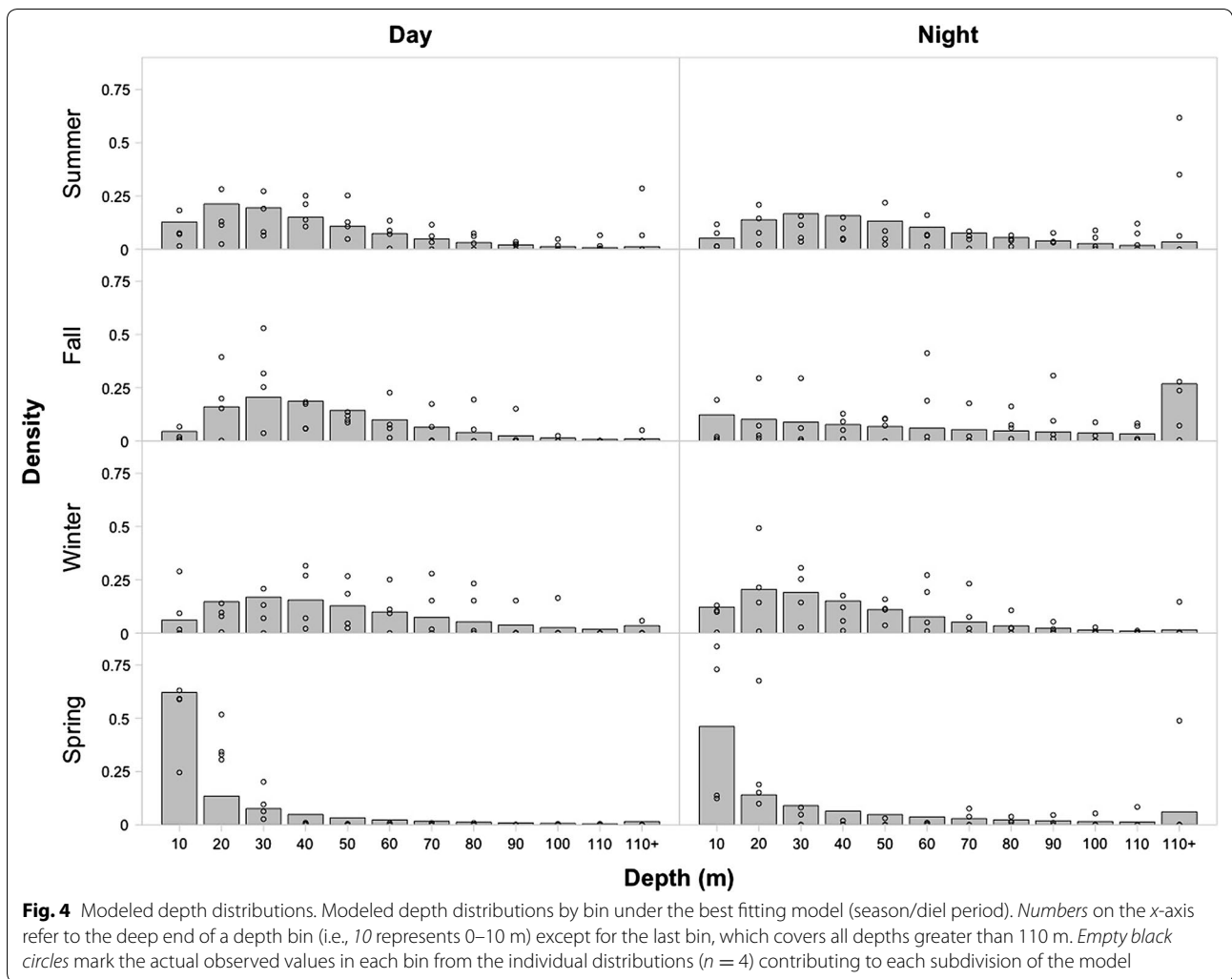


Table 4 Model predicted depth occupancy

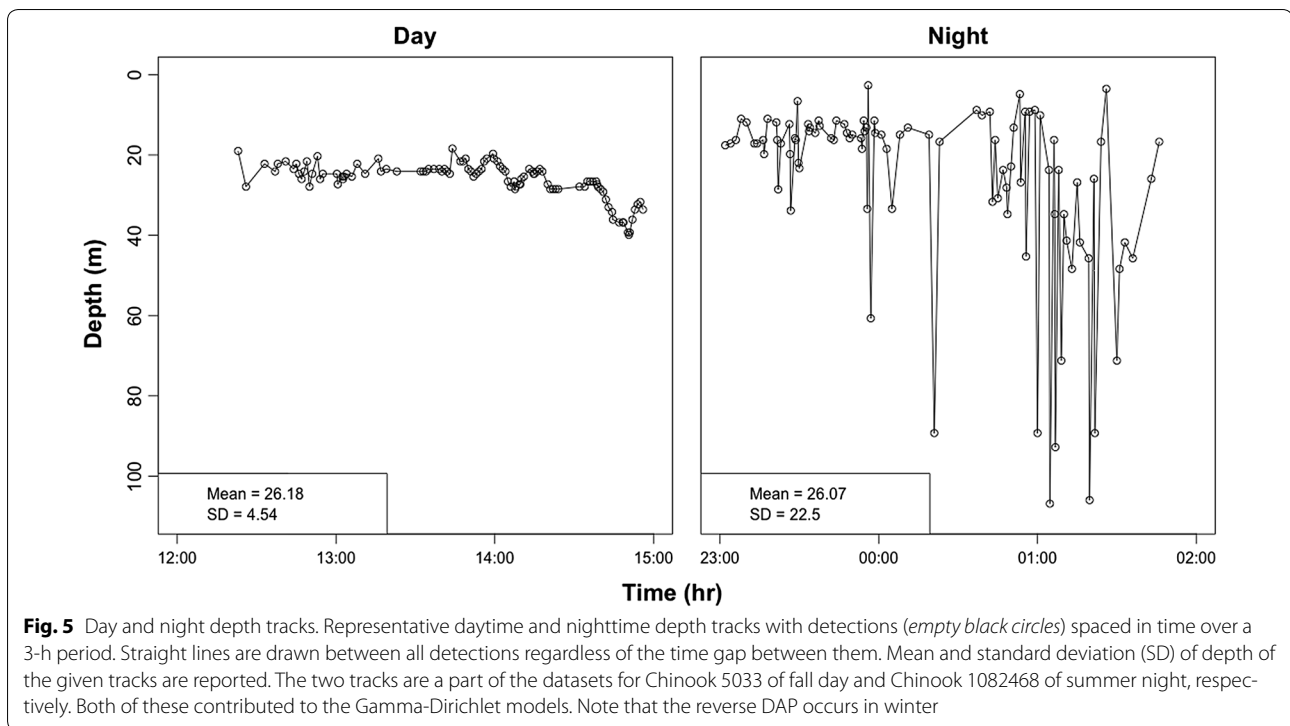
| 50% | Spring | Summer | Fall | Winter |
|-------|--------|--------|-------|--------|
| Day | 5.1 | 28.0 | 34.5 | 37.8 |
| Night | 12.2 | 39.0 | 56.8 | 29.0 |
| 70% | | | | |
| Day | 15.0 | 41.1 | 46.8 | 53.7 |
| Night | 31.1 | 54.8 | 100.4 | 42.6 |
| 90% | | | | |
| Day | 45.5 | 66.2 | 69.1 | 83.6 |
| Night | 83.3 | 84.3 | >110 | 68.6 |

Season/diel period model predicted depths (m) of 50, 70, and 90% occupancy. Depth of percent occupancy is defined as the depth above which the specified cumulative percentage of the distribution occurs. Note that if the predicted depth occurred deeper than 110 m, it was reported here conservatively as “>110” due to the depth limitation of the acoustic tags

The cryptic day–night differences, consistent with DAPs, of Chinook salmon vertical movements highlight the necessity of analyzing the entire distribution of depth

data. Smith et al. [13] reduced variation in the dataset by calculating model predicted average depths derived from hourly means and detected the strong seasonal variation but not the subtle diel variation in depth distribution for Chinook salmon in Puget Sound, WA. Additionally, the framework employed by Smith et al. [13] addressed seasonal variation in depth and DVM, but not DAPs. The 12 Chinook salmon we incorporated into the model were the same fish used in Smith et al. [13], but some of which had generated additional detection data between the end of their study and the beginning of ours. However, the addition of more recent data is not responsible for our supplementary conclusions. Instead, our framework and method inclusive of and capable of differentiating diverse DAPs enabled us to provide more information on Chinook salmon vertical movement behavior.

When changes in depth distribution are particularly pronounced, standard metrics may reveal significant differences across seasons and/or diel periods. For example,



the calculation of mean depths (seasonally, diurnally, hourly, etc.) is a common analysis in telemetry studies, but it can oversimplify vertical movement behavior, and its visual representation does not provide the actual shape of the depth distributions. While mean depths and other metrics can and have revealed much about various species [39–45], they should be accompanied by the analysis and display of full depth distributions that will augment discovery and proper classification of cryptic vertical movement behavior. The Gamma-Dirichlet method employed in this paper utilizes a holistic analysis and presentation of entire depth distributions, thereby enabling detection of particularly fine differences that may otherwise be lost if investigated solely with a standard metric.

Modeling depth distribution data with the Gamma-Dirichlet combination provides substantial benefits in terms of design flexibility and analytical resolution. First, the Dirichlet can estimate proportions over an infinite number of components [46], meaning that few or many depth bins may be used when fitting the gamma. By calculating the α_k of each bin from the α_{mult} and $\hat{p}(k)$, parameterization in each model subdivision is minimized and kept constant. Second, the depth bins may be of any width and need not all be the same width as each other.

Bin width can be expanded or reduced depending upon the depth recorder's resolution and accuracy, and the degree of data coverage. Tags that either record data in bins of varying sizes or that have depth-related limitations are also accommodated by the distribution combination demonstrated here. In conjunction, these flexible aspects of the Gamma-Dirichlet method not only allow the researcher to analyze depth distributions with as much or as little resolution as is desired (and appropriate), but also support the application of this approach to species in different vertical habitats.

For many aquatic species, telemetry studies are ideal for answering questions related to seasonal and diel depth patterns. The primary questions must include: (1) is the depth distribution seasonally variable, (2) does the organism undergo DVM, (3) if it does not undergo DVM, does it follow a DAP, and (4) if it follows a DAP, what is the difference in day–night vertical movement behavior? The framework employed in this paper and the method that assesses the whole depth distribution allow all of these questions to be answered and thoroughly describe the vertical movements of the target species. Future studies should consider using such a framework to describe the seasonal and diel variability in vertical depth distribution and relate it to horizontal movements when appropriate.

Additional files

Additional file 1. Gamma-Dirichlet (Arostegui et al.).R Gamma-Dirichlet Method Code: This is the R code we utilized to analyze our binned detection data with the Gamma-Dirichlet method. It utilizes our dataset, provided in additional file 2, to fit and compare the models.

Additional file 2. Binned_Detection_Data (Arostegui et al.).csv. Binned Detection Data: This is the dataset we utilized in the manuscript and analyzed with the Gamma-Dirichlet method. It consists of the four individual Chinook salmon depth distributions from each season/diel period.

Abbreviations

AIC: Akaike information criterion; DVM: diel vertical migration; DAP: diel activity pattern; SD: standard deviation.

Authors' contributions

MCA developed the Gamma-Dirichlet method, analyzed and interpreted the data, and wrote the manuscript. TEE helped develop the Gamma-Dirichlet method and contributed to manuscript preparation. TPQ obtained funding for the project, coordinated fieldwork and data management, and contributed to manuscript preparation. All authors read and approved the final manuscript.

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Availability of data and materials

The dataset supporting the conclusions of this article is included within the article.

Competing interests

The authors declare that they have no competing interests.

Ethics approval and consent to participate

Permits for the deployment of receivers were obtained from NOAA-Fisheries, the Washington Department of Natural Resources, Washington Department of Fish and Wildlife, and San Juan County. Permits for the capture and handling of fish were obtained from NOAA-Fisheries, the Washington Department of Fish and Wildlife, and the University of Washington's IACUC.

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