Commercially and ecologically valuable forage species selectively use shallow nearshore habitats at fine spatiotemporal scales

by

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Abstract

Nearshore ecosystems provision food and habitat for a diverse community of resident and migratory species, that in turn support coastal fisheries and economies. However, the spatial and temporal dynamics of habitat use by nearshore species are poorly understood in many areas as traditional underwater survey methods (e.g., SCUBA) only capture a snapshot in time, with many species difficult to observe *in situ*. Using timelapse cameras at six sites across two regions on a large nearshore shelf within a temperate inland sea, the Strait of Georgia, we determined community composition and the presence and abundance of forage species between 7 am and 7 pm during the summer of 2024. Timelapse images were paired with environmental data (temperature, current speed) to investigate how abiotic factors influenced dominant forage species. We quantified 16 taxa, including eight groups of forage fish. Community composition varied significantly over time and between regions, with forage species such as *Clupea pallasii* (Pacific herring) dominant earlier in the season and *Doryteuthis opalescens* (opalescent squid) dominant later, with these species being more abundant at different regions. Regional and temporal differences demonstrate that relatively small variations in environmental conditions can affect community composition, underscoring the need for fine-scale monitoring to inform site- and species-specific management. Pacific herring and opalescent squid showed distinct habitat use as the season progressed, with evidence of environmental factors influencing species distributions, particularly during spawning and juvenile stages. Increased temperature negatively influenced herring presence, while increased current had the opposite effect. Conversely, increased current negatively influenced squid presence. These findings have implications for predator-prey interactions, with the distributions of herring and squid likely influencing the presence of their predators, including salmon and rockfish. As climate change continues to alter ocean conditions, understanding how these species respond to environmental variability is essential in predicting shifts in their distributions.

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Introduction

Nearshore ecosystems provision food and habitat for a diverse community of resident and migratory species, many of which are culturally, economically, ecologically, and recreationally valuable (Ayyam et al., 2019; Gregr et al., 2013; Seitz et al., 2014). These ecosystems act as a transition zone between land and sea environments and can be defined as the shallow subtidal region of the coast, ranging from 0-50 metres in depth (Ayyam et al., 2019; Gregr et al., 2013). They are often nutrient rich as they are supplied with both land-based and upwelled nutrients (Ayyam et al., 2019). The shallow nearshore (less than 10 metres in depth) is especially productive, containing a range of marine vegetation, which, in combination with high nutrients, results in high productivity (Ayyam et al., 2019). Vegetation and productivity in the nearshore provide essential nursery and juvenile habitat for many commercial and recreational fishery species (Ayyam et al., 2019; Seitz et al., 2014). Further, nearshore habitats serve as important feeding grounds for resident and migratory species (Ayyam et al., 2019; Seitz et al., 2014).

Nearshore habitats are under pressure from various anthropogenic stressors, including coastal development, habitat degradation, and climate change (Crain et al., 2009). Anthropogenically mediated stressors have the potential to change both the biotic and abiotic factors in the nearshore environment (Crain et al., 2009). Specifically, the degradation of nearshore habitats can be detrimental to their function as nursery and feeding grounds, often to the extent that they can no longer fulfill these roles (Seitz et al., 2014). Moreover, the nearshore environment is highly dynamic, with abiotic factors fluctuating across spatial and temporal scales, influencing species distributions and community composition (Boero, 1994; Noisette et al., 2022). Thus, distributions of marine fish, as well as the timing of spawning and migrations, can be driven by changing abiotic factors (Klimova et al., 2021; Pietrafesa et al., 1986; Tillotson et al., 2021). As such, it is important to develop an understanding of how species in the nearshore use these habitats across varying environmental conditions to inform management and research (Kroeker et al., 2020; Ruppert et al., 2010).

Around the world, small or intermediate-sized pelagic planktivorous fish and invertebrate species (sometimes termed ‘forage fish’) are an important part of marine ecosystems due to their role in marine food webs, supporting fisheries and coastal economies (Gonzalez-Pestana et al., 2022; Nissar et al., 2023; Pikitch et al., 2014). Specifically, forage fish transfer energy between lower

and higher trophic levels by serving as prey for many species of fish, sea birds and marine mammals (Nissar et al., 2023; Rivers et al., 2022). While forage fish themselves can be the basis of important fisheries, they also support fisheries for larger fish, with the economic benefits of forage fish totalling around USD 18.7 billion per year, three times their own estimated catch value (Konar et al., 2019; Nissar et al., 2023). Forage fish abundance is often highly variable and has been found to be driven by climatic variability and changes in oceanic conditions (Fréon et al., 2005; Peck et al., 2014). Habitat use of forage fish species can be influenced by abiotic factors including ocean temperature and current speed, as well as by the time of day and time of year (Almatar, 1984; Beacham et al., 2008; Haslob et al., 2009; Lupandin, 2005; Shaffer et al., 2023). Therefore, understanding changes in habitat use due to varying environmental conditions is crucial. It can help inform where these species are, when they are there, and what influences these patterns of habitat use.

While forage fish have been extensively researched in offshore and estuarine areas, their dynamics and habitat use the nearshore have been less well studied (Munsch et al., 2016; Rivers et al., 2022). Improving our understanding of forage fish dynamics in the nearshore is important for several reasons. First, nearshore habitats are subject to increased anthropogenic pressures ranging from commercial fisheries and recreational activity to the pronounced impact of anthropogenically mediated climate change (Crain et al., 2009). Next, nearshore habitats connect forage fish moving between shallow and deeper waters throughout their life histories (Munsch et al., 2016), and are central habitats for many of their predators (Nissar et al., 2023). Lastly, nearshore habitats are often targets for implementing conservation measures and marine protected areas (Agardy et al., 2011; Cicin-Sain & Belfiore, 2005). As such, due to these unique aspects of the nearshore environment, current knowledge of forage fish dynamics outside of these habitats may not inform how these species use the nearshore. This gap in understanding limits our ability to effectively manage these species across all of their habitats.

Building this understanding in the nearshore is challenging as fish species are difficult to observe *in situ* (Able, 2016). To date, nearshore habitat use of forage fish has typically been monitored using visual (e.g., SCUBA or ROV observations) and fishery-based (e.g., micro-trolling or seine netting) survey methods (Murphy & Jenkins, 2010). These methods are often limited, as they are typically confined to a single area over a short period of time. As such, these methods may target

or exclude certain species due to their logistical constraints. Stationary underwater timelapse cameras offer a potential solution to these limitations, as they allow for non-intrusive, direct observation over long periods of time (Collins et al., 2015). Timelapse imagery is also valuable when direct observations cannot be made due to factors restricting site access, such as poor weather conditions (Balazy et al., 2018). Moreover, it is possible for multiple timelapse cameras to be running simultaneously, allowing a study to cover a larger spatial extent over the same timeframe. Timelapse cameras can inform the diversity and abundance of fish in an area, which can then be used to develop an understanding of community composition and habitat use (Armstrong et al., 1992; Deacy et al., 2016; Kimura & Somerton, 2006; Takahashi et al., 2023).

Two common forage species in the Northeast Pacific are *Clupea pallasii* (Pacific herring) and *Doryteuthis opalescens* (opalescent squid) (Lerner & Hunt, 2024). The latter is considered a forage fish due to its position in the food web, acting as prey for higher trophic levels (Zeidberg, 2013).

Pacific herring (herring) are vital components of the coastal food-web in the Northeast Pacific (Harvey et al., 2012), and have been supporting commercial fisheries for decades (Castañeda et al., 2020). Herring spawns occur along the nearshore in the spring, in the intertidal and shallow subtidal (Hay, 1985; Therriault et al., 2009). After spawning, adult herring move to summer offshore feeding grounds, followed by overwintering areas, after which the annual cycle is repeated (Hay, 1985; Therriault et al., 2009). Once herring hatch, they remain in sheltered nearshore habitats until they metamorphose into juveniles, after which they form schools and move offshore to deeper water until sexual maturity (Hay, 1985). However, relatively less is known regarding habitat use of juvenile herring, limiting efforts to manage herring populations across their life history. In the Northeast Pacific, declines of all major stocks of herring on the west coast of Canada have been observed with no evidence of recovery to date (Forrest et al., 2023; Schweigert et al., 2010). Declines appear to be associated with both local environmental factors (Ito et al., 2015) and anthropogenic pressures (Incardona et al., 2012; Shelton et al., 2014). These declines highlight the importance of effective management to conserve remaining herring populations.

Comparatively, little is known about the life history and population dynamics of opalescent squid (squid) (Walthers & Gillespie, 2002). However, they are an important food source for salmon

and other finfish (Roper et al., 1984). Moreover, the fishery for opalescent squid is California's largest, bringing in USD 73.8 million in revenue in 2010 (Zeidberg, 2013). Each cohort will spawn at one or two years of age (Spratt, 1979), with spawns occurring throughout the year depending on the region (Walthers & Gillespie, 2002). While throughout most of their life they are dispersed and found in deeper water, during spawning they aggregate in larger schools and move to the nearshore (Walthers & Gillespie, 2002). Squid are semelparous, spawning only once in their lifetime and have been found to spawn anywhere from 3-55 metres in depth, often on sandy substrate (Spratt, 1979; Walthers & Gillespie, 2002). The short lifespan of squid has important management implications, as poor recruitment across one spawning season could severely impact subsequent population structure. Squid populations could fluctuate due to the changing climate, specifically oceanographic conditions caused by the El Niño Southern Oscillation (Walthers & Gillespie, 2002).

An important area for studying the dynamics of these species is the Strait of Georgia, the inland marine waters between Vancouver Island and mainland British Columbia, Canada (Quinn & Losee, 2022). Many forage fish species use the nearshore in the Strait of Georgia across their life histories, primarily as nursery habitat (Osgood et al., 2016; Preikshot et al., 2013). Herring and squid have been found to occupy lower trophic levels in the Strait of Georgia (Lerner & Hunt, 2024), highlighting their importance as prey species to higher trophic levels. For example, as the Strait of Georgia provides resident and migratory habitat for native salmonid species (Hendriks, 2024; Quinn & Losee, 2022), understanding the dynamics of salmon prey species, like herring, in this area is vital. Further, some of the largest annual herring spawns on the coast of British Columbia occur in this area (Hay & McCarter, 2006). Herring that hatch in this area have been found to reside near their spawning grounds until they are at least a year old before migrating offshore (Therriault et al., 2009). This further shows the importance of the Strait of Georgia as a nursery, with juvenile herring relying on this habitat throughout their development. The Strait of Georgia can also provide spawning habitat for squid (Timmer, Pers. Comm., 2025), as it has a large area of shallow, sandy coastline (Krassovski et al., 2024), which is considered to be their preferred spawning grounds (Walthers & Gillespie, 2002). The Strait of Georgia is under stress from anthropogenic stressors such as coastal development and changing oceanic conditions due to climate change, such as increasing seawater temperature (Johannessen & Macdonald, 2009). The interaction between coastal development and climate change is likely to increase habitat

degradation in this area, potentially altering habitat use and community composition (Johannessen & Macdonald, 2009). These factors emphasize the need to understand the habitat use of forage fish in this area, particularly herring and squid, as it encompasses important threatened habitats for these species and their predators.

In this study, we use underwater timelapse imagery to investigate community composition and habitat use in the northern Strait of Georgia, across two regions. Sampling took place on the traditional territories of the K'ómoks First Nation across the summer of 2024. Timelapse imagery was coupled with environmental variables (temperature, current speed) to investigate habitat use of Pacific herring and opalescent squid. This work aimed to quantify: (1) how community composition varies across spatial and temporal scales within this area; and (2) how local environmental factors influence the nearshore habitat use of important forage species across these scales. As the two study regions were initially selected based on similar benthic substrate and environmental conditions, we hypothesized that spatially there would not be a large difference in community composition. However, we expected that community composition would vary temporally due to the different life histories of nearshore species and their varying responses to changing abiotic factors. We further hypothesized that stress from abiotic factors such as increased temperature and current speed would decrease the presence and abundance of forage species. This could occur due to increased energy expenditure of individuals in these conditions through increased metabolic rates (Almatar, 1984; Van Noord & Dorval, 2017) or negative impacts on swimming ability and foraging behaviour (McFarland & Levin, 2002; O'Dor, 1982; Utne-Palm & Stiansen, 2002). Increased stress in these conditions will likely result in individuals moving to areas with more favourable conditions, reducing nearshore habitat use by forage species in our study area. We also expect differences in the presence of forage species across hours, with increased presence at dusk and dawn to avoid predation but maximize foraging potential (Brierley, 2014). By examining the spatial and temporal variations in community composition and the influence of environmental factors on forage species, our study provides valuable insights for the management and future research of nearshore habitats in the northern Strait of Georgia.

Methods

Study sites

To investigate community composition and habitat use of forage fish in the northern Strait of Georgia, we surveyed six nearshore sites with timelapse cameras from May to August 2024 over three deployments. Deployment one: May 22nd, 2024, to June 11th, 2024; deployment two: June 19th, 2024, to July 9th, 2024; and deployment three: July 16th, 2024, to August 6th, 2024. Six sites at similar depths, placed about 150 meters apart were located across two regions, Cape Lazo (sites Lazo-1, 2 and 3) and Willemar Bluffs (sites Will-1, 2 and 3), off the coast of Comox (Figure 1). The sites are located north of Baynes Sound, a narrow channel bounded by Denman Island on the east and Vancouver Island on the west (Krassovski et al., 2024) (Figure 1). The northern tip of Denman Island is visible in the bottom right of Figure 1. Willemar Bluffs is closer to the shallower Baynes Sound (40-60 metres), whereas Cape Lazo is located near a large shelf, closer to the more open waters of the Strait of Georgia, with waters up to 200 metres in depth (Figure 1) (Guyondet et al., 2022). The substrate at all six sites is a mix of cobble and boulders, with benthic kelp present and sandy areas containing eelgrass beds closer to Willemar Bluffs (Timmer, Pers. Comm., 2025).

Data collection and camera system

Each camera system was composed of a GoPro (Hero11 Black Model) connected to an external battery (Blue Robotics). We installed GoPro Labs firmware on each camera and configured timelapse settings with GoPro Labs QR Code Creator to take one image every five minutes from 07:00-19:00 for 21 days, after which the data was offloaded. For deployment, we placed the camera and external batteries inside a Blue Robotics watertight housing and attached it to angled rebar rails set in concrete blocks using zip ties. We placed cameras on the substrate at each site, approximately 4-5 metres depth from chart datum. Spare setups were available, so divers would take a full, already running setup down upon each deployment and bring up the old one on the same dive. The cameras faced upwards at an angle of 37.5° with a field of view of 118°-69°-133° (horizontal-vertical-diagonal) that captured the entire water column, from the benthos to the surface of the water. A breakdown of when data was collected for each site is shown in Figure 2. Gaps in data collection other than the periods between deployments are due to either GoPro software malfunction or algae covering the camera. Alongside images, we collected site-level measurements for ocean temperatures (°C) one metre below the surface using BlueEnv

temperature loggers (recorded every half hour). Temperature data was unavailable for Lazo-3 as the mooring with the temperature logger was lost. We also collected current speed approximately 0.5 metres above the benthos in one-second intervals using Marotte HS drag-tilt current meters attached to cinder blocks using zip ties. To determine changes in sea surface temperatures in the Comox region over time, we used data sourced from the Chrome Point lighthouse (Fisheries and Oceans Canada, 2025).

Data processing

We extracted metadata for each site (file name, date, and time of the image) for all GoPro images using 'R' software and organized it in Microsoft Excel. For each image, we recorded all individuals present to the lowest taxa possible and the number of individuals of each taxon. Additionally, for each observation, we noted a measure of certainty on a scale of 1-3 (Table S1) and only observations with a certainty score of two or three were used in the analysis.

When observed in images, herring were commonly schooling in large numbers, most frequently in the hundreds but sometimes thousands of individuals, making accurate counts difficult. We counted a subset of images with herring (one image for every 20 images of herring per week, per site, n = 38), and the mean number of herring individuals was 671 (range 2 - 3,419) (Table S2). As such, for all analyses, we assumed that when herring were detected, a large school was present. For images with all other taxa, counts were completed.

Species data extracted from the timelapse imagery was coupled with environmental data (temperature and current speed). We used unique temperature values for each site in the analysis. For the analysis looking at the impact of abiotic factors on forage species, Lazo-3 was dropped from the analysis as temperature data was not available. As temperature was measured every half-hour and timelapse images were taken every five minutes, each timelapse image was assigned a temperature value corresponding to the nearest preceding half-hour temperature measurement. We processed current data using the MarotteHSConfig software and smoothed current speeds to five-minute intervals, which we matched with the five-minute intervals of timelapse images for analysis. We used unique current values from each site in analysis.

Statistical analysis

All statistical analysis was completed in R v4.3.2 (R Core Team, 2025). To investigate significant differences in environmental variables between regions we used a Mann-U Whitney test. To

evaluate the influence of region and deployment period on community composition, we created a Bray-Curtis dissimilarity matrix using the package 'vegan' v2.6.8 (Okasanen et al., 2025), which described the daily presence and absence of each taxon across all six sites. Metadata included the sampling region and the deployment period. We tested for significant differences in community composition between sampling region and deployment period using permutational multivariate analysis of variance (PERMANOVA) tests with 999 permutations and Bray-Curtis distances using the 'adonis2' function (Okasanen et al., 2025). Bray-Curtis distances were used as this method reduces the influence of highly dominant taxa (Clarke & Warwick, 1997).

We used generalized linear modelling (GLMs) to investigate the influence of (1) temperature (°C), (2) current speed (m/s), (3) hour of the day, and (4) Julian date on the presence of herring and squid. The 'glmmTMB' v1.1.10 package (Brooks et al., 2017) was used for all modelling. Given that abundance data was not recorded for herring, we used a binomial logistic regression to model their presence. For the squid model, we used a zero-inflated negative binomial distribution on the hourly maximum number of individuals (hourly MaxN) in one frame across the study period, split between regions. This approach accounts for both the presence and absence of squid as well as squid abundance, given they are present (Wenger & Freeman, 2008).

We included temperature, current speed, hour, and Julian date as fixed effects in both models. We also included interactions between temperature and current speed, temperature and Julian date, and Julian date and region. In the squid model, we included temperature, current speed, hour, and Julian date in the zero-inflated portion. We modeled temperature, current speed, and Julian date as continuous variables and region as a categorical variable. Hour was included as a quadratic (second order) polynomial to account for the fact that forage fish observations likely peak at a certain time of day. For the herring model, we evaluated residuals, overdispersion, collinearity, and the linearity of log odds, and found all to be reasonable. For the squid model, we evaluated residuals, overdispersion, collinearity, and zero-inflation, and found all to be reasonable. Collinearity for each fixed effect was assessed with variance inflation factors (VIF) which are shown in Table S3. We selected the best-fit model based on the lowest Akaike information criterion (AIC) score while meeting all assumptions.

Results

Environmental data

Data from the Chrome Point lighthouse shows that mean summer sea surface temperatures in the Comox region have been rising at a rate of 0.31 °C per decade (Figure 3). Since 1990, average summer temperatures have been at or above 17 °C 54% of the time, but historically (1960-1990), only 10% of years were this warm (Figure 3). The number of summer days at or above 17 °C has increased by an average of 4.3 days per decade (Figure 3). Between study regions, temperature measured one metre below the surface (°C) and current speed (m/s) both show significant differences (Cape Lazo and Willemar Bluffs) ($p < 0.001$). The mean (all means shown with ± standard deviation) temperatures across each region were 14.92 ± 2.66 °C (range 9.76 – 19.87) and 14.72 ± 2.87 °C (range 9.97 – 20.56) for Cape Lazo and Willemar Bluffs, respectively. Mean current speeds across each region were 0.11 ± 0.073 m/s (range 0.0005 – 0.78) and 0.076 ± 0.049 m/s (range 0.0003 – 0.70) for Cape Lazo and Willemar Bluffs, respectively.

Community composition

In total, we observed 16 different taxa with the timelapse cameras (Table 1). This included eight groups of 'forage fish', six groups of 'demersal fish' and one group of 'pelagic fish' (Table 1). Timelapse cameras also captured one species of sea lion (Table 1). While herring were captured in the most images overall (1.5%), perch species were observed on the most days (78%) (Table 1). Following perch, herring (72%) and squid (48%) were observed on the most days (Table 1). Pacific sand-lance were the only species with a MaxN > 50 over 20% of the time, while perch, squid, and juvenile cod were found in schools of greater than ten more than 20% of the time (Table 2). More than two individuals of salmon species and juvenile rockfish were observed over 15% of the time, while all other taxa were either solitary or in groups of two or less (Table 2).

At Cape Lazo, the three most observed taxa at the daily level were perch (77%), herring (74%), and salmon (40%) (Table 1). In contrast, at Willemar Bluffs, the most observed taxa at the daily level were perch (73%), squid (61%), and herring (22%) (Table 1). Cape Lazo had the highest observations, with six taxa observed on 20% or more of the days sampled, whereas Willemar Bluffs only had four taxa observed on 20% or more of the days sampled (Table 1). Community composition varied significantly between regions (PERMANOVA $p = 0.001$, Figure 4) and the deployment period (PERMANOVA $p=0.001$, Figure 5).

We chose to focus on herring and squid for statistical modelling as they are key prey species for higher trophic levels, both being considered important forage species (Harvey et al., 2012; Lerner & Hunt, 2024; Zeidberg, 2013). Specifically, herring are a primary food source for salmon in the Strait of Georgia, and different squid species also constitute an important part of salmon diets along the coast of British Columbia (Boldt et al., 2024). Both species are also the basis of established fisheries on the coast of British Columbia (Castañeda et al., 2020; Walthers & Gillespie, 2002). Further, both herring and squid had a high number of observations whereas other forage species such as Pacific sand-lance were omitted from analysis due to low observations.

Forage fish presence and abundance

Herring were the most observed species in the timelapse images, with the most herring observed at Cape Lazo ($p < 0.001$) (Figure 6A). Herring were observed on 72% of the days surveyed and in 1.5% of the images captured (Table 1). At the daily level, they were roughly three times more common at Cape Lazo than at Willemar Bluffs and were observed nearly 36 times more frequently there (Table 1). Most herring seen in cameras appeared to be juveniles due to their relative size.

We found that the probability of herring presence decreased across the study period from 15 to 0% ($p < 0.001$, estimate = -0.999) (Figure 7, 8A). We also found that the probability of herring presence decreased with increasing temperature (°C) ($p < 0.001$, estimate = -0.848) (Figure 7). The modelled probability of herring presence with increasing temperatures is shown in Figure 8B, again decreasing from around 15 to 0%, where 95% of herring observations were below 17 °C. We found that the interaction between temperature and Julian date was an important predictor of herring presence ($p < 0.001$), with increased temperatures later in the study period decreasing the probability of herring presence (estimate = -0.588) (Figure 7, 8C). Time of day, modelled as a quadratic, appeared to influence herring presence ($p < 0.01$, estimate = 0.172), with the probability of presence in the mornings and evenings nearly double compared to midday (Figure 9A). We also modelled time of day as a linear effect, but it was not found to be a significant predictor of herring presence ($p > 0.05$), indicating the relationship between time of day and herring presence is nonlinear (Figure 7). Current speed (m/s) had a positive effect on herring presence ($p < 0.01$, estimate = 0.194) (Figure 7). As current speed increased from 0 m/s

to around 0.4 m/s, the probability of herring presence doubled (Figure 9B). We found that the interaction between temperature and current speed was also significant ($p < 0.01$), with this interaction positively influencing herring presence (estimate = 0.190) (Figure 7), indicating that a combination of high temperatures and high current speeds increased the probability of herring presence. We did not find the interaction between Julian date and region to be a significant predictor of herring presence ($p > 0.05$) (Figure 7), suggesting that temporal trends in herring presence are consistent across sites rather than varying between them. Model results for herring are detailed in Table S4.

Squid were the third most observed species both daily and in the number of timelapse images (Table 1). They were found to be in groups greater than two over 50% of the time and in groups greater than ten 24% of the time (Table 2). Squid were roughly twice as common at Willemar Bluffs compared to Cape Lazo across days and images ($p < 0.001$) (Table 1, Figure 6B).

We found Julian date to be an important predictor of squid abundance (hourly MaxN) ($p < 0.001$) (Figure 10A). Modelled probability of hourly MaxN suggests that the predicted hourly MaxN peaks at around Julian date 180 (end of June 2024), with a lower predicted hourly MaxN at the beginning and end of the study period (Figure 11A). We found that the interaction between increasing temperatures and current speed decreased squid abundance ($p < 0.001$, estimate = -1.189) (Figure 10A). This suggests that as temperatures and current speeds increase, the abundance of squid decreases. We also found that current speed, temperature, time of day, and the interactions between Julian date and region and Julian date and temperature were not important predictors of squid abundance ($p > 0.05$) (Figure 10A). The zero-inflation portion of the model shows that the probability of zero hourly MaxN decreased throughout the study period ($p < 0.01$, estimate = -6.140) (Figure 10B). The modelled probability of hourly MaxN shows that squid were not observed at the beginning of the study period, with the probability of seeing squid steadily increasing from the beginning of June through to the end of the study period (Figure 11B). The probability of zero hourly MaxN increased with higher current speeds, with the probability of squid presence decreasing to 0% above 0.2 m/s ($p < 0.05$, estimate = 3.405) (Figure 10B,12). We found that the probability of zero hourly MaxN was not significantly influenced by the time of day or temperature ($p > 0.05$) (Figure 10B). Model results for squid are detailed in Table S5.

Discussion

Our study found that community composition varied significantly across spatial and temporal scales, with important forage fish species significantly influenced by local environmental factors. Overall, 15 groups of fish were observed by timelapse cameras with herring and squid being the most prevalent forage species. Herring and squid presence were both greatly influenced by region, with herring observed across more images and days at Cape Lazo and squid observed across more images and days at Willemar Bluffs. Further, many other fish taxa such as species of groundfish, rockfish, and salmon were observed more often at Cape Lazo. Both herring and squid presence were influenced by time across the study period, with herring presence decreasing and squid presence increasing across the summer. As hypothesized, changing abiotic factors also contributed to predicting the presence and abundance of forage species. Increasing temperatures decreased the probability of herring presence, while increasing current speeds increased the probability of herring presence and decreased the probability of squid presence. Further, we found that the probability of herring presence increased in the mornings and evenings, as expected.

These differences in community composition between the two study regions and across the study period reflect species-specific habitat preferences and the importance of variable environmental factors in determining nearshore habitat use by forage fish. This highlights the need for site- and species-specific monitoring to better understand and protect stocks of key species.

Spatial and temporal community differences

Contrary to what we expected, we found significant differences in community composition between study regions. While the regions surveyed in our study are relatively close together (less than 5 km apart) and were initially selected based on similar benthic and environmental characteristics to one another, we still observed differences in species assemblages between regions. This suggests that habitat characteristics differ between Cape Lazo and Willemar Bluffs, influencing community structure. Cape Lazo's proximity to the cooler deep waters off the Strait of Georgia may allow for periodic upwelling into shallower areas, providing an influx of nutrients (Guyondet et al., 2022). Further, turbulent mixing by the Discovery Passage tidal jet also has the potential to increase nutrient concentrations at the Cape (Haigh & Taylor, 1991). An increase in nutrients could stimulate primary productivity and increase food availability (Haigh

& Taylor, 1991; Olson et al., 2020), subsequently increasing herring presence (Perry & Schweigert, 2008). Increased herring presence can, in turn, increase the presence of predator species such as groundfish, rockfish, and salmon (Godefroid et al., 2019; Murie, 1995). While a higher mean and deviation in current speeds at Cape Lazo compared to Willemar Bluffs could indicate tidal-driven upwelling or increased mixing at the Cape (Guyondet et al., 2022), measurements of other metrics such as nutrient or oxygen concentrations would be necessary to confirm the strength of upwelling or mixing between these regions. However, the observed differences in mean current speed and temperature are small, less than 0.05 m/s and less than 0.5 ºC, with similar variability across regions. As such, the variation in community composition between regions is notable relative to the small temperature and current differences. This suggests that while both regions are relatively similar in oceanographic conditions, even fine-scale differences can drive distinct community composition. Additionally, fine-scale changes in benthic substrate or proximity to other important habitats may also influence community composition. For example, the higher frequency of squid observations at Willemar Bluffs could reflect its proximity to the shallow, sandy Comox Sand Bar, a potential squid spawning area (Walthers & Gillespie, 2002).

As expected, community composition shifted over the study period with significant differences in the presence and absence of different taxa between the three deployments. This is likely driven by the unique life histories of each species, including seasonal migrations, spawning events, and changing oceanographic conditions (Tamario et al., 2019). While these temporal differences are evident, determining the underlying drivers is challenging due to the limited observations of some species and an inability to determine the mechanisms driving shifts in habitat use with the available data. However, for squid and herring specifically, we explored these temporal patterns in greater detail through targeted statistical modelling of these species.

Notably, high frequency of daily observations (e.g., 72% for herring and 48% for squid) do not necessarily correlate with continuous site use (e.g., 1.5% and 0.3% of total images for herring and squid, respectively), indicating that these species are highly mobile but are consistently returning to the study area daily. Frequent daily use suggests that while these habitats are often transient, they remain critical for spawning, feeding or migration patterns (Nagelkerken et al.,

2015). The data does not allow for any conclusions about where or how far individuals are moving when they are not captured in the images, highlighting an area for future research.

Overall, our results suggest that fish taxa are highly selective of nearshore habitat, with small differences in bathymetry or oceanography influencing the presence of individual species and overall community composition. As such, our findings emphasize the importance of fine-scale monitoring to capture localized spatial and temporal patterns of key species in nearshore communities. This ensures that management is suited to the unique ecological conditions of each area. Additionally, understanding patterns of species presence during key life stages such as spawning or migration is important in developing species-specific management strategies.

Factors influencing Pacific herring

Our statistical modelling results suggest that herring habitat use is influenced by a combination of temperature (°C), date, current speed (m/s), and time of day (hr).

As hypothesized, increasing temperatures were negatively correlated with herring presence. A possible explanation for this pattern could be that elevated temperatures increase energetic demand of individuals, corresponding to an increased metabolic rate (Almatar, 1984). An increased metabolic rate can result in several adverse effects on herring individuals. First, increased metabolism may alter swimming capacity, with fish no longer able to maintain sustained swimming without muscular fatigue (Beamish, 1978). Further, to counteract increased metabolism, individuals will need to increase their food consumption which increases the demand for prey (Moyano et al., 2016). As such, as temperatures in the northern Strait of Georgia warm from around 10 to 20 °C over the season, it is possible that herring move to cooler waters either offshore or below the thermocline.

The relationship between temperature and herring is complex as temperature and date are correlated, with temperatures consistently increasing across the study period. The modelled interaction between temperature and date shows that the probability of herring presence increases during cooler periods later in the summer, suggesting herring are moving back into the nearshore when temperatures drop. The interaction also demonstrates that high temperatures earlier in the summer coincide with increased herring presence, with rising temperatures later in the summer decreasing the probability of herring presence. This could be explained as early in the season

warmer temperatures were less frequent and consistent, so overall conditions were still favourable for herring. However, as temperatures rise to a consistent warmer level later in the summer, herring may be ultimately constrained by thermal limits resulting in their movement to cooler waters. Increased herring presence during cooler periods later in the summer likely reflects enhanced productivity from cool water intrusions, providing better forging opportunities (Guyondet et al., 2022). Another consideration is the potential role of ontogenetic shifts where herring move to feeding grounds outside the Strait of Georgia later in the summer (Beacham et al., 2008; Frick et al., 2022). However, Therriault et al. (2009) suggests that juvenile herring in the Strait of Georgia are not partaking in these offshore migrations until they are at least a year old. As such, if the herring we observed with timelapse cameras were indeed juveniles, it is more likely that the herring become thermally constrained and move away from the nearshore to cooler waters within the Strait. The occurrence of migrations could be further investigated with genetic analysis to determine if the herring observed in our study and the individuals observed outside the Strait later in the summer are part of the same stock or age class. It is also possible that increasing temperatures could shift the timing of this migration, prompting earlier movement out of the Strait due to thermal cues rather than a direct metabolic constraint. Ultimately, the mechanisms driving these patterns remain unclear and future research should focus on investigating the thermal limits of herring and tracking individual movement patterns to disentangle the interaction between temperature driven habitat shifts and ontogenetic migrations.

Contrary to what was expected, increasing current speeds had a positive effect on herring presence. This could be due to the influence of current speed on food availability, where stronger currents bring nutrients to the surface, stimulating primary productivity and increasing food availability for higher trophic levels (Guyondet et al., 2022). During calm, summer conditions, phytoplankton activity often depletes surface nutrients, meaning long periods of low current can decrease primary production (Guyondet et al., 2022). To replenish nutrients and fuel primary productivity, bottom, nutrient-rich water intrusions are needed, requiring mechanisms like tidal currents that increase current speeds and bring nutrient-rich water into the shallow nearshore (Guyondet et al., 2022). However, it is important to consider that there may be a lag between changes in current speed and subsequent changes in food availability which suggests there may be other mechanisms influencing increased herring presence with higher current speeds. High current speeds may also benefit herring by reducing the energetic costs of swimming if fish are

swimming along a current, allowing them to travel at a greater speed (Brodersen et al., 2008; Caldwell & Gergel, 2013). Brodersen et al. (2008) found that while migrating fish were more likely to swim at lower current speeds, fish moving during high current velocities could be exhibiting exploratory behaviour. As the herring observed in our study are likely not actively migrating, high current speeds in this area are potentially beneficial for exploratory behaviours such as searching for food. As well, increased currents, up to a point, can increase foraging efficiency by allowing the fish to fall back in the water column to intercept prey instead of expending energy by darting forward (McFarland & Levin, 2002). Additionally, the interaction between current speed and temperature suggests that strong current speeds may mitigate thermal stress, allowing herring to persist in warmer waters. In these conditions, the energetic benefits of greater food availability or decreased swimming effort due to increased currents might outweigh the metabolic costs of higher water temperatures, allowing herring to occupy nearshore habitats despite thermal stress.

Finally, as expected, the quadratic relationship of herring presence with hour likely points to diel-vertical migration patterns, daily small-scale movement where herring are more active in shallow waters during dawn and dusk, likely to optimize foraging while minimizing predation (Brierley, 2014). Diel vertical migration patterns have been observed in herring many times (Haslob et al., 2009; Huse, 2000), confirming that this behaviour is common and expected.

Factors influencing opalescent squid

Results of our statistical modelling suggest that squid presence and abundance is significantly influenced by a combination of date, current speed (m/s), and temperature (°C).

We found that the probability of squid presence increased throughout the study period and hourly MaxN peaked in the middle of the study. These trends could be due to the spawning behaviours of squid. Squid spawning timing is not consistent across their range (Walthers & Gillespie, 2002), with spawning periods seemingly triggered by increasing productivity in the spawning region (Ziedberg, 2013). Spawns in British Columbia have been reported from mid to late summer (Walthers & Gillespie, 2002), and as such, the increasing probability of squid presence later in the summer could be due to squid moving into the area to spawn. The mid-summer peak in hourly MaxN likely also coincides with squid aggregating in schools to spawn (Walthers & Gillespie, 2002). However, the subsequent drop in MaxN is more difficult to explain, as squid

are still predicted to be present in the area but in much lower numbers. It is possible that the largest spawning aggregation occurs mid-summer, around the time of the hourly MaxN peak, and once the spawn is over and these squid die there are still individuals present that have not yet spawned, or new individuals moving into the area to spawn in lower numbers. Nevertheless, data from our study cannot confidently explain the mechanisms driving these patterns of presence and abundance. The dynamics of squid in this area requires further multi-season monitoring as well as sampling to determine the reproductive stage of individuals to confidently explain the seasonal patterns of presence and abundance. Moreover, future monitoring should include determining what characteristics of the Willemar Bluffs habitat are important for squid and if they are found to spawn there.

As hypothesized, we found that increased current speed negatively influenced squid presence. This is likely due to the dual swimming system of squid, which relies on a combination of both fin flapping and pulse jetting (Vidal et al., 2018). At high current speeds, fins become ineffective, reducing swimming efficiency and increasing metabolic rate, resulting in a maximum sustainable swimming speed of 0.4 m/s (O'Dor, 1982, 1988). As a result, squid may be unable to maintain sustained swimming at higher current speeds and are possibly moving to areas with lower currents that are more energetically favourable. In contrast, herring morphology results in an undulating swimming motion which allows them to maintain steady swimming at higher current speeds (O'Dor, 1982, 1988). Additionally, we found that the combined effect of increased current speed and temperature decreased the hourly MaxN of squid. While temperature alone was not a significant predictor of squid abundance in this study, other research has shown that higher temperatures negatively influenced squid abundance (Van Noord & Dorval, 2017). Therefore, the compounded effect of increased current and temperature may increase stress on squid, causing them to move away from the study area.

Ecological implications of climate change on nearshore communities

Summer sea surface temperatures in the northern Strait of Georgia have risen by 0.31 °C per decade, with days above 17 °C increasing by 4.3 days per decade. This observed warming, in conjunction with the fact that 95% of herring observations were below 17 °C, suggests that as warming continues, nearshore habitats may become unsuitable for herring or shift the timing of offshore migrations. Shifts in herring habitat use due to thermal tolerance or migration timing

have the potential to influence associated predator species as well, with predator species moving away from the nearshore along with their prey. Shifts in herring habitat occupancy with increasing temperatures could also result in mismatches in habitat use. For example, while herring and salmon were often seen in the same image, salmon were most abundant later in the summer, when herring observations were at their lowest. As such, if herring are moving away from the area as temperatures increase, that might indicate that there is starting to be a mismatch in herring and salmon habitat use, where herring are not available prey for migrating salmon later in the summer. Additionally, while our study did not find a negative effect of increased temperature on squid presence and abundance, previous work has determined associations with decreased squid abundance and rising temperatures (Van Noord & Dorval, 2017). As such, as temperatures in this area continue to rise it is possible that this will begin to influence squid, decreasing their presence in the nearshore. Further, as maximum temperatures are slightly higher at Willemar Bluffs than at Cape Lazo, ocean warming could result in changing habitat use at a finer scale. For example, species currently spending time at Willemar Bluffs may shift to Cape Lazo, following their thermal preference. Future work should aim to continue monitoring in this area with a focus on the effect of rising temperatures on squid and the shifts in species habitat use between predators and prey to further understand how increasing temperatures influence these species.

Future directions

To expand on this work, future research should include conducting long-term, multi-season monitoring in this area to identify any additional species that make use of these habitats, as well as how the community changes across a full calendar year. Additionally, this study should be repeated annually to gain an understanding of any interannual variability and if patterns that were observed in 2024 are consistent across multiple years. Moreover, to further understand how changing abiotic factors are impacting forage species, conducting a similar study across sites with more distinct characteristics (e.g., different temperature or current regimes) could help inform how these species are responding to more variable conditions. It would also be helpful to continue current monitoring along with measurements of additional abiotic factors that could be influencing community composition and the presence of forage species. For example, measurements of oxygen alongside current speed and temperature could be valuable in disentangling the drivers that are influencing the presence of forage species. Oxygen may be an

especially important variable to consider as previous studies have found differing oxygen saturation tolerances in marine fish, with Atlantic herring specifically avoiding waters with low oxygen concentrations (Neuenfeldt, 2002). Lastly, timelapse images could be further investigated to determine associations of forage fish with their predators across space and time. This could provide more information regarding predator-prey dynamics and the structuring of the ecosystem in this area.

Conclusion

Our study investigated differences in community composition across spatial and temporal scales and aimed to understand how different environmental factors influence the presence and abundance of two key forage species. Results of our study highlight the importance of fine-scale spatial and temporal monitoring to understand spatiotemporal variation in community composition. The observed differences between Cape Lazo and Willemar Bluffs demonstrate that relatively small-scale habitat differences can significantly affect species assemblages, emphasizing the need for site-specific management strategies. Our findings also provide evidence that environmental factors, such as temperature and current speed, play an important role in predicting the presence and abundance of herring and squid. These findings have implications for predator-prey interactions as herring and squid are vital prey for higher trophic levels, with their distributions likely influencing the presence of their predators. Moreover, as climate change continues to alter ocean conditions, understanding how these species respond to environmental variability is essential in predicting future shifts in species distributions. Overall, these insights can help inform conservation strategies, such as habitat protection and fisheries management, while accounting for the effect of environmental conditions and species-specific habitat preferences. Additionally, these findings provide important information on avenues for future research to further develop our understanding of these species.

Figures and Tables

Table 1. Summary of the frequency of occurrence of the taxa observed with timelapse cameras. Frequency of occurrence is summarized per day and total frames captured by cameras (FO day, FO fr). Each metric is further split by region, Cape Lazo (FO day^L, FO fr^L) and Willemar Bluffs (FO day^W, FO fr^W). Taxa are ordered from highest to lowest FO fr. Taxa grouping refers to: FF = Forage fish, D = Demersal fish, P = Pelagic fish, and M = Mammal.

Taxa	Common name	Taxa grouping	FO day	FO day^L	FO day^W	FO fr	FO fr^L	FO fr^W
Clupea pallasii	Pacific herring	FF	0.72	0.74	0.22	$1.5x10^{-2}$	$3.0x10^{-2}$	$8.4x10^{-4}$
Perca sp.	Perch	FF	0.78	0.77	0.73	$1.2x10^{-2}$	$8.2x10^{-3}$	$1.6x10^{-2}$
Loligo opalescens	Opalescent squid	FF	0.48	0.26	0.61	$3.1x10^{-3}$	$2.0x10^{-3}$	$4.1x10^{-3}$
Sebastes sp.	Rockfish	D	0.42	0.39	0.20	$2.3x10^{-3}$	$3.1x10^{-3}$	$1.5x10^{-3}$
Oncorhynchus sp.	Salmon	P	0.40	0.40	0.02	$1.7x10^{-3}$	$3.3x10^{-3}$	$1.3x10^{-4}$
Juvenile *Gadus* sp.	Juvenile cod	FF	0.15	0.16	0.00	$1.6x10^{-3}$	$3.3x10^{-3}$	0.00
Juvenile *Sebastes* sp.	Juvenile rockfish	FF	0.20	0.19	0.02	$9.3x10^{-4}$	$1.8x10^{-3}$	$6.5x10^{-5}$
Hexagrammidae	Greenlings	D	0.26	0.24	0.07	$8.6x10^{-4}$	$1.6x10^{-3}$	$1.9x10^{-4}$
Ammodytes hexapterus	Pacific sand-lance	FF	0.18	0.10	0.17	$5.6x10^{-4}$	$6.1x10^{-4}$	$5.2x10^{-4}$
Aulorhynchus falvidus	Tube-snout	FF	0.08	0.06	0.02	$2.3x10^{-4}$	$4.1x10^{-4}$	$6.5x10^{-5}$
Platichthys stellatus	Starry flounder	D	0.03	0.03	0.00	$1.0x10^{-4}$	$2.0x10^{-4}$	0.00
Squalidae sp.	Dogfish	D	0.05	0.00	0.07	$1.0x10^{-4}$	0.00	$1.9x10^{-4}$
Cottidae	Sculpin	FF	0.02	0.00	0.02	$3.3x10^{-5}$	0.00	$6.5x10^{-5}$
Hydrolagus sp.	Ratfish	D	0.02	0.02	0.00	$3.3x10^{-5}$	$6.8x10^{-5}$	0.00
Pleuronectiformes	Flatfish	D	0.02	0.02	0.00	$3.3x10^{-5}$	$6.8x10^{-5}$	0.00
Zalophus californianus	California sea lion	M	0.02	0.02	0.00	$3.3x10^{-5}$	$6.8x10^{-5}$	0.00

Table 2. Summary of the abundance (MaxN) of the taxa observed on timelapse cameras. MaxN is defined as the most individuals observed in a single image over the study period. MaxN is further split by region, Cape Lazo ($MaxN^L$) and Willemar Bluffs ($MaxN^W$). The proportion of observations where each taxa had a MaxN of greater than 2, 10, and 50 is also included. Taxa are ordered from highest to lowest MaxN. Pacific herring are not included in this table, as counts were not completed for all images with herring.

Taxa	Common Name	Max N	Max N^L	Max N^W	Prop. MaxN >2	Prop. MaxN >10	Prop. MaxN>50
Perca sp.	Perch	1100	1100	184	0.58	0.39	0.19
Ammodytes hexapterus	Pacific sand-lance	536	34	536	0.82	0.59	0.35
Loligo opalescens	Opalescent squid	194	194	173	0.57	0.24	0.076
Juvenile *Gadus* sp.	Juvenile cod	124	124	0	0.79	0.43	0.16
Juvenile *Sebastes* sp.	Juvenile rockfish	34	34	1	0.25	0.14	0
Oncorhynchus sp.	Salmon	11	11	1	0.18	0.019	0
Aulorhynchus falvidus	Tube-snout	2	2	2	0	0	0
Sebastes sp.	Rockfish	2	2	1	0	0	0
Cottidae	Sculpin	1	0	1	0	0	0
Hexagrammidae	Greenlings	1	1	1	0	0	0
Hydrolagus sp.	Ratfish	1	1	0	0	0	0
Platichthys stellatus	Starry flounder	1	1	0	0	0	0
Pleuronectiformes	Flatfish	1	1	0	0	0	0
Squalidae sp.	Dogfish	1	0	1	0	0	0
Zalophus californianus	California sea lion	1	1	0	0	0	0

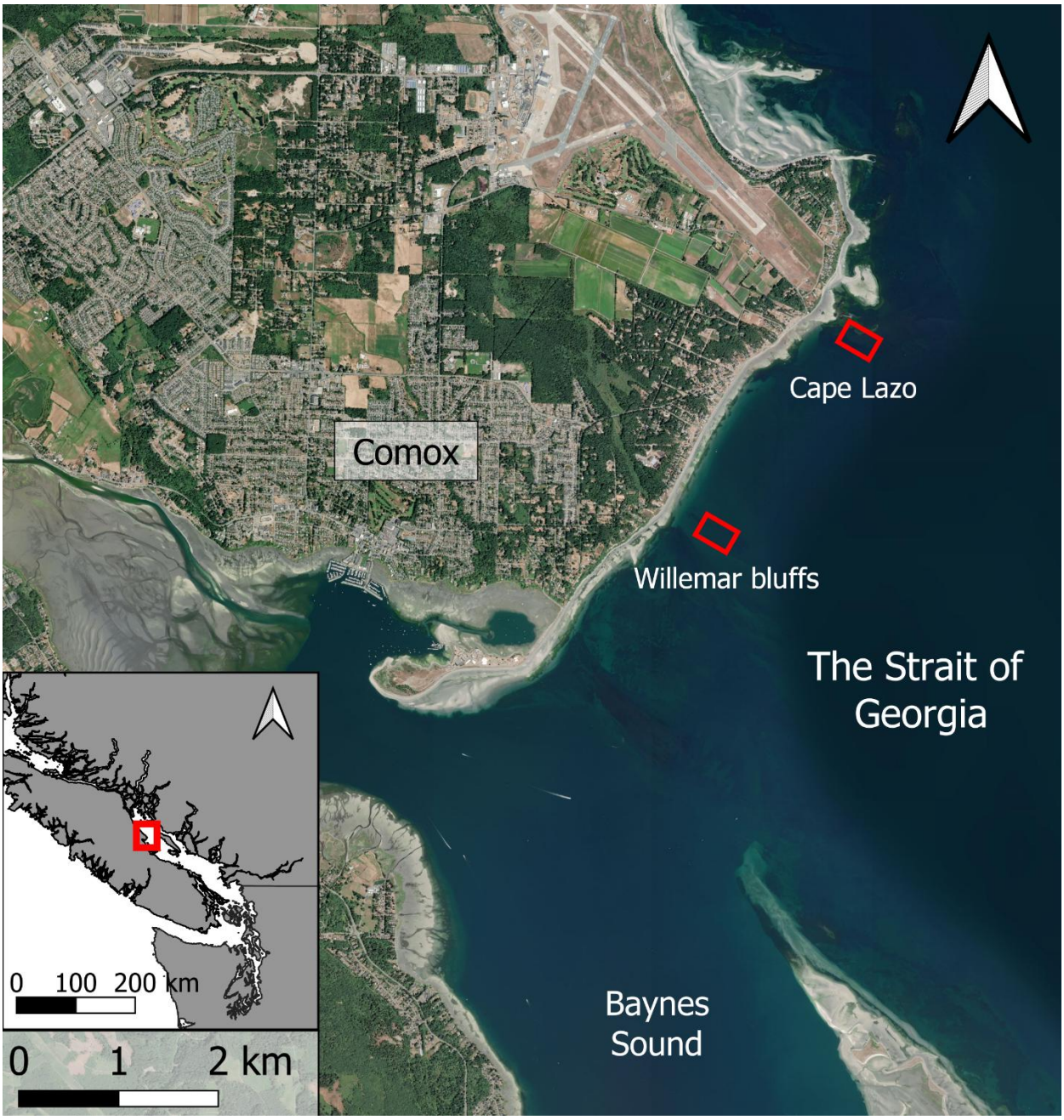

Figure 1. Map of the two study regions, Cape Lazo and Willemar Bluffs (red boxes), in the northern Strait of Georgia off the east coast of Vancouver Island. Three sites with similar depths were placed about 150 m apart within each region. The inset shows the position of the study area (red box) relative to the west coast of British Columbia and Vancouver Island.

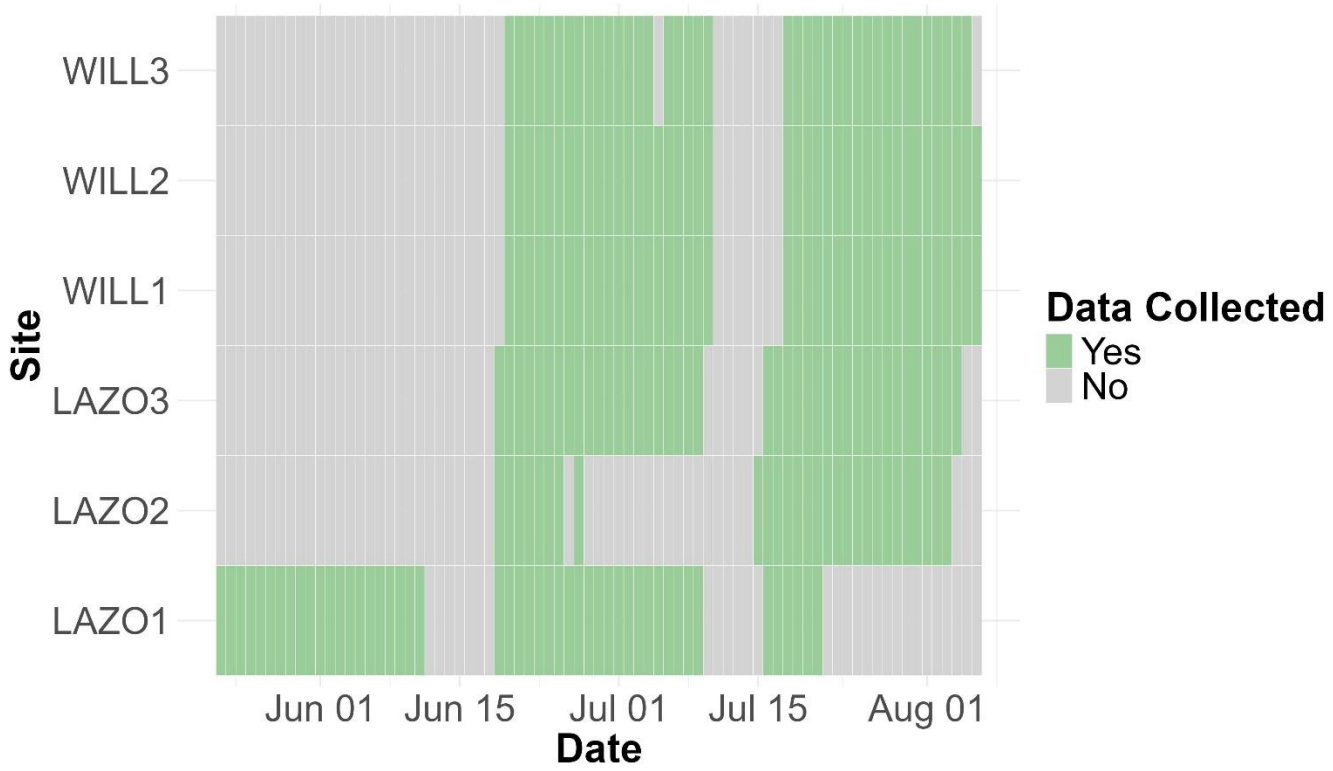

Figure 2. Distribution of days when remote timelapse cameras were running at the study sites during the summer of 2024. Green indicates that data was collected, and grey shows days when timelapse cameras were not running or when algae covered the camera. Time between deployment periods is indicated by days where data is not being collected at any of the six sites.

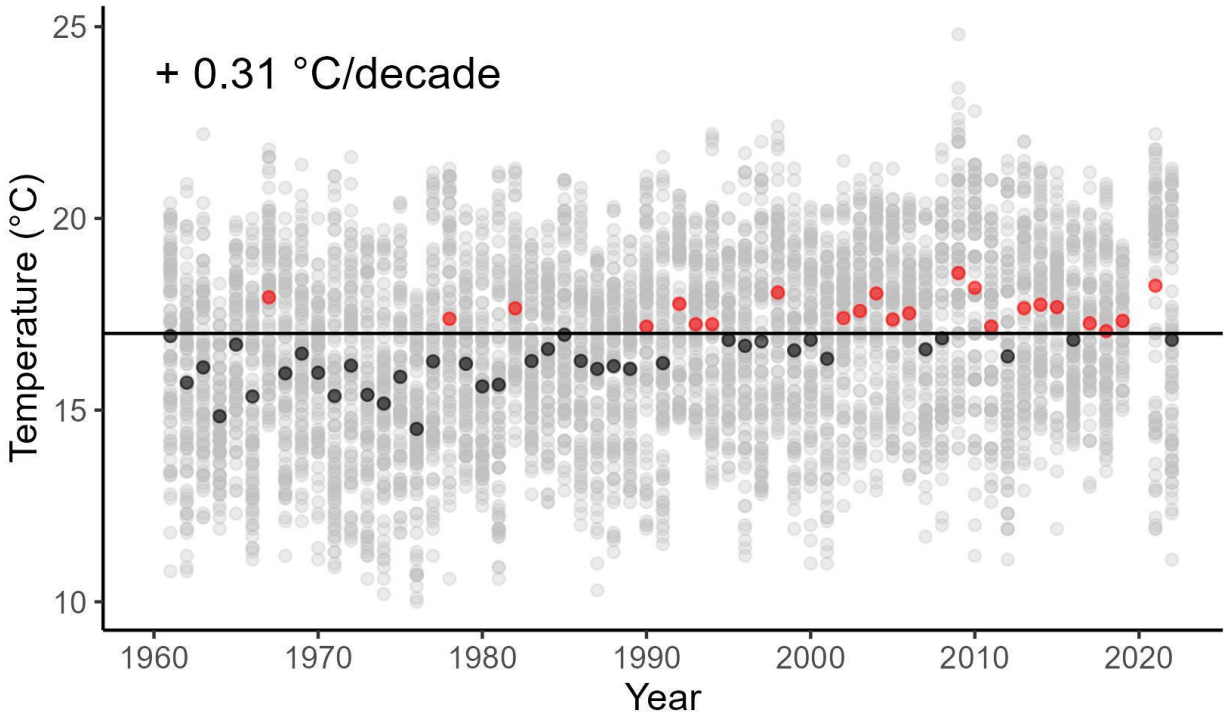

Figure 3. Mean summer sea surface temperatures (June, July, August) in the northern Strait of Georgia sourced from the Chrome Point lighthouse. The solid black line denotes 17 °C where black points are the years when the mean summer temperature was below 17 °C and red points are years when the mean summer temperature was above 17 °C.

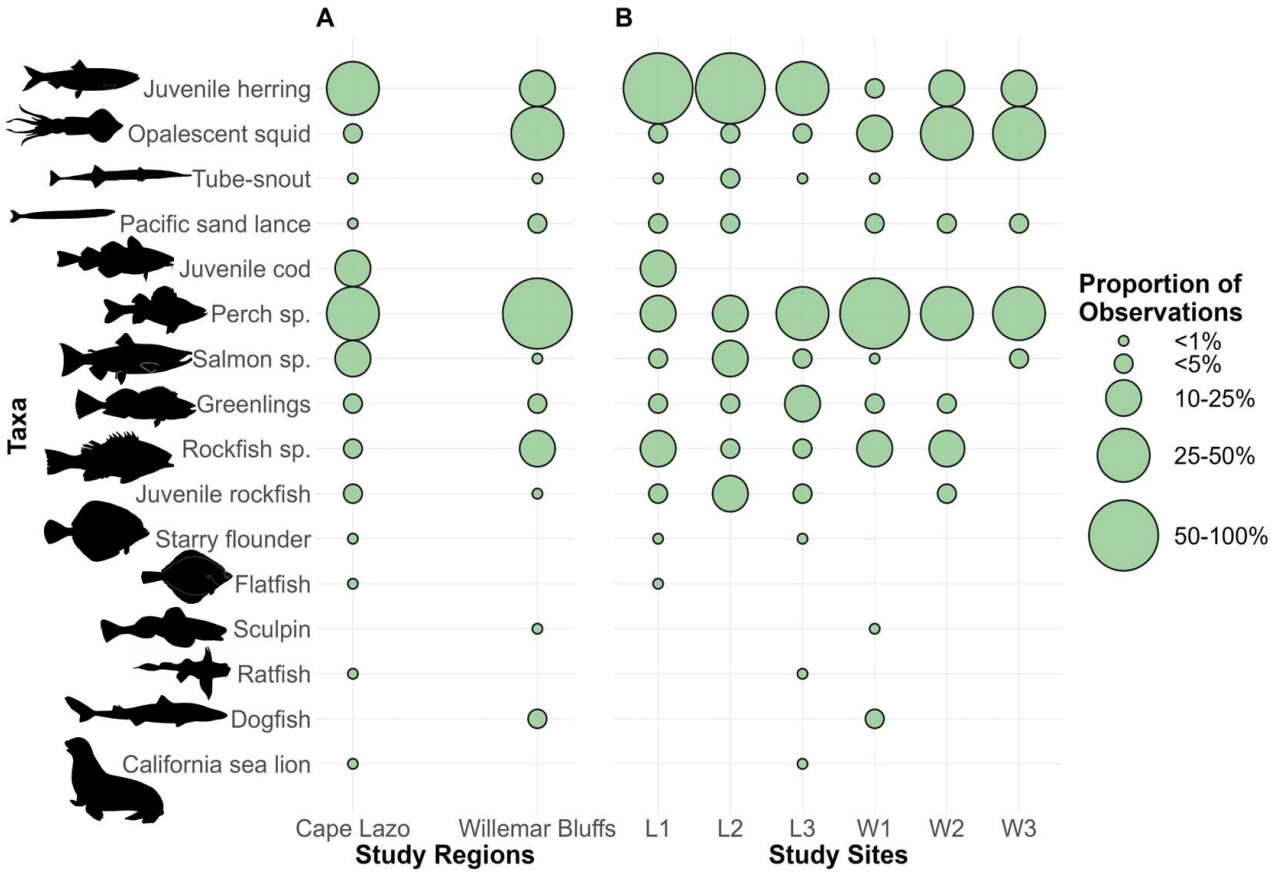

Figure 4. The binned proportion of observations for each taxa observed at: (A) each of the two study regions, and (B) each of the six study sites within the two regions (where L is Cape Lazo and W is Willemar Bluffs). Species icons are not to scale. Icons sourced from phylopic.

Figure 5. The binned proportion of observations for each taxa observed across deployments throughout the study period for (A) Cape Lazo sites and (B) Willemar Bluffs sites. Deployment one: May 22nd, 2024, to June 11th, 2024; deployment two: June 19th, 2024, to July 9th, 2024; and deployment three: July 16th, 2024, to August 6th, 2024. Species icons are not to scale. Icons sourced from phylopic.

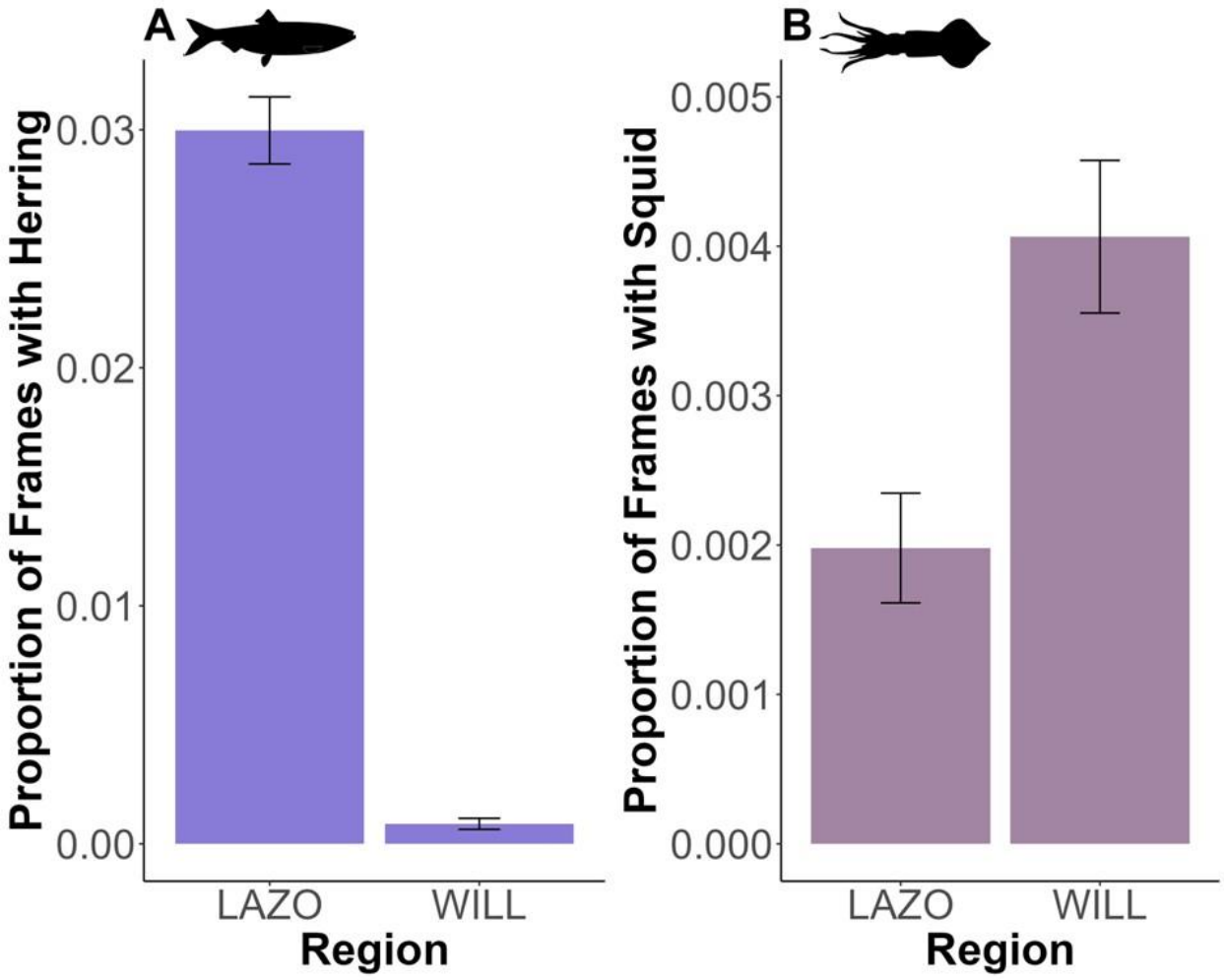

Figure 6. Bars representing the proportion of frames with (A) Pacific herring and (B) opalescent squid between the two study regions, Cape Lazo and Willemar Bluffs. The standard error is plotted for each bar.

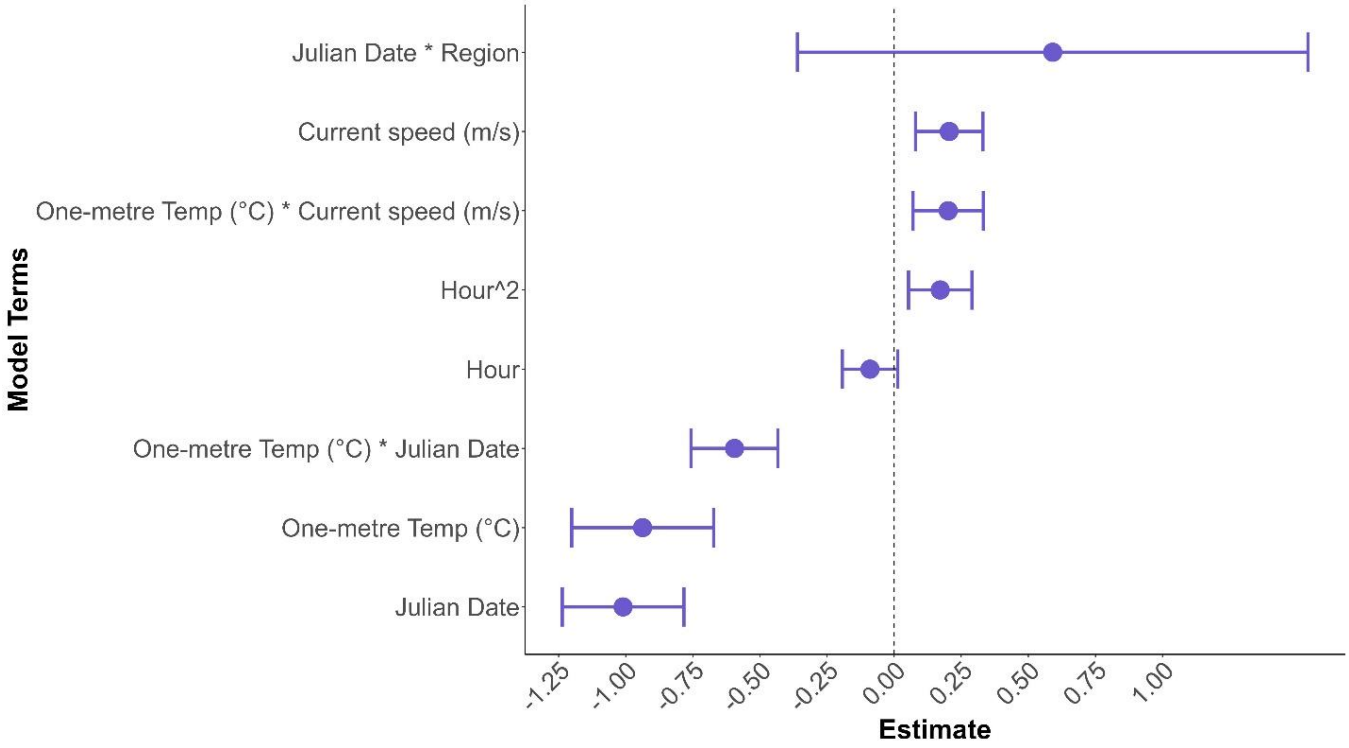

Figure 7. Effect sizes of Pacific herring model terms with 95% confidence intervals from the binomial logistic regression ran for herring presence across all six sites. Terms overlapping the zero dashed line are not significant.

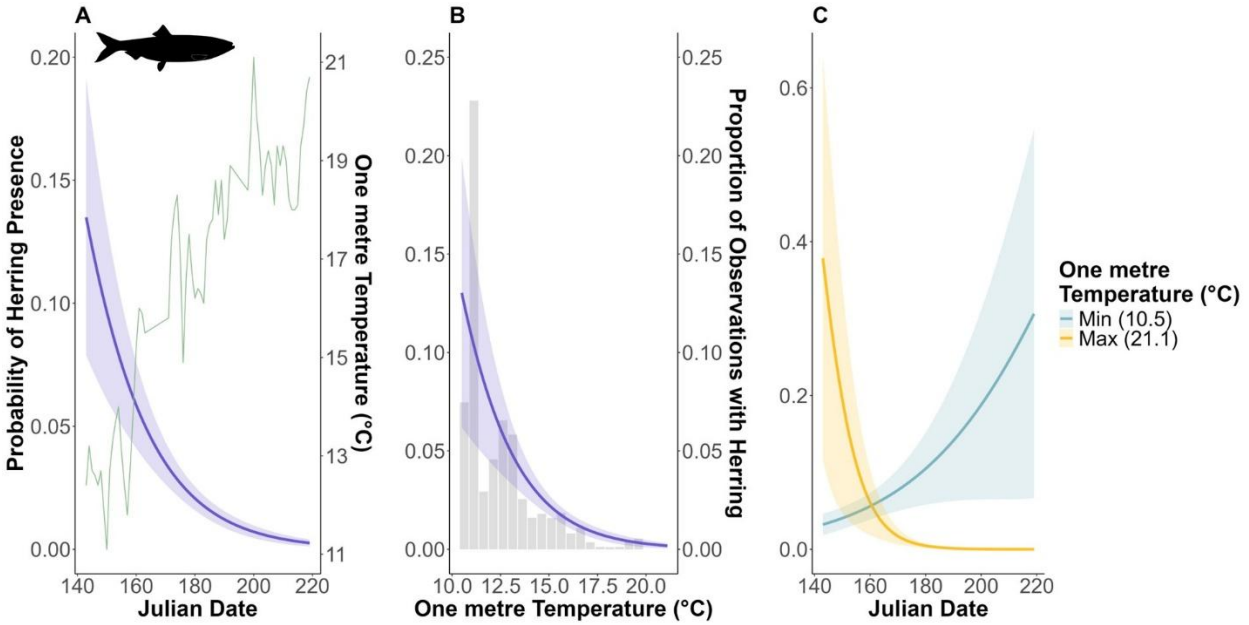

Figure 8. The modelled probability of herring presence (blue line) with shaded 95% confidence intervals showing a decrease in herring presence over (A) days of the study (Julian Date) and (B) temperature (°C). In panel A, the green line shows the average maximum temperature at one metre depth on each day of the study. In panel B, the grey bars represent the proportion of images with herring present by 0.5 °C increments. Depicting the interaction between herring presence and temperature, panel C shows the modelled probability of herring presence over time for two specific temperatures: the minimum (in blue) and maximum (yellow) temperatures recorded during the study. Predictions were generated by holding all other fixed effects at their mean. Note the difference in y-axis scales.

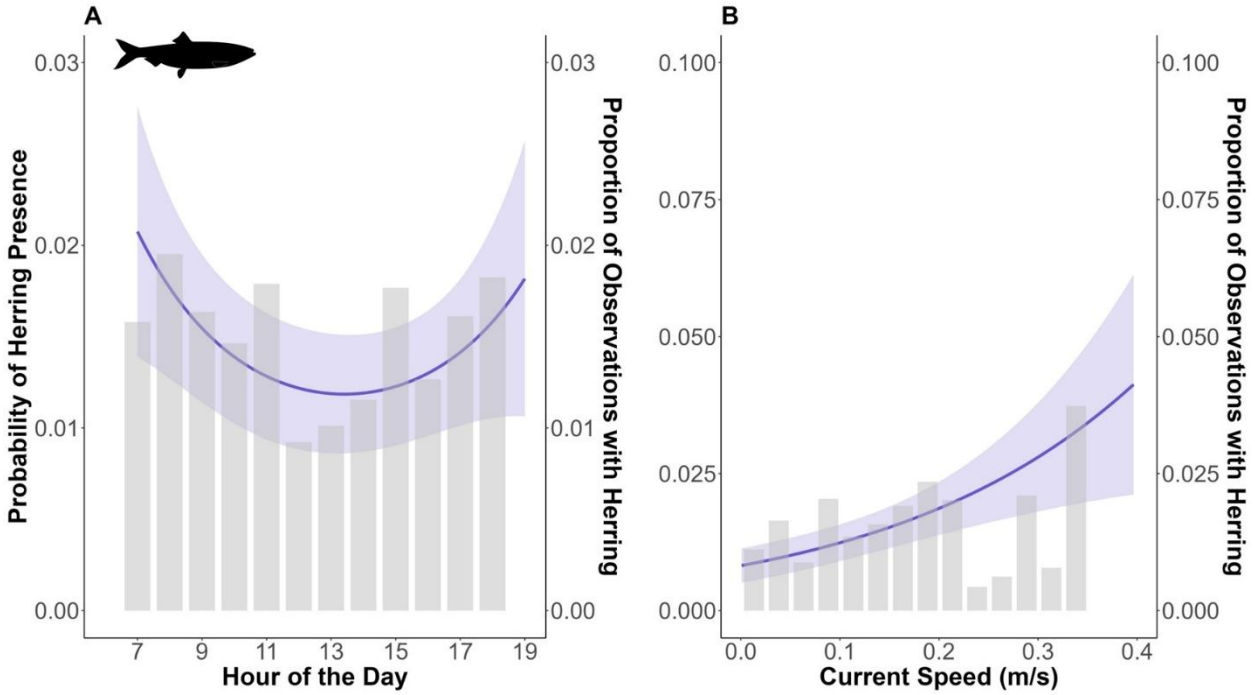

Figure 9. The modelled probability of herring presence (blue line) with shaded 95% confidence intervals across hours of the day (07:00 -19:00) (A) and current speed (m/s) (B). In panel A, the grey bars represent the proportion of images with herring present each hour. In panel B, the grey bars represent the mean proportion of images with herring present by 0.025 m/s increments. Predictions were generated by holding all other fixed effects at their mean. Note the difference in y-axis scales.

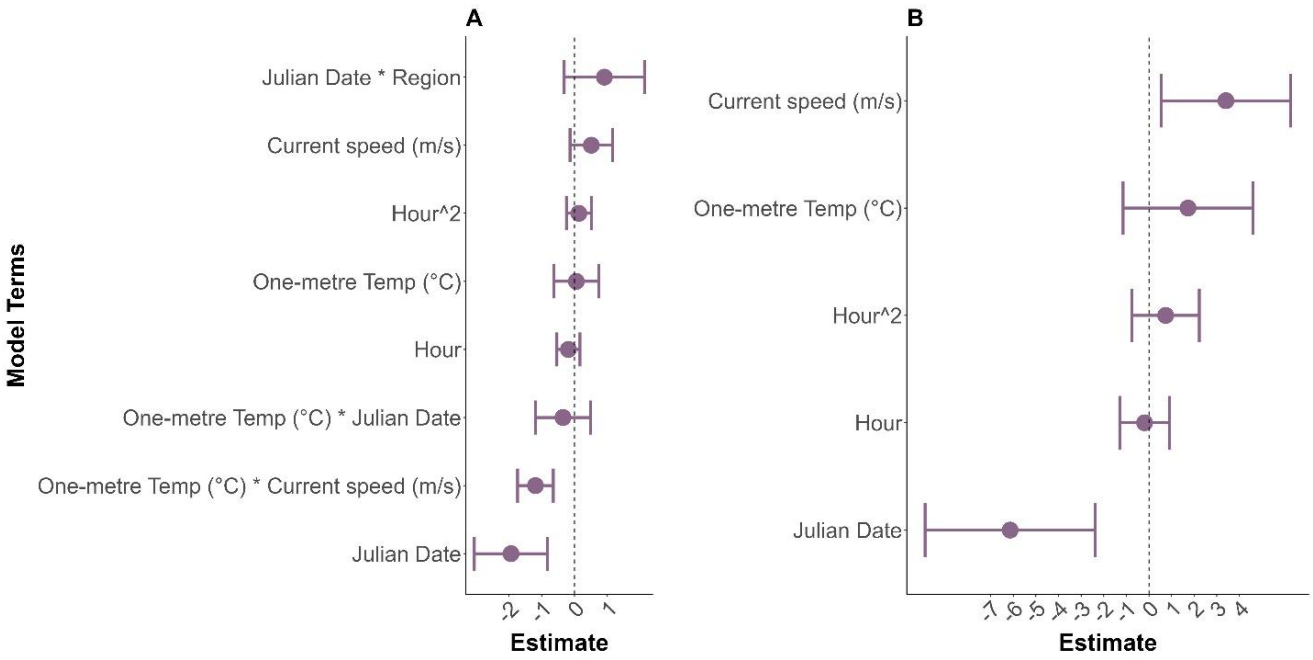

Figure 10. Effect sizes of opalescent squid model terms with 95% confidence intervals for the zero-inflated negative binomial model ran for squid hourly MaxN across the study period. Where (A) represents the conditional model terms and (B) represents the zero-inflated model terms. Terms overlapping the zero dashed line are not significant. Note the difference in x-axis scales.

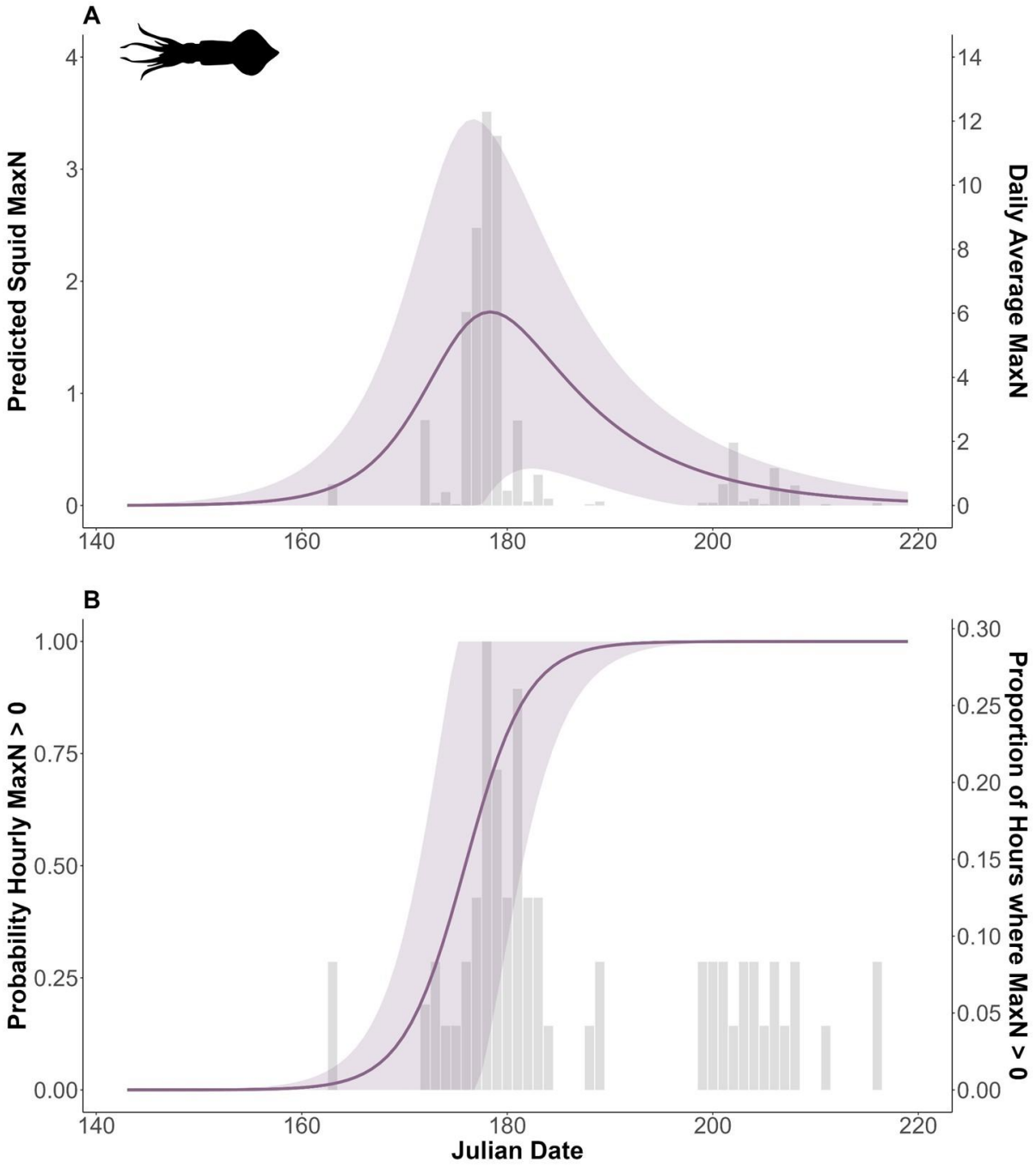

Figure 11. The modelled probability of: (A) predicted opalescent squid hourly MaxN over the study period, with the grey bars representing daily average hourly MaxN and (B) predicted probability of opalescent squid MaxN being greater than zero in a given hour across the study period, with the grey bars representing the proportion of hours per day where MaxN is greater than zero. The purple line represents model predictions with shaded 95% confidence intervals. Predictions were generated by holding all other fixed effects at their mean.

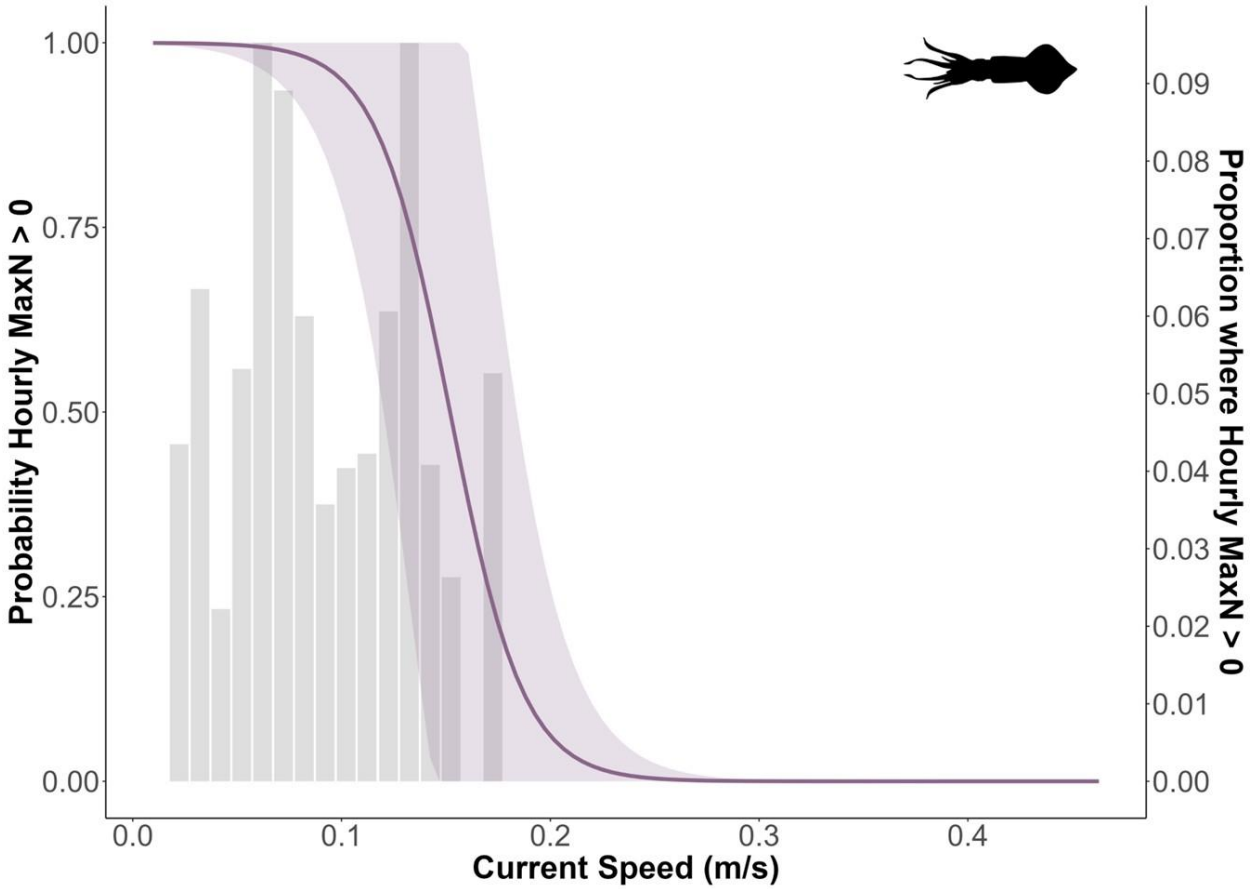

Figure 12. The modelled probability that opalescent squid MaxN is greater than zero in a given hour (purple line) with shaded 95% confidence intervals across current speeds (m/s). The grey bars represent the proportion of hourly MaxN values in each 0.010 m/s current speed block greater than zero. Predictions were generated by holding all other fixed effects at their mean.

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Appendix

Table S1. Certainty scores assigned to each observation in timelapse images.

Certainty Score	Description
1	Challenging to assign the ID in the given image, but the same fish appears in an adjacent frame with more characteristics visible.
2	Some characteristics of the described category are visible but may not be clear. Correct ID is likely.
3	All characteristics of the described category are clearly visible. Correct ID is certain.

Table S2. The subset of images with herring that were counted where one image for every 20 images of herring was counted per week, per site (n=38). Images counted were determined by a random number generator based on the total number of images of herring that week at that site.

Site	Week	Total images with herring	# images counted	Herring counts
Lazo 1	1	5	1	299
	2	83	4	376,313,144,827
	3	148	7	1434, 344, 250,111, 714, 2895, 218
	4	24	1	1222
	5	4	1	691
	6	1	1	255
	7	2	1	155
Lazo 2	1	62	3	323, 357, 927
	2	6	1	1005
	3	4	1	205
	4	8	1	3419
	5	11	1	339
Lazo 3	1	52	3	754, 206, 433
	2	14	1	2384
	3	8	1	341
	4	0	0	NA
	5	5	1	1933
	6	8	1	882
Will 1	1	1	1	2
	2	1	1	521
	3-5	0	0	NA
	6	1	1	118
Will 2	1	1	1	103
	2	5	1	82
	3-4	0	0	NA
	5	1	1	856
	6	0	0	NA
Will 3	1	2	1	44
	2-3	0	0	NA
	4	1	1	46
	5-6	0	0	NA

Table S3. Variance inflation factor results for the fixed effects used in Pacific herring and opalescent squid models.

Model	Model Terms	GVIF	GVIF^(1/(2*Df))
Pacific herring			
	Temperature (°C)	3.594503	1.136485
	Hour	1.046658	1.011466
	Current speed (m/s)	2.777427	1.185606
	Julian date	1.401283	1.034314
	Region	4.342726	1.277302
Opalescent squid			
	Temperature (°C)	3.116191	1.120372
	Hour	1.049921	1.012253
	Current speed (m/s)	4.050899	1.262579
	Julian date	1.732281	1.056481
	Region	5.506855	1.328874

Table S4. The model estimates, standard errors, and p-values for the fixed effects and interactions included in the top model for the binomial logistic regression ran for Pacific herring presence.

Fixed effect	Estimate	Estimate Std. Error	P-value
Temperature (°C)	-0.84815	0.12563	1.46e-11
Hour	-0.09313	0.05262	0.07672
Hour^2	0.17151	0.06037	0.00450
Current speed (m/s)	0.19383	0.06040	0.00133
Julian date	-0.99900	0.11441	< 2e-16
Temperature*Current speed	0.19011	0.06316	0.00261
Temperature*Julian date	-0.58822	0.08170	6.03e-13
Julian date*Region	0.58445	0.48002	0.22340

Table S5. The model estimates, standard errors, and p-values for the fixed effects and interactions included in the top zero-inflated negative binomial model ran for the hourly MaxN of opalescent squid.

Model	Fixed effect	Estimate	Estimate Std. Error	P-value
Conditional model				
	Temperature (°C)	0.05552	0.34942	0.873760
	Hour	-0.18528	0.17905	0.300766
	Hour^2	0.13310	0.19313	0.490708
	Current speed (m/s)	0.51197	0.33170	0.122709
	Julian date	-1.93447	0.56973	0.000685
	Temperature*Current speed	-1.18932	0.27790	1.87e-05
	Temperature*Julian date	-0.35060	0.42754	0.412189
	Julian date*Region	0.91052	0.62349	0.144195
Zero-inflation model				
	Temperature (°C)	1.7293	1.4657	0.23807
	Hour	-0.1922	0.5613	0.73200
	Hour^2	0.7390	0.7592	0.33040
	Current speed (m/s)	3.4049	1.4624	0.01990
	Julian date	-6.1402	1.9196	0.00138