Characterizing seasonal dormancy and the physiological threshold for survival in Pacific sand lance (*Ammodytes personatus*)

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Abstract:

Pacific sand lance (*Ammodytes personatus*) go dormant through the winter. As foraging decreases, sand lance experience a decline in body condition. Natural mortality may occur due to starvation if body condition decreases beneath a physiological "threshold of survival". To quantify the threshold, juvenile Pacific sand lance were gathered from Jackson Beach on San Juan Island, Washington, and adults were collected from the San Juan Channel sand wave field. Fish were placed in tanks separated by life stage/source location. One juvenile tank contained sediment, while the other juvenile tank and the adult tank did not. This caused natural mortalities to occur earlier in the season and be observed during the study period.

To verify that the tank environments closely resembled natural habitats, condition over time data were compared from in-situ sampling and tank observations in 2018 and 2019. There was no statistically significant difference in the natural decline in condition trend between in-situ and tank observations for juveniles; there was a significant difference for adults. However, this is likely due to sampling variability. Morphometrics and condition were taken for fish which died of starvation. This condition at mortality data was compared over time and across life stages to gauge if the threshold of survival was consistent through the overwintering period and within/between life stages.

Results indicated that the threshold was consistent through time, suggesting that mortalities occurred due to fish reaching a "floor" of condition, regardless of if the death occurred early or late into the overwintering period. Condition at mortality differed significantly between life stages, with adults dying at a higher condition factor. Separate probability of mortality curves (eCDFs) were created for juveniles and adults to characterize the likelihood that an individual will reach mortality soon given a particular body condition. The threshold of survival was dictated by the condition at which fish have a 50% probability of mortality occurring soon. Juveniles were found to have a threshold at a condition factor (*K*) of 16.8, while the threshold for adults was 20.

This threshold likely exists for other fishes and may be an important consideration for fisheries management. Juveniles of various fish species are disproportionately affected by winter mortality. Variable mortality could have large effects on abundance and year class strength. Since mortality rates differ by life stage and based on environmental conditions year to year,

managers could reference mortality curves and oceanographic conditions to make better informed regulations which incorporate considerations for years with high mortality rates.

Introduction:

Pacific sand lance are small, burrowing forage fish which occupy coastal, benthic habitats of the North Pacific (Robards et al. 1999). In the San Juan Archipelago of Washington, sand lance can be found both in nearshore habitats and in deeper sand wave fields. Protected, shallow areas such as Jackson Beach are continually occupied by juveniles (Rood 2010). As autumn progresses, adults move from beach shores into deeper wave fields, such as those found in the San Juan Channel (Sisson and Baker 2017).

Sand lance are a critical component of pelagic ecosystems, providing essential and high-quality nutrients for higher trophic levels (Cury et al. 2011; Piatt et al. 2018). A limited number of forage fish species compose the intermediate trophic level in pelagic ecosystems. Thus, forage fish represent the constriction in a “wasp-waist” ecosystem (Cury et al. 2000). Since energy must pass through a few key species of forage fish before reaching higher trophic levels, gauging the body condition of these fish is important.

Through winter, Pacific sand lance enter a state of dormancy. This period is characterized by a reduction in foraging and overall inactivity. It has been observed in other forage fish such as various sand eels (*Ammodytes spp.*) and the European eel (*Anguilla anguilla*) (Deurs et al. 2010; Westerberg and Sjöberg 2015). Growth is limited by changes in temperature and food abundance (Baker et al. 2019; Robards et al. 2002). Thus, sand lance remain burrowed in sediment when they are not foraging to avoid predation and maintain energy reserves (Quinn 1999; Robards et al., 1999). As foraging decreases through the fall and winter, Pacific sand lance experience a natural decline in body condition (Baker et al. 2019). Seasonal depletion of energy reserves and decline in condition is similarly observed in other pelagic and estuarine fish (Foy and Paul 1999; Geissinger et al. 2021; Schultz and Conover 1999).

Fish which reach a low enough condition from winter starvation experience natural mortality (Dutil and Lambert 2000). Specifically, juvenile fish are greatly impacted by their first winter. With limited energy reserves, natural mortality rates are high for the first year of a juvenile teleost’s life (Sogard 1997). Some studies indicate that an individual’s probability of survival is not affected by size or the amount of energy reserves present (Shultz and Conover, 1999). However, contrasting evidence suggests that an individual's size is positively correlated with overwinter survival. High growth rates occurring late in the growth season may be a critical factor in survival (Huss et al. 2008).

This study aims to characterize a condition threshold of survival in Pacific sand lance and examine how it varies with fish demographics. It is hypothesized that there is a set minimum condition which is required for continued survival through the winter; fish which fall below this threshold are likely to experience natural mortality. Such a threshold likely occurs naturally and is approached as food availability declines in the winter. Given the physiological differences present between juveniles and adults, it is hypothesized that there may be different, but constant, critical conditions for each life stage. With limited energetic reserves, juveniles may fall below the threshold more frequently, leading to the observed high rates of first-year mortality. Variable declines in the number of juveniles may affect trends in stock abundance and year-class strength.

Establishing a threshold illustrates a concrete "floor" for survival. The condition of sampled Pacific sand lance may be compared to it when gauging population health. Rather than only comparing the condition of sand lance from a given year to historical data, which may be subject to shifting baselines, a threshold of survival may inform scientists about a population's condition relative to their own physiological requirements.

Methods:

Specimen Collection

From 2018 through 2023, juvenile Pacific sand lance were collected from Jackson Beach on San Juan Island, Washington and adults were obtained from the San Juan Channel sand wave field (Figure 1). Sampling in 2023 was conducted from October 28th through November 15th. In 2018 through 2022, sample collection occurred over approximately the same period, occasionally extending until early December.

To obtain fish from Jackson Beach, seines were conducted every 5 days. On each occasion in 2023, seines began just before sunrise and occurred under various tidal conditions. Two researchers dragged a 16.14 m^2 surface area, 0.5 cm diameter, knotless seine net at a depth of 1 meter parallel to the shoreline for a total of 2 minutes. The net was then pulled ashore, and

Pacific sand lance were retained. 5 seines were conducted sequentially on each sampling occasion.

To collect specimens from the San Juan Channel wave field, Van Veen grabs were performed aboard the University of Washington's R/V *Kittiwake*. Cruises occurred once per week for a total of 6 weeks. The Van Veen Grab Sampler was set in an open position and lowered to the seafloor. After reaching the ground, the Van Veen closed and was immediately raised carrying 0.12 m^2 of sediment and benthic organisms. Van Veen samples were sifted through on board. Pacific sand lance were retained for later processing.

Sample Processing

The majority of collected Pacific sand lance were euthanized so that morphometric data could be gathered. Fish were placed in seawater with MS-222 for a minimum of 5 minutes. For each individual, the following were recorded: a unique identification number, total length in millimeters, wet weight in centigrams, and whether the fish had been injured in collection in a manner that may affect morphometric measurements. A body condition factor (K) was calculated from mass (m, in centigrams) and length (l, in millimeters) according to the equation (Bagenal and Ricker 1978):

$$K = m \times 10^7 \times l^{-3}$$

Tank Experimental Set-Up

A subset of the Pacific sand lance collected during early-season sampling events were retained live in tanks in each year from 2018-2023. For mortality studies, 2023 samples were sourced from Jackson Beach and San Juan Channel and kept in tanks with and without sediment (Table 1). Tanks without sediment prevented individuals from resting as often as they would otherwise; this caused energy to be expended more quickly and allowed for natural mortalities which may have occurred later in the season to be observed during the study period. Tanks kept from 2018-2022 had various specimen source locations and experimental set-ups. This study references only historical data from tanks containing Jackson Beach fish kept with sediment and San Juan Channel fish kept without sediment. Source location was used as a proxy for fish life stage with juveniles occupying Jackson Beach and adults occupying San Juan Channel.

Data Collection: Mortalities and End-of-Season Sacrifices

For the purpose of this study, "mortality" refers to natural deaths which occurred in the tanks due to a seasonal decline in body condition, whereas "sacrifice" refers to fish which survived until early December in tanks and were euthanized. Fish which experienced natural mortality were carefully examined for indications of unrelated trauma; individuals which were determined to have died from external factors were excluded from the dataset.

Tanks were monitored daily for fish mortalities. Pacific sand lance which were swimming or had visibly moving gills were left undisturbed. Fish which were laying down were slightly moved using a net to check for responsiveness. Dead individuals were removed from the tanks. Morphometrics were taken for all mortalities according to the standard sample processing procedure described previously. Dead fish were then individually labeled and stored at -80°C for potential future analyses. Fish which survived through the study period were sacrificed and processed in the first two weeks of December of every year from 2018-2023.

Inclusion of historical data

Historical data from 2018-2023 were considered for incorporation. Condition-at-mortality data came from the 2023 experiment, as there was consistent monitoring for mortalities and record keeping of morphometrics. In-situ versus in-tank condition data were derived from 2018 and 2019 experiments, as these years included tanks with sediment for juveniles and adults. For 2018 and 2019, data was included from sampling events throughout the fall season and sacrifices at the end of the season. Morphometrics which might have been affected during the specimen collection process were excluded from the dataset.

Data Analysis

A variety of plot types and statistical tests were applied in R (version 2023.09.0+463) and used to analyze mortality and condition data. Histograms were created to visualize body condition-at-mortality in juveniles versus adults (Figure 2). To determine if there was a significant difference in condition-at-mortality between life stages, boxplots, ANOVAs, and Tukey tests were generated.

For each treatment, scatterplots of condition-at-mortality by Julian date and linear regressions were created to determine if time of mortality (through the overwintering period) affected condition-at-mortality. A general additive model (GAM) was applied to gauge the influence of time through the overwintering period on condition-at-mortality. Additionally, a GAM was used to illustrate if mortalities occurring early in the season may be due to trauma from capture rather than a natural decline in condition; mortalities deemed to be caused by trauma from capture were excluded from further analysis.

To quantify the probability of a condition-related mortality occurring for an individual of a given condition (or a sample average), empirical cumulative distribution functions (eCDFs) were produced. As juvenile and adult fish differ morphometrically, separate eCDFs were made for each life stage.

To verify that tank environments resembled natural habitats and did not introduce confounding variables, data from tank experiments were related to in-situ data in condition-over-time scatterplots. The slope of linear models representing the decline in condition in-situ and in tanks were compared. For in-situ data, fish were gathered during sampling events throughout the fall, sacrificed, and processed; this group represented the condition factor for the population on the day they were sampled. For tank observation data, a subsection of fish were put in three tanks, while others from the same sampling event were sacrificed and processed. To obtain an initial condition for tank fish, condition factors from fish which were processed on the same day that others were put in tanks (in early October) were used. The final condition factor for tank fish (taken in December) came directly from tank fish which survived through the fall. ANOVA and Tukey tests were applied to gauge significance. From this data, scatterplots were created of in-tank body condition by day of the year for 2018 and 2019. Separate scatterplots of in-situ condition by day of the year were generated for each source location (Jackson Beach and San Juan Channel) in 2018 and 2019. The slopes of in-tank and in-situ based scatterplots were compared to gauge the similarity between results observed in tank experiments and what occurs in natural habitats. An alpha level of 0.05 was set for all statistical tests.

Results:

Effect of time on condition at mortality

The influence of time of mortality on final condition was analyzed for both juveniles and adults kept without sediment. An initial scatterplot and linear model of juvenile condition at mortality by date was generated (Figure 3). The linear model had a statistically significant negative slope ($p = 0.0458$).

High outliers which occurred soon after fish were put in tanks indicated the need to generate a general additive model (GAM) (Figure 4). There was a positive influence of time on condition at mortality from the initial date of October 9th, 2023 through October 21st, 2023. There was negligible influence of time on condition at mortality from October 22nd, 2023 through November 30th, 2023.

A secondary scatterplot and linear model of juvenile condition at mortality by date was created, omitting mortalities from October 9th, 2023 through October 21st, 2023 (Figure 5). The slope of the linear model was not significantly different from 0 ($p = 0.1199$).

For adults, a scatterplot and linear model was created which omitted mortalities before October 22nd (Figure 6). The slope of the linear model was not significantly different from 0 (0.4258).

Effect of life stage (juvenile versus adult) on condition at mortality

Box plots of condition at mortality for the three groups (juveniles kept with sediment, juveniles kept without sediment, and adults kept without sediment) were generated (Figure 7). An ANOVA test highlighted a significant difference between groups ($p = 5.17 \times 10^{-5}$). A Tukey test found a significant difference between adults kept without sediment and juveniles kept without sediment ($p = 0.0001$) as well as between adults kept without sediment and juveniles kept with sediment ($p = 0.0011$). There was not a significant difference between juvenile groups ($p = 0.6974$).

Probability of mortality curves

Separate empirical cumulative distribution functions (eCDFs) were created for juveniles and adults based off the previous histogram (Figure 2). For juveniles, the 0.50 probability of mortality aligned with a condition factor of 16.8 (Figure 8). For adults, the 0.50 probability of mortality fell at a condition factor of 20 (Figure 9).

Comparison of historical tank and in-situ data

Scatterplots with linear models were generated, characterizing the decline in condition over the fall as observed in tanks and in-situ in 2018 and 2019 for juveniles (Figure 10) and adults (Figure 11). For juveniles, there was not a significant difference in slopes modeling decline in condition in tanks versus in the wild in 2018 ($p = 0.4576$) or 2019 ($p = 0.0571$). For adults, there was a significant difference in slopes modeling decline in condition in tanks versus in the wild in 2018 ($p = 1.988\times10^{-7}$) and 2019 ($p = 0.0004$).

Discussion:

With the goal of understanding the energetic requirements for Pacific sand lance to survive through the winter, this study aimed to quantify and test for the validity of a body condition "threshold of survival". This included testing whether the threshold was impacted by time through the overwintering season or the life stage of individuals. Additionally, it was verified that findings from the tank experiment could be generalized to wild habitats.

Verifying the similarity of tank and natural environments

Similar slopes for seasonal decline in condition were observed for juveniles (Figure 10) and adults (Figure 11), in-situ and in tanks. If tanks had introduced additional stressors which may act as confounding variables, data may have shown a stronger decline in condition (that is, a steeper linear model slope) in tank data as compared to in-situ data. Visually, all trends appear similar between in-situ and in tank environments. Among juveniles, there was no significant difference, indicating that the tank did not introduce confounding variables and that all findings could be generalized to the wild. Among adults, there was a significant difference. However, this may be due to sampling variability, which was greater in tank observations compared to in-situ. Since fish must be sacrificed before calculating condition, the initial condition recorded for tank fish did not come from the actual tank fish, whereas the final condition data did. This difference in individuals may increase sampling variability and lead to significant, but not meaningful, differences. However, it is interesting that differences were only observed for adults and not juveniles; future studies could examine if physiological needs differ for adults in a manner that may be negatively impacted by a tank environment. Within the range of this study, it is assumed that the tank environment adequately resembled a natural habitat and that results may be generalized to the wild.

Effect of time on condition at mortality

With a statistically flat trendline over time, Figure 3 indicates that time of mortality does not impact condition at mortality. That is, a juvenile will die if it hits a consistent minimum condition threshold, whether that occurs early or late in the overwintering season. Notably, three mortalities displayed in Figure 3 occurred soon after fish were put into tanks. All three fish died in relatively good condition. This indicated that the cause of death may not have been due to a natural decline in condition, but rather injury or stress from being caught and placed in tanks. To substantiate this hypothesis, a general additive model was applied to test if the influence of time on condition at mortality was consistent or variable. Figure 4 shows that time had a large influence on the condition at mortality from October 9th, 2023 (when the first mortality occurred, a week after individuals were placed in the tank) through October 21st, 2023. This justified the exclusion of early outliers from further analysis. With early mortalities omitted, Figures 5 (for juveniles) and 6 (for adults) also display statistically flat trendlines over time. It may therefore be concluded that time does not substantially impact the condition at mortality in juveniles or adults. Conceptually, this suggests that the threshold of survival, the minimum body condition at which a sand lance will continue to survive, is consistent through the season.

Effect of life stage on condition at mortality

Given the physiological differences present in juvenile and adult fish, it was hypothesized that the threshold may vary between life stages. In contrast to adults, juveniles must allocate energy for growth as well as building energetic reserves (Cui et al. 1996). Reaching a large body size is especially important for survival in juveniles; large larvae and juveniles experience higher winter survival rates (Sogard 1997; Stige et al. 2019). Winter mortality often occurs due to depleted energy reserves (Huss et al. 2008). Thus smaller juveniles may be more susceptible to it than adults. This is reflected in Figure 7. The threshold between adults and juveniles is statistically different, with adults dying at a better condition than juveniles. Because the condition factor at mortality does not differ between groups of juveniles, it is reasonable to conclude that the threshold is consistent within life stages.

Probability of mortality curves

Empirical cumulative distribution functions (Figures 8 and 9) were used to conclude that juveniles with a condition factor of 16.8 or lower have a 50% or greater probability of mortality in the near future. Similarly, adults with a condition factor of 20 or lower have a 50% or greater probability. Though 50% was highlighted as the "threshold of survival" for the purpose of obtaining a straightforward figure, it is important to note that the likelihood of reaching mortality in the near future increases with decreasing body condition. Data indicate that juveniles with a condition of 12.5 or lower, and adults with a condition of 15 or lower, have a near 100% probability of reaching mortality soon. Though statistics cannot be run between the two thresholds, there is a substantial difference in condition thresholds for adults versus juveniles. This is further evidence that the threshold varies with life stage and occurs at a greater condition in adults compared to juveniles.

The probability curve may be used as a reference to gauge the health of individuals or samples from a larger population. The condition factor of an individual, or an average condition factor from a sample, may be used to find the probability that the group of interest will reach mortality in the near future. This could be beneficial in several ways. Sampling for fish likely excludes individuals which have reached or are near mortality, as they may be more subject to predation. The health of sand lance populations could be gauged by comparing the condition of sampled fish from a given year to that of previous years. However, using the probability of mortality curve may enable scientists to gauge a fish's health by comparing it to the minimum condition that an individual could reach before starving. Essentially, the curve can help to compare a sample's health relative to their own physiological base requirements. Used in conjunction with condition-over-time studies, scientists may assess the health of a population both over time and within biological limits. It is important to recognize that the probability of mortality curves were based solely on data from sampling done in 2023, as it was the first year morphometrics on tank fish mortalities were regularly recorded. Overall Pacific sand lance condition varies over years (Baker 2023*). Therefore, if the probability of mortality curve were to be applied to data from other years, it would be valuable to build on the dataset and reduce bias toward the average condition of fish in 2023.

Broader Implications

The existence of a consistent threshold of survival in Pacific sand lance implies that a threshold exists for other fishes. Researchers observed similar seasonal declines in nutritional status in Pacific herring (*Clupea pallasi*) when metabolic needs exceeded the energy that could be obtained through foraging. Concurring with the present study, juveniles were found to be more affected by starvation (Foy and Paul 1999).

Mortality rates may vary both between life stages and based on year-specific conditions. This must be considered as an important factor in stock abundance and year-class strength. For gizzard shad (*Dorosoma cepedianum*), unusual winter and spring conditions caused an estimated 10% of the population to starve. "Severely stressed" (though surviving) fish had significantly lower condition factors and lipid stores (Adams et al. 1985). If juveniles were disproportionately affected, as was observed with Pacific sand lance and herring, this abnormally large mortality event may have affected recruitment, having lasting impacts on population size and structure. This effect likely occurs for a wide range of mid-level fishes.

To effectively assess fish populations, managers should also consider oceanographic factors which may affect mortality levels. In a review of studies on the causes of winter mortality on fishes, Hurst concludes that the likelihood of winter starvation in fishes is impacted by both thermal regime and prey availability (2007). As these factors differ year-to-year, and may be subject to larger global change, it is reasonable to conclude that mortality rates may vary greatly over time. However, little research has been conducted on whether the probability of mortality given a certain body condition varies with environmental conditions, or if the threshold for survival is inherent and consistent regardless of non-physiological factors. Future studies could compare probability of mortality curves across a range of species and years to understand if they may be universally applicable, or year specific.

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Tables and Figures:

Figure 1: Study sites around San Juan Island, Washington including the San Juan Channel sand wave field (outlined in orange) and Jackson Beach.

Table 1: Experimental set-up of tanks holding pacific sand lance of various source locations and life stages with and without sediment.

Source location	Life stage of fish	Sediment presence	Original sample size
Jackson Beach	Juvenile	Present	n = 65
Jackson Beach	Juvenile	Absent	n = 65
San Juan Channel	Adult	Absent	n = 55

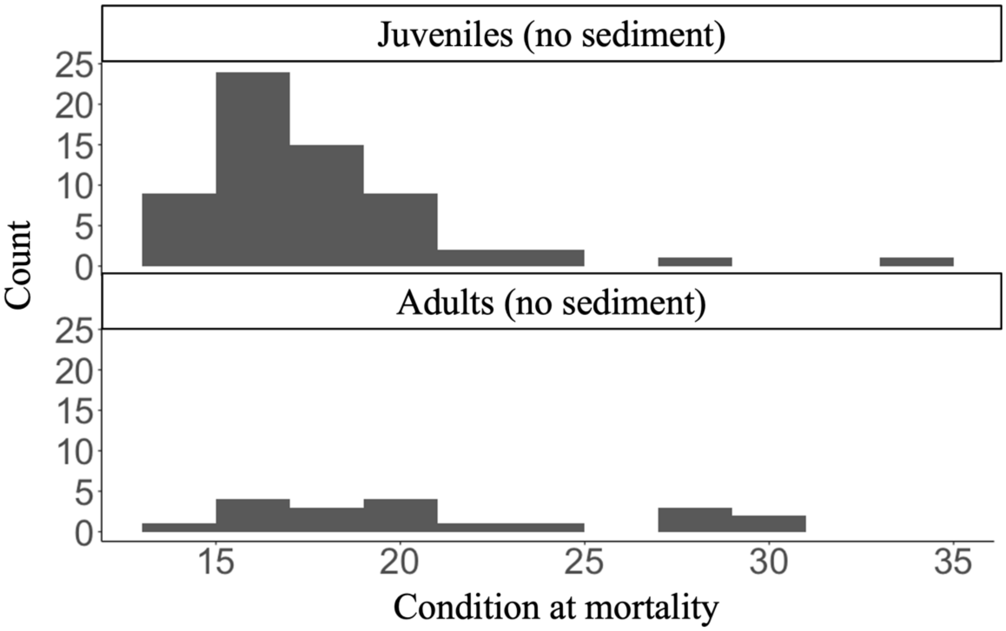

Figure 2: Histograms displaying the condition factor (K) at mortality for juveniles from Jackson Beach and adults from San Juan Channel kept in tanks without sediment. Recorded mortalities occurred between October 22nd, 2023 and November 30th, 2023.

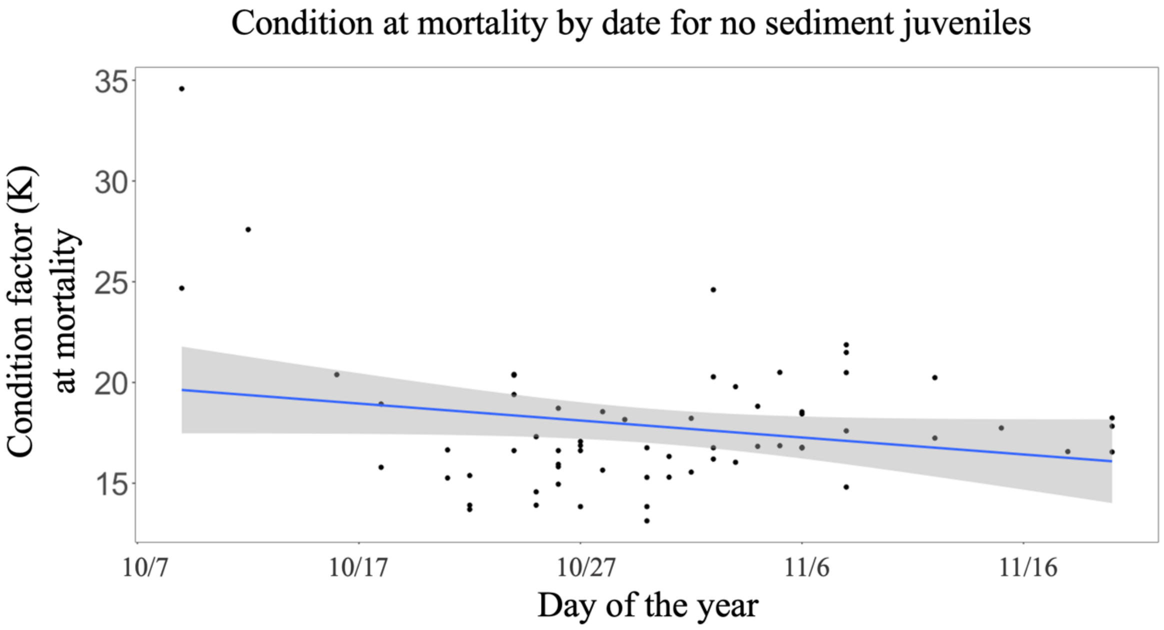

Figure 3: Scatterplot with an overlayed linear model comparing the condition factor (K) at mortality for juveniles kept in tanks without sediment to the date of mortality (day of the year). Recorded mortalities occurred between October 9th, 2023 and November 30th, 2023.

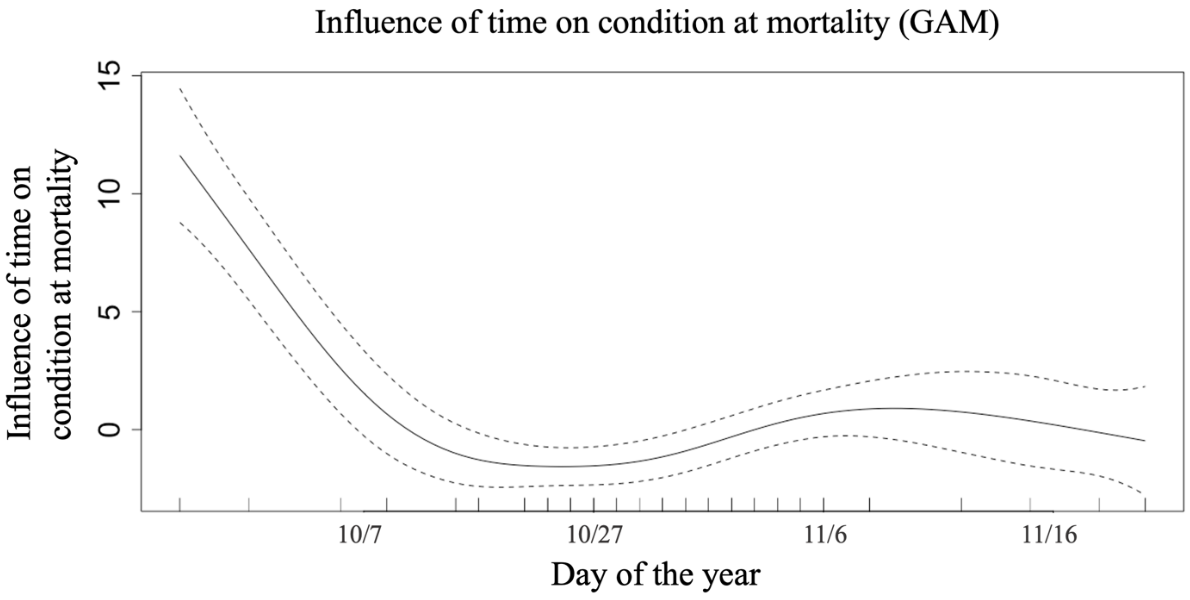

Figure 4: General additive model describing the influence of time on the condition factor (K) at mortality for juveniles kept in tanks without sediment. Recorded mortalities occurred between October 9th, 2023 and November 30th, 2023.

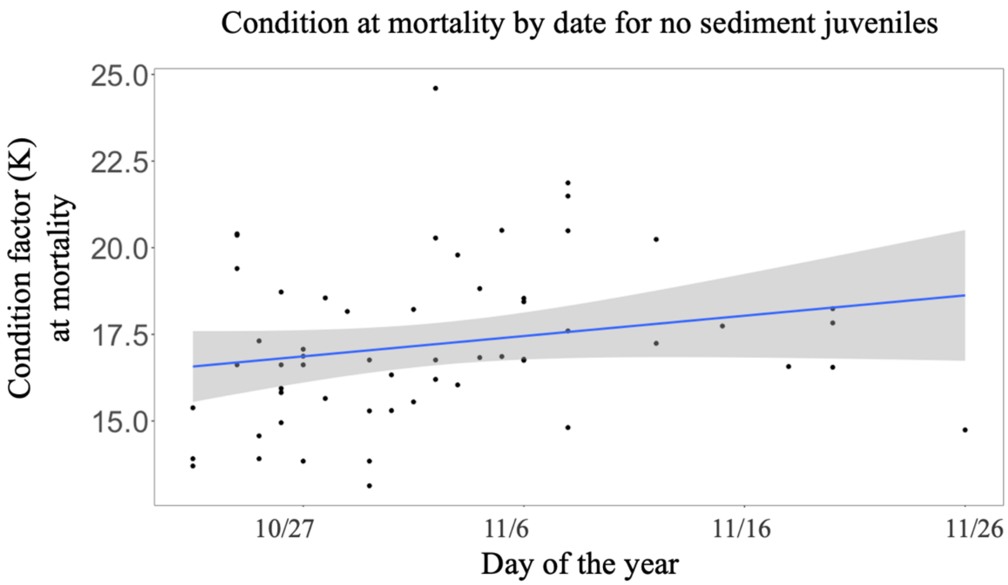

Figure 5: Scatterplot with an overlayed linear model comparing the condition factor (K) at mortality for juveniles kept in tanks without sediment to the date of mortality (day of the year). As compared to Figure 3, Figure 5 omits mortalities occurring before October 22nd, 2023. Recorded mortalities occurred between October 22nd, 2023 and November 30th, 2023.

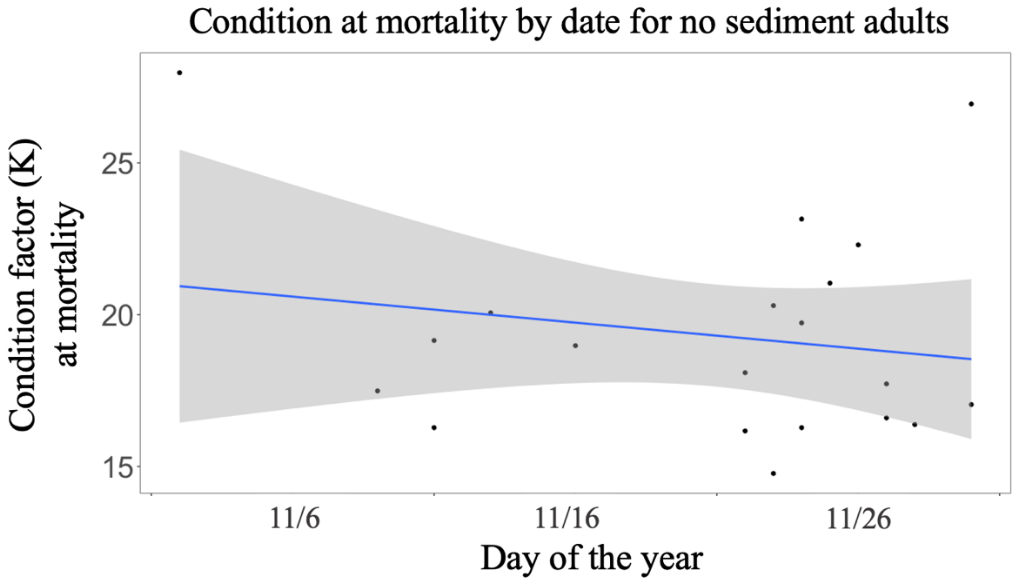

Figure 6: Scatterplot with an overlayed linear model comparing the condition factor (K) at mortality for adults kept in tanks without sediment to the date of mortality (day of the year). Recorded mortalities occurred between November 2nd, 2023 and November 30th, 2023.

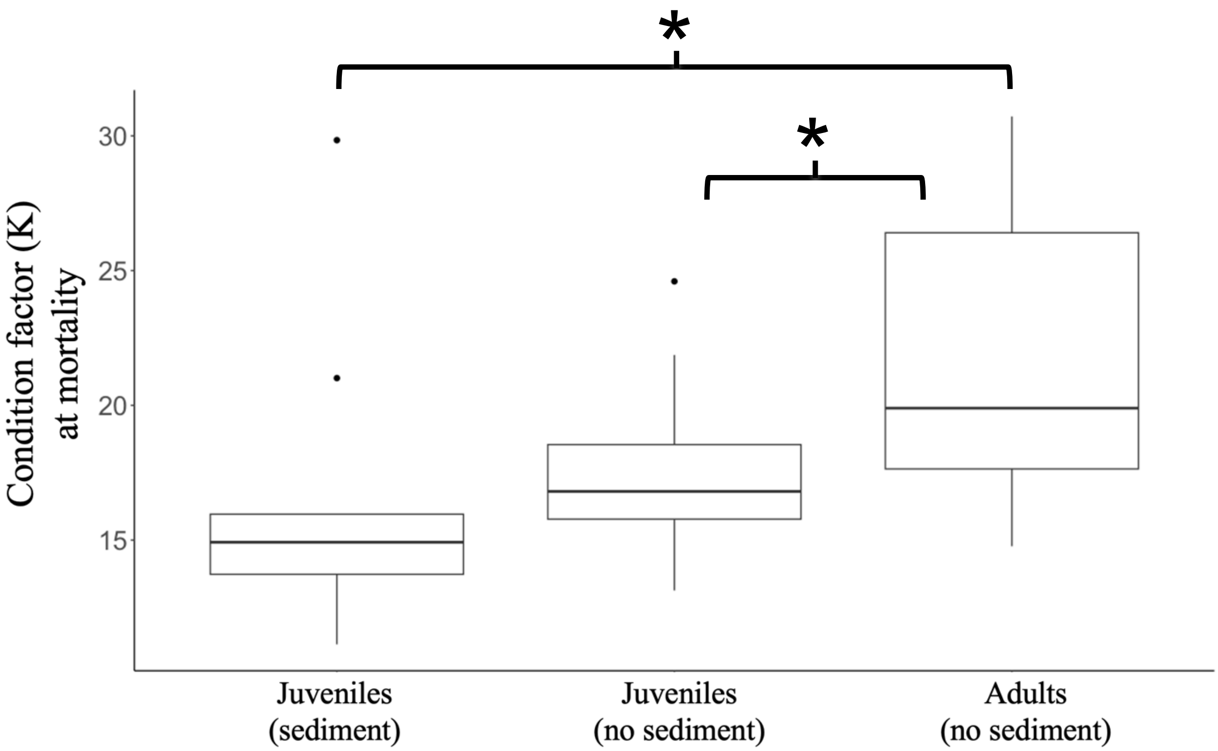

Figure 7: Boxplots illustrating the difference in condition factor (K) at mortality for juveniles kept in tanks with sediment, juveniles kept without sediment, and adults kept without sediment. Recorded mortalities occurred between October 22nd, 2023 and November 30th, 2023. Statistically significant differences are signified with asterisks.

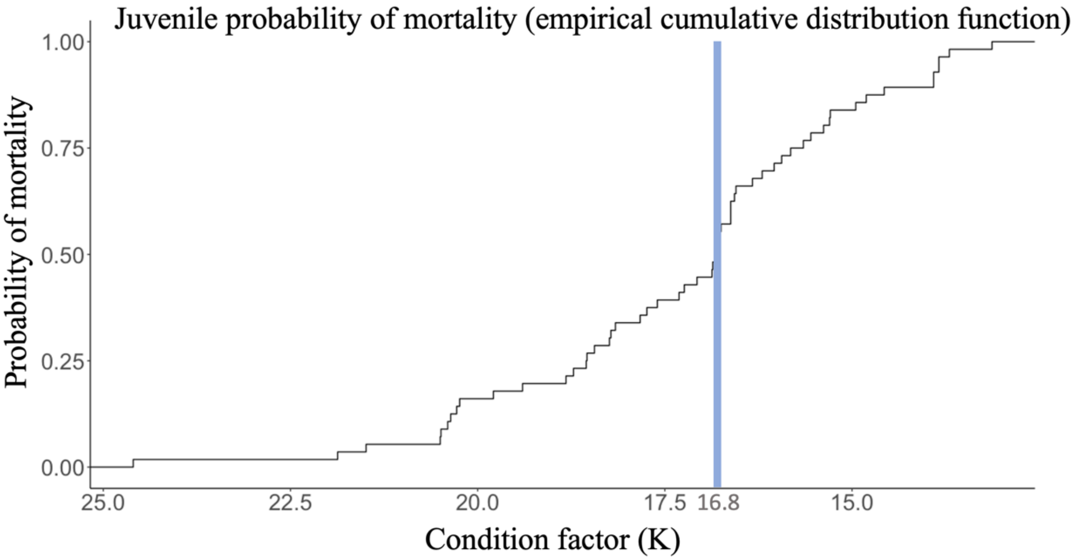

Figure 8: Empirical cumulative distribution function (eCDF) depicting a probability of mortality curve for a Pacific sand lance juvenile from Jackson Beach, San Juan Island. Condition factor (K) is plotted against the probability of mortality. The curve is based on mortalities occurring between October 22nd, 2023 and November 30th, 2023. The vertical blue line denotes the threshold of survival (with a condition factor of 16.8 and a 0.50 probability of mortality).

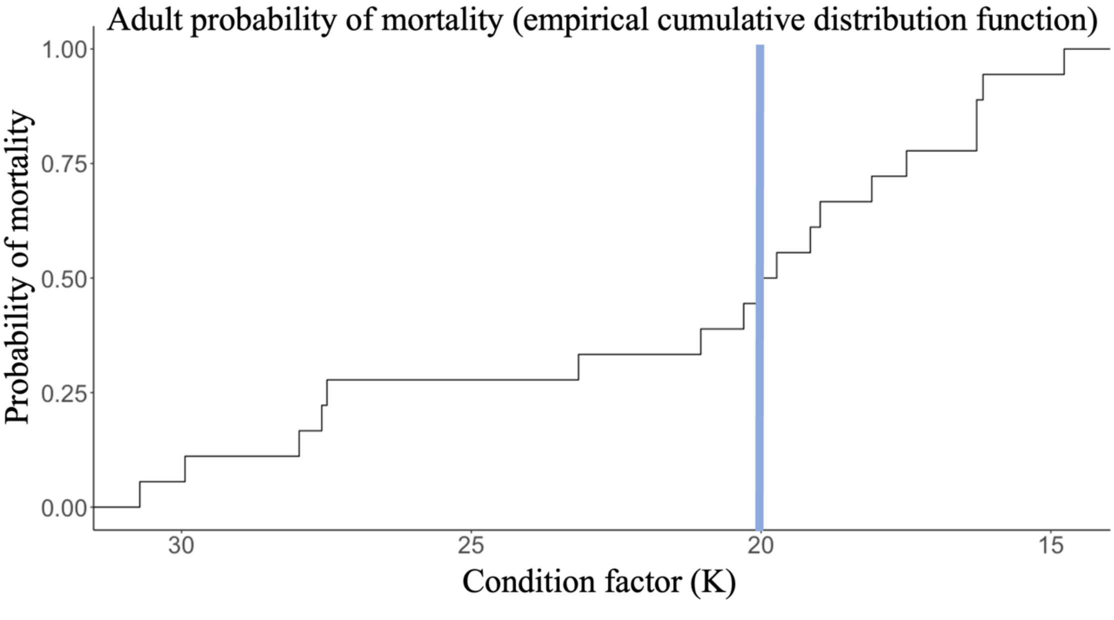

Figure 9: Empirical cumulative distribution function (eCDF) depicting a probability of mortality curve for a Pacific sand lance adult from San Juan Channel. Condition factor (K) is plotted against the probability of mortality. The curve is based on mortalities occurring between November 2nd, 2023 and November 30th, 2023. The vertical blue line denotes the threshold of survival (with a condition factor of 20 and a 0.50 probability of mortality).

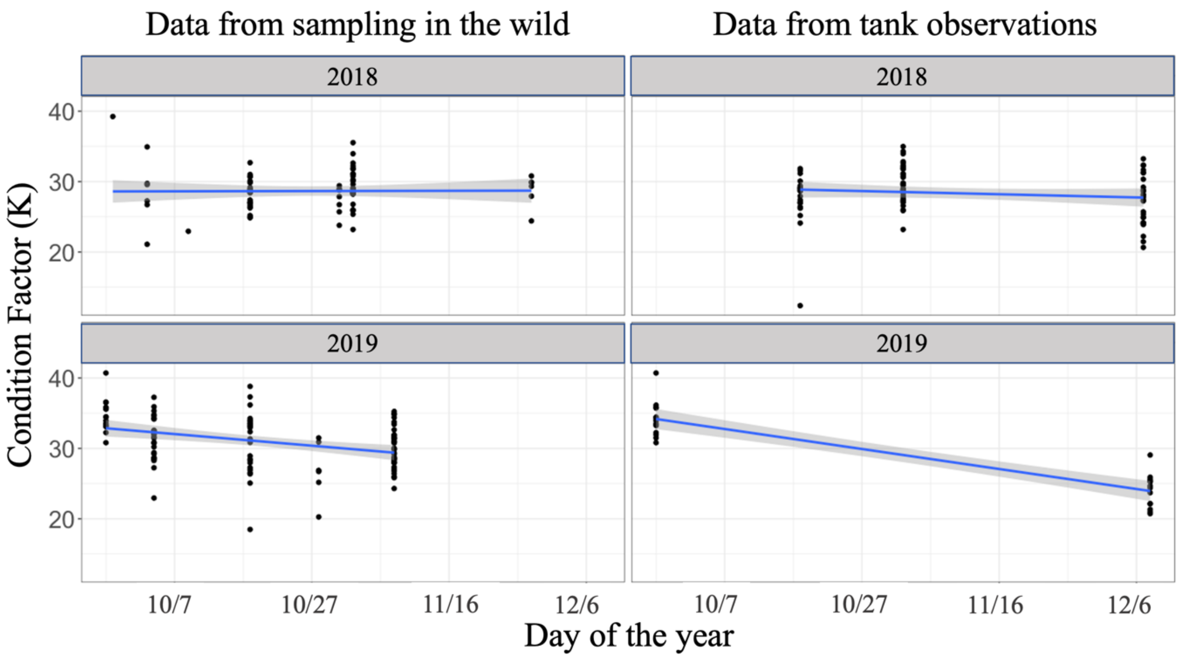

Figure 10: Scatterplots with linear models illustrating a historical data comparison of juvenile decline in condition through the fall as observed in the wild (left column) and in tanks (right column) in 2018 and 2019. Columns of points represent the condition factors of all individuals processed from one sampling event.

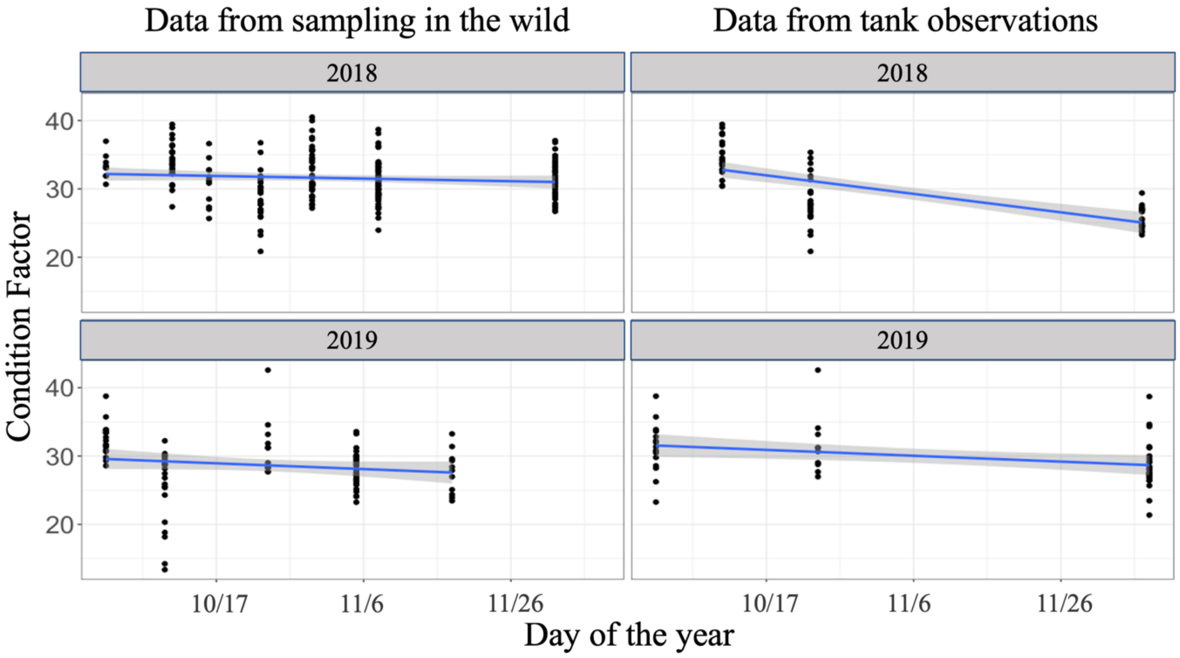

Figure 11: Scatterplots with linear models illustrating a historical data comparison of adult decline in condition through the fall as observed in the wild (left column) and in tanks (right column) in 2018 and 2019. Columns of points represent the condition factors of all individuals processed from one sampling event.