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Monograph

Does the extent of glacial cover across watersheds and discharge periods affect dietary resource use of nearshore fishes in the Northern Gulf of Alaska?

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ABSTRACT

Northern high-latitude glaciers impact nearshore marine ecosystems through the discharge of cold and fresh waters, including nutrients and organic matter. Fishes are important integrators of ecosystem processes and hold key positions in the transfer of energy to higher trophic positions in such systems. This study used a natural gradient in space and time, including watershed glacial cover (0–60%) of five adjacent estuaries and three sequential discharge periods (pre-peak, peak, post-peak) in the northern Gulf of Alaska (Kachemak Bay) to test whether differences in glacial cover of watersheds upstream of estuaries affect dietary resource use of nearshore fishes. Dietary resource use was assessed using stomach content and stable carbon and nitrogen isotope analyses to determine fish diet composition and trophic niche width. Crescent gunnel (*Pholis laeta*), a mostly sedentary species, was our focal species for comparisons across estuaries and discharge periods. Discharge period had a greater influence on diet composition and trophic niche width of crescent gunnels than watershed glacial coverage. Niche width of crescent gunnel was larger during the post-peak discharge period compared to pre-peak and peak periods, coincident with a shift in prey spectrum. However, watershed glacial cover was not a suitable predictor of niche width of crescent gunnel. Trophic resource use was also considered along this glacial cover gradient for two other fish species, Pacific staghorn sculpin (*Leptocottus armatus*) and starry flounder (*Platichthys stellatus*), but within the post-peak discharge period only. These species exploited a larger prey base compared to crescent gunnel, likely due to their greater mobility. Similar to crescent gunnel, there were no relationships in trophic niche width associated with watershed glacial coverage for these other species during the post-peak discharge period. Instead, trophic resource use of these three nearshore fish species was influenced by a more complex set of dynamic environmental variables (salinity, temperature, turbidity, and discharge), as well as static watershed characteristics, especially vegetation cover. Such drivers can act through changes in metabolic rates, modulating foraging strategies and trophic connectivity, as well as terrestrial nutrient delivery to support estuarine production. The environmental conditions associated with the glacially influenced estuaries during our study period (2020−2021) seemed within a range that allowed nearshore fishes to maintain energy pathways and prey bases across these estuaries, but it is unknown how these estuarine food webs may be influenced in years of extreme conditions such as during heat waves, droughts, or floods.

1. Introduction

Glaciers influence nearshore ecosystem processes due to freshwater and nutrient input provided through melting (Arimitsu et al., 2016; Hopwood et al., 2020). The effects of climate change are magnified in high-latitude estuarine systems, such as those in Alaska, where temperatures are rising, precipitation levels are increasing, and glaciers are receding at unprecedented rates (Anderson and Piatt, 1999; O'Neel et al., 2015; Wuethrich, 2000). Warmer summers generally increase glacial melt and, therefore, freshwater flux (Hodge et al., 1998; Motyka et al., 2001; Neal et al., 2002; Spencer et al., 2014). Glacial runoff can cool coastal water temperatures, decrease salinity, and increase turbidity and nutrients in high-latitude estuaries (Arimitsu et al., 2016, 2017; Hopwood et al., 2020; Pitman and Moore, 2021). Climate change

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has shifted the magnitude and seasonality of precipitation and glacier runoff to estuaries, with an increase in precipitation in coastal regions of Alaska by 8% between 1949 and 2016 (Wendler et al., 2016).

The increased freshwater and nutrient discharge from glaciers transport bioavailable particulate organic matter (POM) and dissolved organic matter (DOM) into coastal estuaries, although the promotion of marine primary production from glacier melt is more pronounced in marine-terminating than land-terminating glaciers (Hopwood et al., 2020). Glacial runoff can impact food web dynamics as allochthonous organic matter or by stimulating phytoplankton blooms (Dierssen et al., 2001; Hood and Scott, 2008; Possamai et al., 2020). For example, terrestrial organic matter that enters the nearshore via estuarine watersheds may be utilized by lower trophic level primary consumers, which may then be transferred to higher trophic levels via predation (Whitney et al., 2018; Reddy et al., 2022). The POM and DOM influx from glaciated watersheds is strongly correlated with the glacial coverage of the watershed (Hood et al., 2009; Fellman et al., 2010) and can diversify the food web pathways in the downstream estuaries, potentially adding to the dietary niche width of organisms that occupy these habitats. In addition, temporal variability such as from different glacial discharge periods can create niche diversity and promote trophic diversity and species coexistence (Chesson, 2000).

The extent to which spatial and seasonal watershed dynamics drive estuarine nearshore food webs, particularly dietary resource use by nearshore fishes, may differ depending on the species (e.g., Thorman, 1982; Munsch et al., 2016; Whitney et al., 2017). Various fish species either reside in, or temporarily inhabit, nearshore ecosystems providing links to the surrounding areas through nutrient flow (Sheaves, 2009). For example, habitat use and food sources may differ between more sedentary versus more mobile fish species or other aspects of their feeding strategy (e.g., morphology). Further, estuarine fishes can respond differently to environmental conditions depending on their physiology or life history (Frimpong and Angermeier, 2010; Winemiller et al., 2015; Teichert et al., 2017). Understanding how nearshore fish species respond to glacial melt influence may improve understanding of future coastal ecosystem functioning in an increasingly warming climate that continues to erode glacial cover.

Here, we focused on trophic niche use of three estuarine species including crescent gunnel (*Pholis laeta* [Cope, 1873]), Pacific staghorn sculpin (*Leptocottus armatus* [Girard 1854]), and starry flounder (*Platichthys stellatus* [Pallas, 1787]) in a glacially influenced high-latitude fjord system located in Southcentral Alaska (Kachemak Bay). Gunnels (Pholidae) are common resident fishes in high-latitude nearshore marine ecosystems. They occupy a mid-level trophic position, generally consuming benthic organisms, mainly crustaceans (Rutenko et al., 2022), and provide a stable food source for various predators such as larger fishes, River Otter (*Lontra canadensis* [Schreber, 1777]), American Mink (*Mustela vison* [Schreber, 1777]), and Pigeon Guillemot (*Cepphus columba* [Pallas, 1811]) (Cote et al., 2008; Shorty and Gannon, 2013; Buckner et al., 2022).

In contrast to the crescent gunnel, two common coastal species – Pacific staghorn sculpin and starry flounder – employ broader habitat use and behavior in the nearshore (Gross et al., 2018). While Pacific staghorn sculpin are mostly resident in the nearshore, the species' habitat use is broader by exhibiting diel migrations between shallower estuaries during the day and deeper subtidal and offshore habitats at night (Gross et al., 2019). Pacific staghorn sculpin consume a wide variety of invertebrate prey items and, as adults, also prey on other fish species (Dinnel et al., 1990; Hughes et al., 2014). Starry flounder are the most transient of our study species and move among habitat patches in search of resources (Rountree and Able, 2007). Starry flounder primarily feed on a wide range of invertebrates, including some highly mobile species (Orcutt, 1950; Cailliet et al., 2000). The comparison of common estuarine fishes that differ in morphology, behavior, and habitat use strategies (e.g., Chalifour et al., 2019) can provide information on how intra- and inter-specific patterns in dietary resource uses vary in association with watersheds of different glacial cover for mid-trophic level consumers.

Dietary niche width represents the multi-dimensional niche in which an organism uses resources, in this case for dietary use (sensu Bearhop et al., 2004). It is a key metric of resource use, which can be sensitive to changes in environmental conditions, competition, and prey abundance. Dietary niche width can be quantified from stomach content analysis, defined as the number and type of prey species consumed (Bearhop et al., 2004). Stomach contents provide a detailed snapshot of the most recent diet of a consumer, allowing for quantification of the diversity and abundance of individual prey species (Buckland et al., 2017). Complementary niche width metrics include stable carbon and nitrogen isotope values of fish tissues, parameters that integrate consumer diets over weeks to months, depending on tissue-specific turnover rates (Peterson and Fry, 1987; Post, 2002). The combination of these two approaches (stomach content and stable isotope analysis) is useful to discern the dietary resource use of common nearshore fish species by linking snapshot and integrated approaches to inform diet variability (Winemiller et al., 2007).

The overall objective of this study was to understand how glacial cover of a watershed influences resource use and dietary niche width of fishes in downstream estuaries. Using a series of adjacent estuaries connected to watersheds with variable glacial coverage, we hypothesized that watershed glacial cover influences estuarine fish dietary resource use as glaciers drive proximate factors known to influence fishes, prey, and food web interactions (e.g., through water temperature, salinity, nutrients; Arimitsu et al., 2017; Hood and Scott, 2008). Discharge period was explicitly included in this analysis to account for the seasonality of glacial influences. Understanding if and how the diet and trophic resource use of nearshore fishes is influenced by variables associated with glacial cover informs a current information gap for predicting fish and ecosystem responses as glaciers continue to recede in association with a warming climate.

2. Methods

2.1. Study sites

A gradient in glacial cover of five land-terminating glaciers within the study region served as a natural experiment, following a space-for-time substitution approach where watersheds of varying glacial coverage were selected to reflect stages in the decline of glacier mass over time with climate warming (Hood and Berner, 2009). The present study was conducted across five estuaries downstream from land-terminating glaciers in the northern Gulf of Alaska, Kachemak Bay, Alaska, USA (Fig. 1), here referred to as sites. These sites represented a gradient in percent glacial cover (Jenckes et al., 2023) of the watershed, ranging from 0 to 60%: 0% (Jakolof Bay), 8% (Tutka Bay), 16% (Halibut Cove), 27% (Wosnesenski River), and 60% (Grewingk Glacier) (Fig. 1, hereafter sites are referred to by the percent glaciation of the respective watershed). Importantly, we note these watersheds are adjacent and part of the larger Kachemak Bay system; thus, our study sites experience similar overall atmospheric conditions (e.g., air temperature and precipitation).

2.2. Sampling design

Crescent gunnel, Pacific staghorn sculpin, and starry flounder were collected at each of the five study sites. Up to ten crescent gunnel per site were collected once per month: June – September 2020, and April – May 2021. Monthly samples were grouped within three discharge periods: time before peak glacial discharge (pre-peak: April, May), peak discharge (peak: June, July), and post-peak discharge (post-peak: August, September) (following Whitney et al., 2017; Jenckes et al., 2023). Up to a total of 23 Pacific staghorn sculpin and 17 starry flounder were collected at each site in August and September 2020 to compare

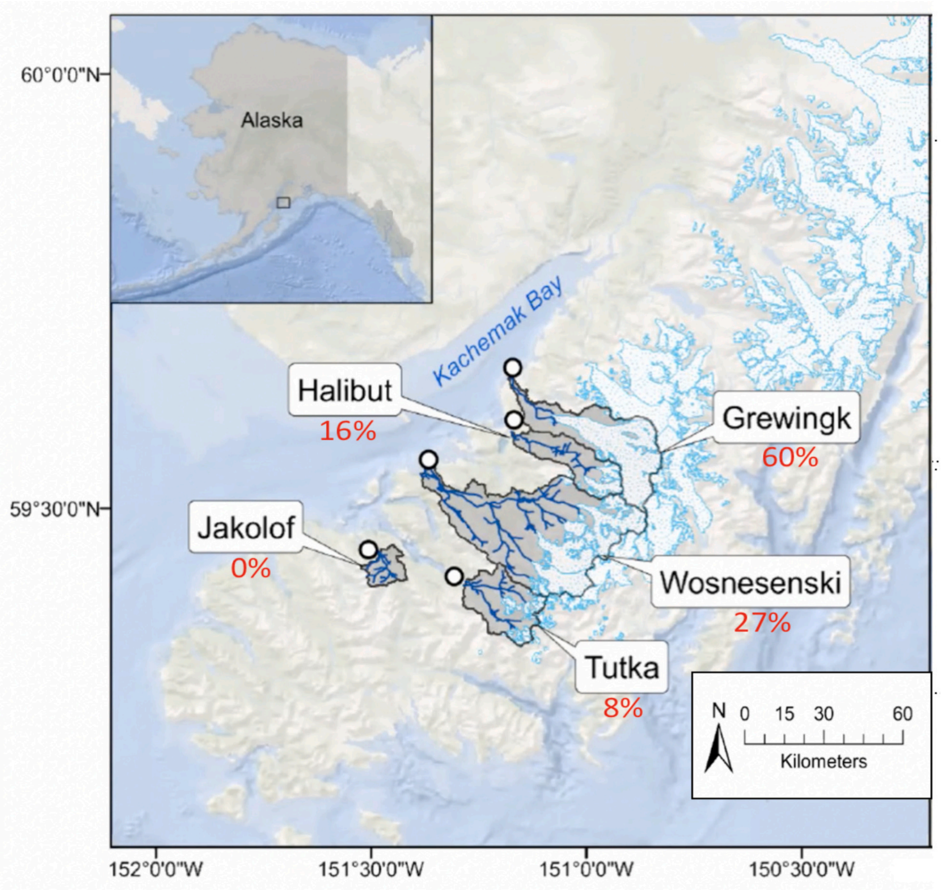

Fig. 1. Study sites within Kachemak Bay, Northern Gulf of Alaska, indicating the percent glacial cover (Jenckes et al., 2023) of the sampled watersheds. White circles represent the fish sampling locations. The black outlines show the respective watershed areas with white/blue color representing the glacial coverage and blue lines the rivers discharging from the watersheds. The inset map shows the location of Kachemak Bay within Alaska. Jakolof = Jakolof Bay, Tutka = Tutka Bay, Halibut = Halibut Cove, Wosnesenski = Wosnesenski River, Grewingk = Grewingk Glacier. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

spatial patterns in food resource use among the three different fish species during the post-peak discharge period only, due to logistical constraints. Species accumulation curves for each species, site, and discharge period confirmed that samples sizes of ten or more individuals per discharge period were sufficient to characterize the diet of these fish species (data not shown; Cortés, 1997).

Sampling occurred during the first low tide cycle of each month. Fishes were collected using a 15-m long, 2.5-m wide, white beach seine with a square mesh size of 1.2 cm. Five beach seine hauls were conducted per site per sampling event at approximately 1-m depth around low tide. The seine net was spread out and pulled between two people parallel to shore for the duration of approximately 5 min, before closing the net and pulling it onto the beach (following Whitney et al., 2017). Fishes caught in the seine were immediately removed from the net and placed into containers with aerated saltwater obtained from the sampling site. Individuals selected for diet analysis were placed in a lethal solution of MS-222 of >200 mg l^{-1} in seawater before being individually labeled, bagged, and stored on ice for transport to the lab and processing. Fishes were then kept frozen at −20 °C until processing for stomach content and stable isotope tissue sampling. Prior to diet analysis, each fish was thawed, exact length (tip of snout to end of tail) measured in the lab and wet weight taken (0.1 g accuracy) (Iken, 2023). All fishes were collected following University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC) guidelines (protocol #1238650), and Alaska Department of Fish and Game permits (CF-20-043 and CF-21-037).

2.3. *Stomach content analysis*

Stomachs were removed from each fish and the contents processed for prey taxonomic diversity and relative abundance. First, a complete prey list at the greatest possible taxonomic resolution was recorded from visual inspection of the stomach contents. Then, stomach content items were quantified based on a point system in a gridded petri dish (Hyslop, 1980; Lima-Junior and Goitein, 2001; da Silveira et al., 2020). The benefit of the point method is that it accounts for both the abundance (number) and size (proxy for relative weight) of the prey, as large prey items will cover more than one point (Zacharia, 2017). The partial degradation state of some fish prey made actual counts or volumetric assessment of prey biomass difficult. For the point system, lines drawn onto a petri dish created a grid with a defined number of points of line intersections that were used to quantify stomach content elements. Depending on fish size, a 6.5-cm-diameter dish with 25 grid intersection points (fish <200 mm) or a 10-cm-diameter dish with 50 grid points (fish ≥ 200 mm) was used for the quantification process. The stomach content was spread evenly across the dish and each grid point was analyzed for the type of prey item (if any) covering it. Stomach content was estimated as the total number of points for each prey item or blank point (no prey) and then converted into a percentage of total stomach content based on the total number of points. Prey items that were present in the stomach based on the complete prey list, but were not encountered on any point, were assigned a small proportion (0.0001%) in the quantitative prey taxon list to indicate their presence. Fish stomach content data are archived in Iken (2023).

2.4. Stable isotope analysis

Fish dietary resource use was also determined using bulk stable carbon and nitrogen isotope values of fish liver tissue. Liver tissue was chosen to maximize the detection of potential diet trends over relatively short periods of time (on the order of several weeks) (Post, 2002; Buchheister and Latour, 2010). Stable carbon and nitrogen isotope analysis was performed on approximately ten fish per species per site and sampling event, using the same individuals used for stomach content analysis; however, not all specimens analyzed for stable isotopes were analyzed for stomach content analysis. Liver tissue samples were dried at 60 °C for at least 24 h and until reaching a constant weight. Liver tissue is high in lipid content, which is depleted in ^{13}C relative to other major biochemical components (Schlechtriem et al., 2003; Logan et al., 2008; Skinner et al., 2016). Because common chemical extraction methods may also alter the nitrogen stable isotope values to varying degrees (Logan et al., 2008; Skinner et al., 2016), we compared the carbon stable isotope values (see below) of select samples, where one tissue aliquot was chemically extracted (three treatments with 2:1 chloroform:methanol) and the other aliquot was not extracted (Supplementary Material, Table S1). We then compared the extracted carbon stable isotope values to those that would be derived when applying various mathematical correction functions to the non-extracted tissue values, using six equations from the literature (Supplementary Material, Table S2). Based on those results, all liver carbon stable isotope values were mathematically corrected using the approach by McConnaughey and McRoy (1979) (for details, see Supplementary Material Table S2 and Fig. S1), which also allowed for using non-extracted samples for nitrogen stable isotope values.

Carbon and nitrogen stable isotope ratios were measured from dried and homogenized liver tissue samples and measured at the Alaska Stable Isotope Facility (ASIF) at the University of Alaska Fairbanks. Stable isotope data were obtained using continuous-flow isotope ratio mass spectrometry (CF-IRMS). This method utilizes a Thermo Scientific Flash 2000 elemental analyzer and Thermo Scientific Conflo IV interfaced with a Thermo Scientific DeltaV^{Plus} Mass Spectrometer (Breman, Germany). Stable isotope values are expressed in the common delta (δ) notation as parts per thousand (‰) according to the equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Pee Dee Belemnite and atmospheric N_2 served as standards for carbon and nitrogen, respectively. Instrument error was determined from all standard runs ($n = 86$) and was calculated as ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Stable carbon and nitrogen isotope data for all fish species are archived in Iken and Schloemer (2022).

2.5. Environmental measurements

We used several static (i.e., did not change over the time of our study, Table 1a, after Schloemer et al., 2024) and dynamic (i.e., changed across discharge periods, Table 1b) environmental variables to assess potential environmental drivers of nearshore fish dietary resource use. Static watershed characteristics that could influence downstream estuarine conditions were taken from Schloemer et al. (2024) for the same watersheds (0–60% glaciated in Kachemak Bay). These characteristics included total watershed area (km^2), mean slope (%), mean elevation (m), river length (km), and percent cover of vegetation (%) (Table 1b). These static metrics were derived from a digital elevation model and multispectral imagery (see Schloemer et al., 2024 for details). Dynamic variables included temperature (°C) and salinity measured from HOBO conductivity loggers (Onset Computers, Bourne, MA, USA), and dissolved oxygen (DO, mg l^{-1}) measured from miniDOTs (Precision Measurements Engineering, Vista, CA, USA). All loggers were continuously deployed as an instrument package at about 1-m below mean lower low water (MLLW) at each study site. Temperature, salinity and DO measurements were averaged over the first 12 days of each sampling month to encompass the variability across the time of monthly sampling, which always occurred within the first ten days of a month. Using the first 12 days of each month allowed us to create distinctly different time sections to distinguish conditions for subsequent sampling months. Turbidity was determined from the location of the instrument package and from surface waters 50-m offshore from the site once during each sampling event; water samples were analyzed using a Hach 2100P TurbidiMeter (Ames, IA, USA) as Nephelometric Turbidity Units (NTU). Discharge volume (m^3 s^{-1}) was measured for each site and month as described in detail in Jenckes et al. (2023). Discharge values were not available for every collection month; in those cases, discharge values from the same month, but from the previous year were used. While we cannot expect discharge rates to be the exact same in a given month every year, the overall magnitude of monthly discharge at the various sites will likely still be similar across years and sufficiently different among watersheds to be a reasonable representation of discharge. This is especially the case when combining several months into discharge periods (see below), which will mute some of the inter-annual differences at a given site. Discharge volume was then standardized to watershed area and is reported as standardized discharge (m^3 s^{-1} km^{-2}). Monthly values for dynamic variables including salinity, temperature, DO and standardized discharge were averaged to present data for the pre-peak (April – May), peak (June – July) and post-peak (August – September) discharge periods (Table 1b), following the approach applied for fish stomach content and stable isotope data.

Table 1a
Static environmental variables for the five study sites (0%, 8%, 16%, 27%, and 60% glaciation). Data from Schloemer et al. (2024).

Site (% glaciated)	Watershed area (km^2)	Slope (%)	Elevation (m)	Vegetation (%)	River length (km)
0%	18.9	21.0	1140.0	64.7	3.9
8%	65.7	45.0	1275.0	18.5	23.3
16%	55.6	26.0	1494.0	7.1	14.8
27%	256.6	20.0	1569.0	17.6	25.8
60%	111.5	14.0	1641.0	3.7	6.3

2.6. Statistical analyses

Stomach content composition was compared using multivariate statistics in Primer-e V7 (Clarke and Gorley, 2015). To test for spatio-temporal differences in diet composition of crescent gunnels, data were fourth-root transformed and a Bray-Curtis similarity resemblance matrix applied as the basis of a PERMANOVA with site and discharge period as fixed factors. Fish size was considered by including length as a covariate in the PERMANOVA. Diet composition of the three species (crescent gunnel, Pacific staghorn sculpin, and starry flounder) from the post-peak discharge period were analyzed using PERMANOVA with site as a fixed factor, and fish length included as a covariate. The significance level for all analyses was set at $\alpha = 0.05$. Dietary overlap was visualized using non-metric multidimensional scaling (nMDS) plots: crescent gunnel diets by discharge period, and diet of the three fish species within the post-peak discharge period. Ellipses were added representing the 95% confidence level for multivariate t-distribution in R (version 4.0.3, ggplot2 statellipse; Wickham, 2016; R Core Team, 2020). Trophic resource niche width based on stomach content analysis was calculated based on the similarity (nMDS ordinations) of diet composition using multivariate dispersion (MVdisp, Primer-e V7) for each group shown in the nMDS plots, as well as for all data by site within discharge periods.

Trophic resource use represented by stable carbon and nitrogen isotope values of fish liver tissue was compared by site and discharge period (for gunnels), or among sites (for the three species separately) using PERMANOVA as described above for stomach contents. Isotopic niche overlap among these groups was visualized as carbon and nitrogen stable isotope biplots. Isotopic dispersion (SIdisp) following

Table 1b

Dynamic environmental variables for the five study sites (0%, 8%, 16%, 27%, and 60% glaciation) for the three discharge periods (pre-peak, peak, post-peak). DO – dissolved oxygen, NTU – Nephelometric Turbidity Units. Stand. discharge – discharge standardized to watershed area.

Site (% glaciated)	Discharge period	Salinity	Temperature (C)	DO (mg l^{-1})	Turbidity near (NTU)	Turbidity 50 m (NTU)	Stand. discharge (m^3 s^{-1} km^{-2})
0%	Pre-Peak	22.0	4.4	8.6	16.6	11.6	0.009
8%	Pre-Peak	26.4	3.9	11.3	16.6	7.9	0.132
16%	Pre-Peak	25.6	4.3	9.7	41.3	8.7	0.058
27%	Pre-Peak	25.1	4.2	9.2	36.5	7.2	0.042
60%	Pre-Peak	25.3	4.3	11.4	3.0	2.7	0.047
0%	Peak	26.5	9.7	8.7	68.9	4.2	0.014
8%	Peak	20.0	9.4	12.5	1.8	1.3	0.201
16%	Peak	23.6	10.8	11.2	37.1	2.5	0.105
27%	Peak	25.0	9.2	10.9	501.9	38.1	0.350
60%	Peak	23.5	10.5	11.0	4.0	2.6	0.299
0%	Post-Peak	22.0	11.6	8.6	6.3	1.2	0.009
8%	Post-Peak	22.4	11.3	7.8	6.3	4.7	0.135
16%	Post-Peak	15.2	12.1	8.5	6.8	4.9	0.133
27%	Post-Peak	20.1	11.3	8.7	70.4	26.8	0.527
60%	Post-Peak	20.8	12.0	8.8	20.5	3.4	0.474

Cucherousset and Villeger (2015) was calculated for each grouping as a measure of isotopic niche width.

Environmental data were tested for skewness and transformed accordingly (log transformation for both turbidity measurements). Collinearity among variables was tested with Pearson correlations. None of the variables had correlation coefficients ≥ 0.95; thus, all environmental variables were retained. Prior to analysis, all variables were normalized to achieve a consistent reference frame. Environmental conditions at sites and across discharge periods (dynamic variables only) were visualized using principal components analysis (PCA) in Primer-e V7. The effect of the combined dynamic and static variables on fish diet from stomach content analysis and stable isotope composition was then determined using the BEST-BIOENV analysis in Primer-e V7.

3. Results

3.1. Environmental setting

Study sites were well separated based on static environmental variables, with high vegetation cover characterizing the 0% glaciation site, long river run and steep slopes at the 8% site, while the 16% site was intermediate in all static variables (Table 1a, 2a, Fig. 2a). The 27% site had the largest watershed area and river length, while the 60% site was characterized by high elevation. Based on the dynamic variables, sites aligned by discharge period within the PCA ordination, especially for the pre-peak period (Fig. 2b), where all sites had lower temperatures and higher salinities and tightly grouped at the positive end of PC1 (Table 1b, 2b, Fig. 2b). PCA groupings were less tight during the other two discharge periods, displaying variable conditions at the sites during these discharge periods. During the peak period, sites separated diagonally mostly along a gradient in turbidity (PC1 and PC2) (Fig. 2b). Similarly, sites during the post-peak period were aligned within the PCA along a gradient in turbidity but also based on standardized discharge. Sites during post-peak conditions were separated from those during peak conditions mostly by warmer temperatures (Table 1b, 2b, Fig. 2b).

Table 2a

Principal components analysis (PCA) results for static variables characterizing sites (based on percent glacial cover; Jenckes et al., 2023), computed using Primer-e V7 (Clark and Gorley, 2015). Given are the Eigenvectors of the variables (vector loadings making up the principal components) and the principal component scores for the sites along principal components (PC) 1 and 2, as shown in Fig. 2a.

Eigenvectors		
Variable	**PC1**	**PC2**
Watershed area	0.519	−0.016
Slope	−0.145	−0.737
Elevation	0. 569	0.272
Vegetation	−0.514	0.075
River length	0.349	−0.615
Principal Component Scores		
Site (% glaciated)	**Score 1**	**Score 2**
0%	−2.451	0.721
8%	−0.464	−1.960
16%	0.240	0.004
27%	1.815	−0.218
60%	0.866	1.453

3.2. Dietary resource use in crescent gunnel

A total of 289 crescent gunnel were analyzed for stomach contents across all sites and discharge periods, ranging in total length from 39 to 194 mm (mean ± SD: 131 ± 32 mm). Crustaceans were the most prominent diet category in crescent gunnel stomachs at all sites and discharge periods (Fig. 3), comprising mostly harpacticoid copepods, gammarid amphipods, and hermit crabs. Diet composition in crescent gunnel stomachs was related to site, discharge period, and their interaction (PERMANOVA, all three terms $p = 0.001$) after accounting for fish length (Table 3). Of these, discharge period had the largest effect (pseudo-F = 7.10; Table 3). During the peak discharge period, the contribution of the diet category “other” increased (i.e., unidentifiable tissue remains or other taxa that had otherwise very small proportional contributions to overall diet). During the post-peak period, there was a noticeable increase of mollusks in the diet of crescent gunnel, particularly at the 8%, 16%, and 60% glacial cover sites, while the amount of “other” (unidentifiable tissues) decreased. The relative contributions of annelids and macroalgae also increased at most sites during the post-peak period.

There was overlap in crescent gunnel diet composition across the three discharge periods when all sites were combined, as seen by overlap of the ellipses in the nMDS ordination (Fig. 4a). Dietary niche width, as measured by MVdisp, was largest during the post-peak discharge period (MVdisp = 1.12) and lowest during the peak discharge period (MVdisp = 0.87) (Fig. 3a). There was no obvious trend in trophic niche width at the individual sites along the glacial cover gradient within any discharge period (Fig. 4b–d).

Both site and discharge period significantly predicted stable carbon and nitrogen isotope values of crescent gunnel liver tissues, after accounting for fish length (PERMANOVA, $p < 0.05$; Table 4). Of these factors, discharge period had the largest effect (pseudo-F = 29.68), about double the effect of site (Table 4). The δ^{13}C range of crescent gunnels was similar for all three discharge periods, but there were noticeable differences in δ^{15}N ranges (Fig. 5a). During the pre-peak

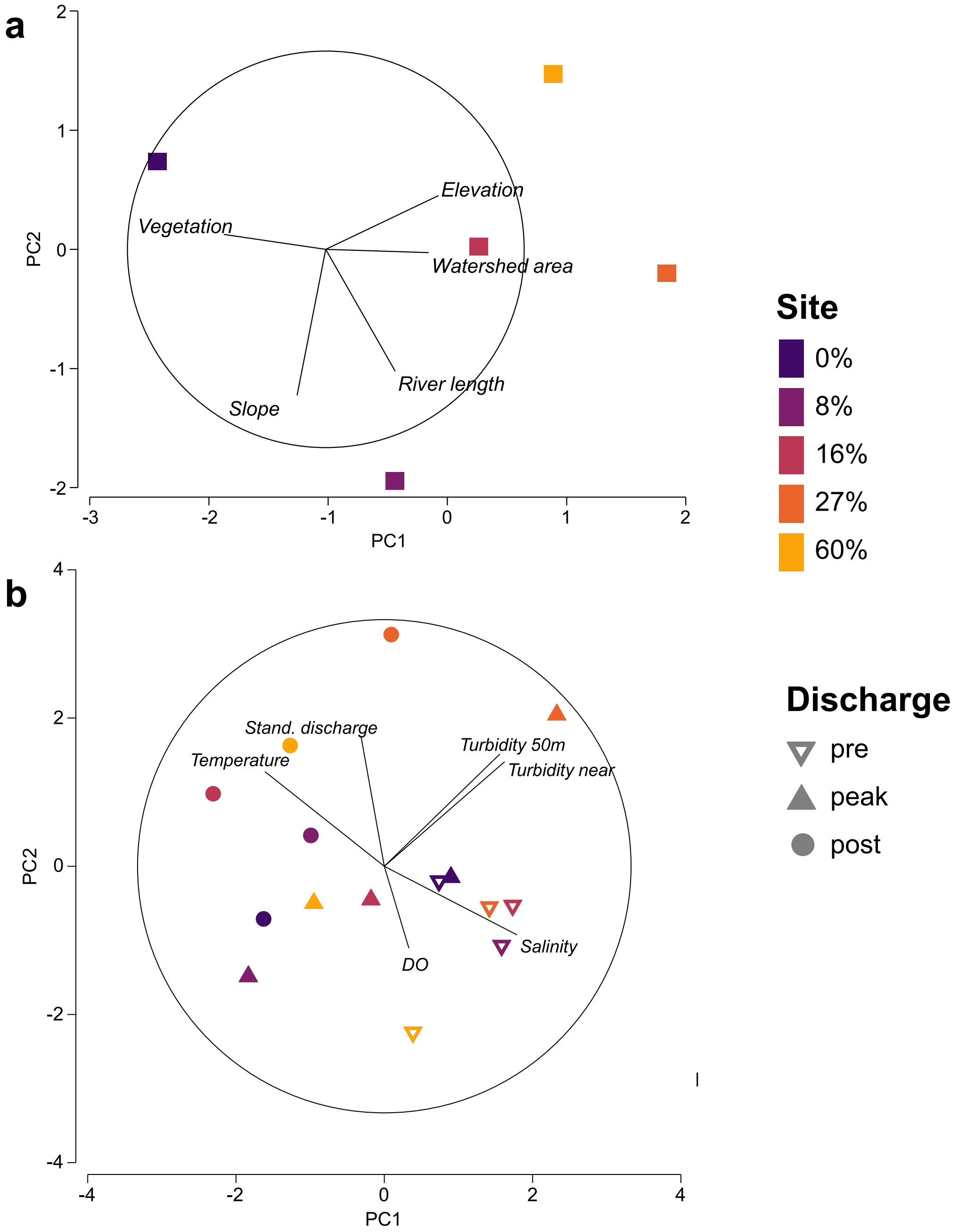

Fig. 2. Principal components analysis (PCA) of sites (ranging in glacial cover from 0 to 60%; Jenckes et al., 2023) based on static watershed characteristics (a) and of sites and discharge period (pre-peak, peak, and post-peak) based on dynamic environmental variables (b). See Table 2 for PCA results.

period, crescent gunnel had, on average, slightly higher δ^{15}N values (12.3 ± 1.0‰), intermediate values during the peak period (11.2 ± 1.1‰), and lowest values occurred during the post-peak period (10.8 ± 1.0‰). Therefore, the average δ^{15}N values dropped by about 1.6‰ from pre-peak to post-peak periods. Trophic niche width, measured as SIdisp, was similar during the three discharge periods (Fig. 5a). Crescent gunnel stable isotope values differed by site within each discharge period (PERMANOVA, $p < 0.01$; Table 4), although there were no consistent trends according to the glacial gradient in trophic niche width. SIdisp varied by site, but in no particular order of percent glacial cover in either discharge period (Fig. 5b–d). For example, during the pre-peak discharge period, crescent gunnel SIdisp was highest at the 27% glacial cover site and lowest at the 16% glacial cover site, while during peak discharge, crescent gunnel SIdisp was highest at the 16% glacial cover site and lowest at the 0% glacial cover site. During the post-peak discharge period, the highest SIdisp of crescent gunnel was also found at the 60% glacial cover site and the lowest occurred at the 8% glacial cover site (Fig. 5b–d).

Among the dynamic and static watershed variables tested, the combination of salinity, temperature, and standardized discharge volume, together with watershed area and slope were predictors of the crescent gunnel stomach composition (Spearman rank correlation coefficient $\rho = 0.458$; BEST-BIOENV analysis). When considering crescent gunnel stable isotope values, the combination of the dynamic environmental variables temperature and standardized discharge, together with the static variable of river length resulted in the highest Spearman rank correlation coefficient of $\rho = 0.512$ (BEST-BIOENV analysis).

Table 2b

Principal components analysis (PCA) results for dynamic variables characterizing sites (based on percent glacial cover; Jenckes et al., 2023) and by discharge period (pre-peak, peak, post-peak), computed using Primer-e V7 (Clark and Gorley, 2015). Given are the Eigenvectors of the variables (vector loadings making up the principal components) and the principal component scores for the sites grouped by discharge period along principle components (PC) 1 and 2, as shown in Fig. 2b.

Eigenvectors		
Variable	**PC1**	**PC2**
Salinity	0.538	−0.279
Temperature	−0.484	0.384
DO	0.100	−0.333
Turbidity near	0.488	0.424
Turbidity 50 m	0.468	0.454
Stand. discharge	−0.095	0.528

Principal Component Scores			
Site (% glaciated)	**Discharge period**	**Score 1**	**Score 2**
0%	Pre-Peak	0.814	−0.262
8%	Pre-Peak	1.600	−1.140
16%	Pre-Peak	1.700	−0.587
27%	Pre-Peak	1.470	−0.626
60%	Pre-Peak	0.331	−2.290
0%	Peak	0.838	−0.146
8%	Peak	−1.870	−1.460
16%	Peak	−0.170	−0.451
27%	Peak	2.330	2.070
60%	Peak	−0.965	−0.451
0%	Post-Peak	−1.620	−0.746
8%	Post-Peak	−1.000	0.373
16%	Post-Peak	−2.280	0.990
27%	Post-Peak	0.068	3.110
60%	Post-Peak	−1.250	1.620

3.3. Patterns of dietary resource use among three nearshore fish species

The diet composition of all three fish species was significantly (PERMANOVA, $p = 0.001$) and comparably (similar F-statistics across species) affected by site during post-peak discharge (Table 5). Fish length was not related to diet composition in any species examined during this post-peak period; crescent gunnel size ranged from 47 to 180 mm (mean ± SD = 133 ± 31 mm; $n = 117$), Pacific staghorn sculpin size ranged from 111 to 338 mm (216 ± 54 mm; $n = 97$), and starry flounder size ranged from 100 to 449 mm (159 ± 60 mm; $n = 38$). As noted earlier, crustaceans comprised the majority of crescent gunnel diets during the post-peak discharge period at all five sites with variable contributions from mollusks and macroalgae among sites (Figs. 3, 6). Pacific staghorn sculpin diet included major contributions from several prey categories across sites, with crustaceans, teleost fishes, macroalgae, and "other" (mostly unidentifiable material) making up the largest proportions of their diets at all five sites. Starry flounder diets were

Table 3

PERMANOVA results comparing prey proportions of crescent gunnel in stomach contents (Iken, 2023) by site (watersheds with varying degrees of glacial cover at the headwaters ranging from 0 to 60%, from Jenckes et al., 2023) and discharge period (both as fixed factors), as well as the interaction between site and discharge period; fish length was included as a covariate. Results show degrees of freedom (df), sum of squares (SS), mean squares (MS), pseudo-F-values, and p-values (P(perm)). The PERMANOVA was run as 999 unique permutations. Significant p-values ($\alpha = 0.05$) are noted in bold (Primer-e V7 software, Clark and Gorley, 2015).

Source	df	SS	MS	Pseudo-F	P(perm)
Length	1	3454.00	3454.00	5.22	**<0.01**
Site	4	10,280.00	2569.90	3.89	**<0.01**
Discharge	2	9394.10	4697.00	7.10	**<0.01**
Site x Discharge	8	16,537.00	2067.20	3.13	**<0.01**

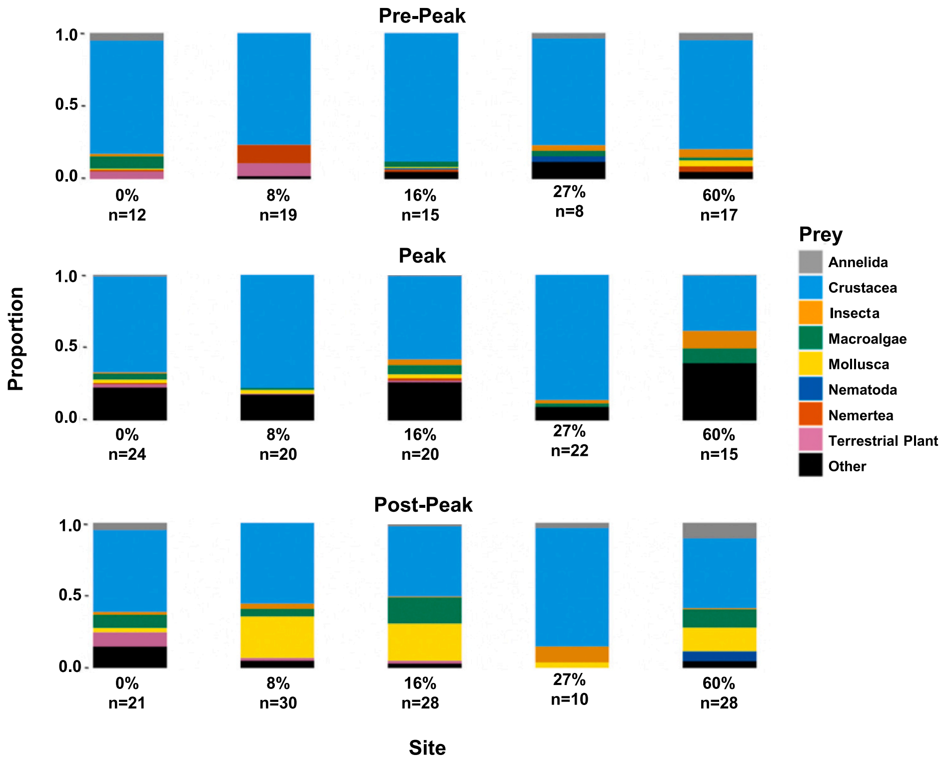

Fig. 3. Relative proportions of prey categories from stomach content analysis of crescent gunnel during pre-peak, peak, and post-peak discharge periods at sites varying in the percent glacial cover, ranging from 0 to 60% (Jenckes et al., 2023). Sample sizes are given for each site-discharge combination. Data available in Iken (2023).

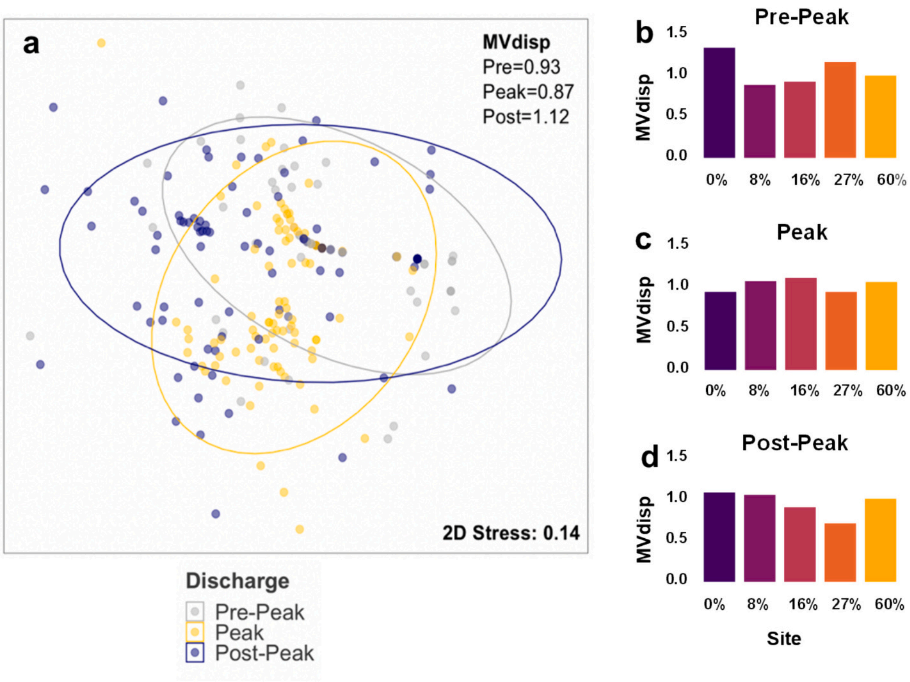

Fig. 4. Non-metric multi-dimensional scaling (nMDS) plot showing crescent gunnel diet composition collected during three glacial discharge periods: pre-peak, peak, and post-peak (a). All sites (0–60% glacial cover; Jenckes et al., 2023) were combined by discharge period. Ellipses represent 95% confidence level for a multivariate t-distribution. Multivariate dispersion (MVdisp) values for the three discharge periods are listed in the top right corner. Mvdisp values for each site (0–60% glacial cover) for each of the three discharge periods are plotted as bar graphs b = pre-peak, c = peak, and d = post-peak. Sample sizes as in Fig. 3 and data available in Iken (2023).

Table 4
PERMANOVA table of results comparing stable carbon and nitrogen isotope values of crescent gunnel liver tissue (Iken and Schloemer, 2022), by site (estuaries with varying degrees of watershed glacial cover ranging from 0 to 60%; Jenckes et al., 2023) and discharge period (pre-peak, peak, post-peak). Fish length (mm) was included as a covariate. Results show degrees of freedom (df), sum of squares (SS), mean squares (MS), pseudo-F-values, and p-values (P (perm)). The PERMANOVA was run as 999 unique permutations. Significant p-values ($\alpha = 0.05$) are noted in bold (Primer-e V7 software, Clarke and Gorley, 2015).

Source	df	SS	MS	Pseudo-F	P(perm)
Length	1	15.82	15.82	5.20	**<0.01**
Site	4	182.89	45.72	15.03	**<0.01**
Discharge	2	180.57	90.29	29.68	**<0.01**
Site x Discharge	8	52.58	6.57	2.16	**<0.01**

primarily mollusks and “other” (mostly unidentifiable material) in their stomachs, with crustaceans prominent at the 16% glaciation site, but diet composition varied greatly among sites (Fig. 6). This diverse diet in starry flounders was reflected in the largest niche width (MVdisp = 1.14) compared to those in crescent gunnels (MVdisp = 0.98) and Pacific staghorn sculpins (MVdisp = 1.01) when all sites were combined (Fig. 7a). In addition, trophic niche width (MVdisp) across sites did not seem to increase or decrease in a linear fashion relative to the glacial gradient for crescent gunnel or Pacific staghorn sculpin (Fig. 7b–d). Starry flounder niche width did increase at sites with higher glacial cover, but sample sizes were only adequate for this analysis at three of the five sites (0%, 16%, 27%, Fig. 7d).

Site was a significant predictor of stable carbon and nitrogen isotope values of liver tissue with fish length included as a covariate for each of the species (PERMANOVA, $p < 0.01$) (Table 6). Length as a covariate was a significant predictor of stable isotope values for crescent gunnel and Pacific staghorn sculpin, but not for starry flounder. Site had a larger influence on the stable isotope composition of crescent gunnel (pseudo-F = 9.57) and starry flounder (pseudo-F = 9.48) than Pacific staghorn sculpin (pseudo-F = 2.69). Pacific staghorn sculpin generally had higher average δ^{15}N values compared with crescent gunnel and starry flounder, which had similar δ^{15}N values to each other (Fig. 8a). All three species had similar isotopic trophic niche width, measured as SIdisp, when all sites were combined (Fig. 8a). No specific trend relative to the glacial cover of the sites was observed for either crescent gunnel or starry flounder trophic niche width based on SIdisp (Fig. 8b–d), while SIdisp for Pacific staghorn sculpin peaked at the 27% mid-glacial cover site.

The effect of environmental drivers on the diet composition from stomach content analysis of the three fish species was extremely weak. The best combination was with the dynamic estuary variables turbidity at 50 m and standardized discharge volume, and the static watershed characteristics slope and river length ($\rho = 0.08$, BEST-BIOENV analysis). Turbidity at 50 m (dynamic variable) and the static watershed characteristics slope, percent vegetation and river length resulted in the highest correlation with the stable carbon and nitrogen isotope values of the three fish species ($\rho = 0.361$, BEST-BIOENV analysis).

4. Discussion

A better understanding of the trophic ecology of glacially influenced, high-latitude estuaries may inform management about ecological changes related to climate warming. Our space-for-time substitution study design used a natural gradient in glacial coverage of adjacent watersheds to study the impact of various levels of glacial cover on nearshore fish diet. In addition, we also included repeated sampling over the course of the summer to identify changes in trophic ecology across discharge periods within these glacial systems. Contrary to our expectation, we found more evidence of shifts in dietary resource use across the discharge periods within an estuary than among estuaries associated with different glacier cover watersheds. This result indicates that the amount of glacial cover of a watershed itself is not a useful metric, or direct driver, of dietary resource use of nearshore fishes during the study period (2020–2021). As glaciers tend to melt from the surface and the

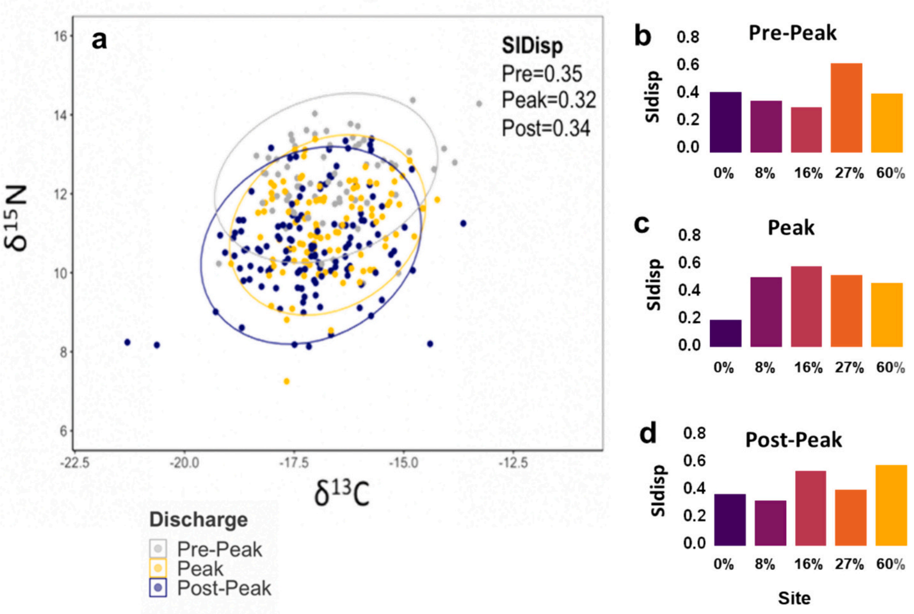

Fig. 5. Stable carbon and nitrogen isotope biplots of crescent gunnel liver tissue (Iken and Schloemer, 2022) over three discharge periods (pre-peak, peak, post-peak) (a). Ellipses represent 95% confidence level for a multivariate t-distribution. Isotopic dispersion (SIdisp) is listed in the top right corner. SIdisp values for each site (0–60% glacial cover; Jenckes et al., 2023) for each of the three discharge periods are plotted as bar graphs b = pre-peak, c = peak, and d = post-peak. Sample sizes were pre-peak: 0% *n* = 11, 8% *n* = 19, 16% *n* = 14, 27% *n* = 8, 60% n = 14, peak: 0% *n* = 24, 8% *n* = 21, 16% n = 19, 27% *n* = 22, 60% *n* = 15, post-peak: 0% *n* = 13, 8% *n* = 20, 16% *n* = 17, 27% n = 14, 60% *n* = 18.

Table 5
PERMANOVA table of results comparing stomach content composition (Iken, 2023) of crescent gunnel, Pacific staghorn sculpin and starry flounder by sites, which consist of estuaries with varying degrees of glacial cover (from Jenckes et al., 2023) at the headwaters ranging from 0 to 60% (all during the post-peak discharge period). Fish length (mm) was included as a covariate. Results show degrees of freedom (df), sum of squares (SS), mean squares (MS), pseudo-F-values, and p-values (P(perm)). The PERMANOVA was run as 999 unique permutations. Significant p-values (α = 0.05) are noted in bold (Primer-e V7 software, Clark and Gorley, 2015).

Source	df	SS	MS	Pseudo-F	P(perm)
Crescent gunnel					
Length	1	1782.30	1782.30	2.10	0.13
Site	4	85,652.00	848.04	4.07	**<0.01**
Pacific staghorn sculpin					
Length	1	1439.80	1439.80	1.69	0.18
Site	4	14,516.00	36,290.00	4.25	**<0.01**
Starry flounder					
Length	1	1654.30	1654.30	2.07	0.12
Site	4	15,700.00	3925.00	4.90	**<0.01**

edges (Rossini et al., 2018), the percent glaciation alone may not be a suitable representation of the complex effects and interactions this melt and flow through the watershed has on the downstream estuary. Instead, some of the static environmental factors associated with glaciated watersheds and the dynamic variables in the downstream estuaries were important predictors of fish trophic resource use. Static drivers such as vegetation cover, river length, and slope can determine the mobilization of terrestrial nutrients to support estuarine production. Dynamic drivers (temperature, salinity, discharge, turbidity) can influence fish foraging by affecting their metabolic rates, the prey field, or visibility at foraging locations. Strong seasonal changes in these dynamic variables can then explain the significant effect of discharge period on dietary resource use, especially of resident crescent gunnels. The overall similar patterns in trophic niche width across all sites during the discharge periods suggest that discharge conditions create a wide range and overlap of environmental conditions at all sites. This aligns with ecological theory that strong seasonality maintains diversity (here: trophic diversity) and allows locations that appear to offer different habitat conditions to maintain similar food web structure (Livingston et al., 1997; McMeans et al., 2020).

We had originally hypothesized that the glacial cover of a watershed would be related to the diet and trophic niche width of nearshore fish species, because larger glacial cover could indicate more discharge into the estuarine system. Possible effects on fish diets could then be related to associated factors such as cooler water temperatures, lower salinity, less terrestrial vegetation, and differences in terrestrial nutrient inputs and production (Arimitsu et al., 2017; Whitney et al., 2017). This hypothesis was not supported, as increasing glacial cover of a watershed did not systematically relate to any fish diet metrics examined. Estuarine processes of a watershed are more complex than can be represented by glacial cover alone (St. Pierre et al., 2022; Jenckes et al., 2023). Accordingly, the static or the dynamic variables included in our study also were not systematically related to glacial coverage. For example, even when corrected for watershed area, standardized discharge was much higher during the peak and post-peak periods at the 27% than the 60% glacial cover site despite having half the area of glacial cover. As the geometry of a glacier (surface area and edge length) influences glacier melt the most, the actual glacial area rather than the percent glaciation might have been more informative. Similar to our study results, glacial cover in Southeast Alaska only marginally influenced the diet of estuarine fish species (Whitney et al., 2018), again supporting the idea that glacier cover alone is not a good representation of the complex influences of the glaciated watershed on downstream estuarine conditions. Our results are also similar to lower-trophic level invertebrate diets within the same study watersheds in Kachemak Bay; invertebrate diets were driven by a combination of river length, slope, and percent vegetation, and estuarine characteristics, including turbidity, instead of glacial cover of the watersheds (Schloemer et al., 2024). Similarly, benthic invertebrate diets in Southeast Alaska estuaries were related to forest cover in addition to overall glacial cover of the watersheds

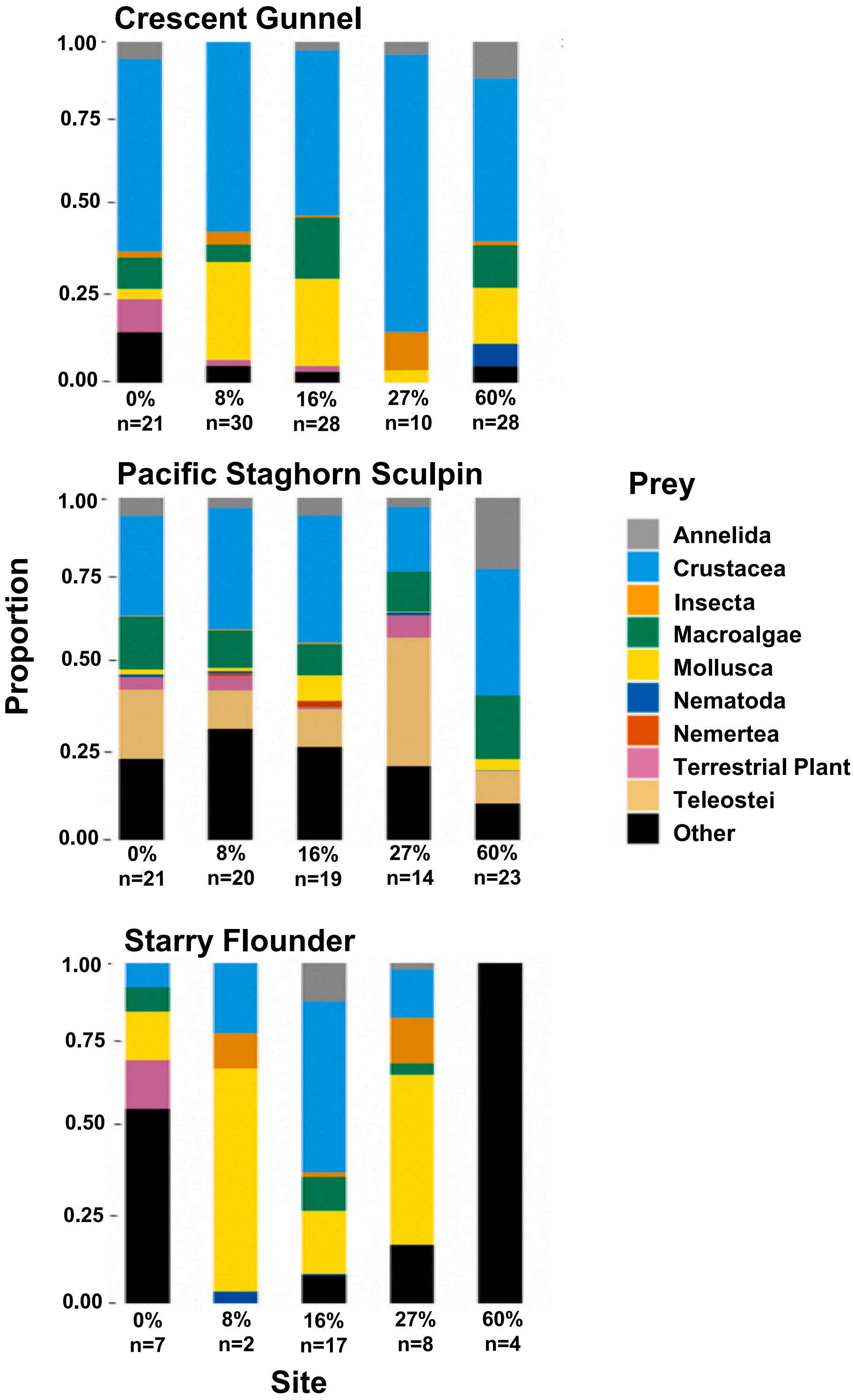

Fig. 6. Relative proportions of major diet categories of crescent gunnel, Pacific staghorn sculpin, and starry flounder during the post-peak discharge period at sites with varying degrees of glacial cover (0–60%; Jenckes et al., 2023). Sample sizes are given for each site and species and data available in Iken (2023).

(Whitney et al., 2018). Watershed characteristics of vegetation, river length, and slope, in particular, play a role in the mobilization and weathering of organic matter, as well as the input of cold and turbid freshwater into the downstream estuaries. Fishes are commonly a part of a benthic, detrital pathway in estuaries (e.g., Vander Zanden and Vadeboncoeur, 2002; Akin and Winemiller, 2006), so that mixing of multiple organic matter sources from glacial discharge in the detrital pool may complicate the detection of a glacial signal in the estuaries for fishes such as the species included in this study and their prey. In particular, such detrital mixing could obscure if the organic matter input from vegetation was part of a glaciated or a non-glaciated system, which differ in the quantity and quality of organic matter input into the downstream estuary (Pain et al., 2020). In addition to detrital mixing, the highly dynamic hydrographic conditions in the study region (strong tides, circulation; Muench et al., 1978; Johnson, 2021) may have muted any glacial effects in the estuaries.

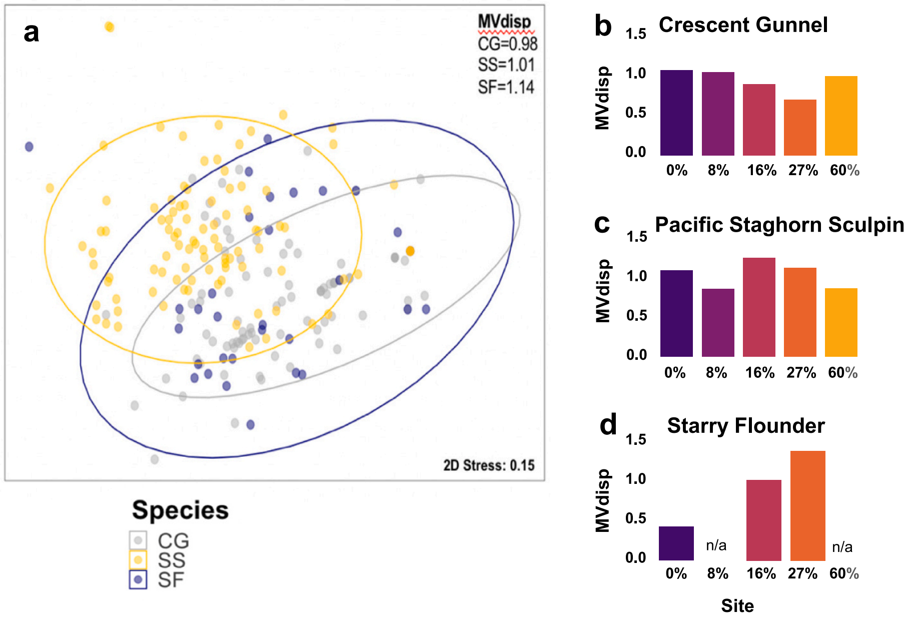

Fig. 7. Non-metric multi-dimensional scaling (nMDS) plots for diet composition based on stomach contents among three nearshore fish species, crescent gunnel (CG), Pacific staghorn sculpin (SS), and starry flounder (SF). All sites (0–60% glacial cover; Jenckes et al., 2023) were combined by fish species. Ellipses represent 95% confidence level for a multivariate t-distribution. Multivariate dispersion (MVdisp) values for each species are listed in the top right corner. MVdisp values for each species by site (0–60% glacial cover) are plotted as bar graphs b = crescent gunnel, c = Pacific staghorn sculpin, and d = starry flounder. n/a indicates insufficient sample size to calculate MVdisp. Sample sizes as in Fig. 6 and data available in Iken (2023).

Table 6
PERMANOVA table of results comparing carbon and nitrogen stable isotope values of crescent gunnel, Pacific staghorn sculpin and starry flounder (Iken and Schloemer, 2022) by site, which consist of estuaries with varying degrees of glacial cover at the headwaters and are denoted by their percent glacial cover (0–60%; Jenckes et al., 2023). Fish length (mm) was included as a covariate. Results show degrees of freedom (df), sum of squares (SS), mean squares (MS), pseudo-F-values, and p-values (P(perm)). The PERMANOVA was run as 999 unique permutations. Significant p-values ($\alpha = 0.05$) are noted in bold (Primer-e V7 software, Clark and Gorley, 2015).

Source	df	SS	MS	Pseudo-F	P(perm)
Crescent gunnel					
Length	1	14.52	14.52	4.31	**0.01**
Site	4	129.01	32.25	9.57	**<0.01**
Pacific staghorn sculpin					
Length	1	171.94	171.94	14.50	**<0.01**
Site	4	127.38	31.84	2.69	**0.02**
Starry flounder					
Length	1	5.22	5.22	2.44	0.09
Site	4	81.26	20.32	9.48	**<0.01**

Discharge period had a strong influence on the trophic ecology of crescent gunnel. Diet composition became more varied and trophic niche width became wider from pre-peak to peak and post-peak discharge periods. Seasonal changes in diet are typical for fishes in temperate regions, where a broadening of trophic niche width has been linked to seasonal variation in prey distribution and abundance (Akin and Winemiller, 2006) and in organic matter sources supporting trophic pathways (Neves et al., 2020; St. Pierre et al., 2022). Harpacticoid copepods and amphipods were the dominant prey items for crescent gunnel during pre-peak and peak discharge periods, while other diet items such as mollusks and macroalgae increased during post-peak discharge. Trophic diversification has been observed in other estuarine systems, where increased resource availability during periods of higher river flow resulted in increased trophic niche width of fish species (Akin and Winemiller, 2006; Howe and Simenstad, 2015; McMeans et al., 2020). This may be reflective of a change in the prey community composition in the nearshore, mostly driven by the seasonal recruitment of many invertebrate and macroalgal taxa (McCabe and Konar, 2021). Additionally, the prey community could change seasonally based on an increased influx of freshwater fauna into the estuaries during high flow conditions (Williams and Williams, 1998).

The effect of discharge period on crescent gunnel stomach content composition can also be related to the specific environmental conditions encountered during the three discharge periods. We found that the standardized discharge rate, salinity, and temperature were significant drivers of gunnel diet composition across the three discharge periods. Typically, salinity decreased after the pre-peak period, consistent with the increase in freshwater discharge. While we expected temperatures to drop with higher discharge, temperatures actually increased and peaked during the peak discharge period at all sites. It should be noted that resolution of averaged temperatures over a 2-month time period for each of the discharge periods may not reflect the occurrence of periodically high or low temperatures associated with particularly high or low discharge events. It is likely, however, that the increase in temperatures with discharge periods are a result of seasonal warming, which appears to supersede a possible cooling effect from the glacial discharge. Therefore, the changes in trophic resource use across discharge periods may be associated with higher temperatures during the late summer, causing a higher metabolic demand in poikilotherm fishes, resulting in a more varied diet (Elliott, 1976; Alfonso et al., 2020).

The trophic position of crescent gunnel decreased about half a trophic level (1.6‰) from pre-peak to post-peak discharge periods, based on stable isotope data. This decrease in trophic level could be explained by the observed increase of macroalgae in crescent gunnel stomachs during that time frame, i.e., increased consumption of lower-trophic level primary producers and, as such, feeding on a lower trophic level. It should be noted, however, that actual assimilation of macroalgal material is often temperature-limited in temperate fish species (Floeter et al., 2005). A more likely explanation might be a change in the isotope values of the prey consumed by the crescent gunnels. This would

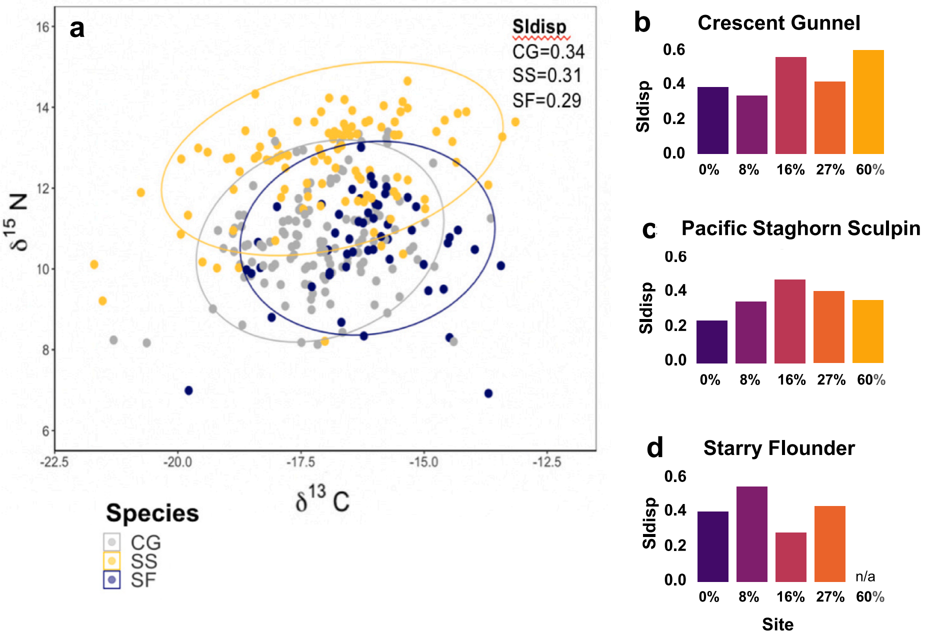

Fig. 8. Stable carbon and nitrogen isotope biplot, including all samples of crescent gunnel (CG), Pacific staghorn sculpin (SS), and starry flounder (SF) from the post-peak discharge period (a). Ellipses represent 95% confidence level for a multivariate t-distribution. Isotopic dispersion (SIdisp) is listed in the top right corner. SIdisp values for fish species at each site (0–60% glacial cover; Jenckes et al., 2023) are plotted as bar graphs b = crescent gunnel, c = Pacific staghorn sculpin, and d = starry flounder. n/a indicates insufficient sample size to calculate SIdisp. Samples sizes were: crescent gunnel: 0% n = 13, 8% n = 20, 16% n = 17, 27% n = 14, 60% n = 18, staghorn sculpins: 0% n = 21, 8% n = 21, 16% n = 19, 27% n = 18, 60% n = 24, starry flounders: 0% n = 8, 8% *n* = 12, 16% n = 20, 27% *n* = 9, 60% *n* = 3. Data available from Iken and Schloemer (2022).

indicate a diet shift occurring at lower trophic levels that, ultimately, is reflected in a shift in the isotope composition of the fish consumer. In the same study region, and across the same discharge periods as the present study, the diets of intertidal periwinkles (*Littorina* spp.) and limpets (*Lottia* spp.) shifted from predominantly macroalgal-fueled during the pre-peak discharge period, to predominantly POM-fueled (i.e., phytoplankton) during peak and post-peak discharge periods (Schloemer et al., 2024). A corresponding decrease in δ^{15}N of the prey may then be reflected in a decrease in δ^{15}N values in crescent gunnels.

Changes in trophic level in estuarine fish consumers have often been observed in relation to seasonal changes in river flow regimes (e.g., Carlier et al., 2007; Vinagre et al., 2011; Olin et al., 2013; Howe and Simenstad, 2015). Accordingly, we found standardized discharge to be an important driver of crescent gunnel stable isotope values. Increased freshwater flow from river discharge (including glacial discharge) may change the flushing of the estuary, thus increasing food web connectivity with surrounding habitats. If watershed drainage occurs through vegetated areas, the resulting discharge also carries nutrients such as dissolved nitrogen (Hood et al., 2009) and lithogenic minerals (Calleja et al., 2017; St. Pierre et al., 2022) into the estuary. Longer rivers increase the mobilization potential and type of nutrients and carbon stores, which is known to influence watershed primary production (Sutfin et al., 2016). This, in turn, could cascade through the food web to higher trophic level fish consumers. This may be a reason for the significant effect of discharge volume on the stable isotope composition of crescent gunnels we observed. Such seasonal effects can be expected to be particularly strong in high-latitude systems like the glacially influenced estuaries in Kachemak Bay, where discharge rates vary considerably across the melting season (Curran and Biles, 2021; Jenckes et al., 2023).

The morphology (e.g., body size, gape size), behavior, and life history stages of the three nearshore fish species investigated here likely played a role in the observed interspecific variability in dietary resource use. For example, starry flounder had the broadest array of prey in stomach contents among the three species, indicating a diverse diet and high individual variation in prey composition. Starry flounder are a highly mobile species, known for moving in and out of the nearshore system, more so than crescent gunnel and Pacific staghorn sculpin (Dean et al., 2000). This movement across coastal habitats would expose them to more diverse prey availability, which is a known mechanism that contributes to the food web connectivity and stability in coastal systems (Guest and Connolly, 2005; Howe and Simenstad, 2015). This difference in mobility and reliance on various adjacent coastal habitats by the three species may be the reason for the generally very low explanatory power of the local environmental variables on diet composition based on stomach content analysis. Turbidity was identified as one of the environmental metrics that influenced, albeit weakly, the diet composition based on stomach content data in the three fish species. High turbidity decreases the foraging success of visual predators in estuaries, such as fishes (Lunt and Smee, 2015). Hence, more resident fish species such as crescent gunnel may be more restricted in their prey spectrum and their feeding radius, leading to overall smaller trophic niche width, compared with the more mobile species such as starry flounder.

The three fish species differed in their tropic level, based on stable isotope data. Pacific staghorn sculpin fed at a higher trophic level, as shown by higher δ^{15}N values, compared to crescent gunnel and starry flounder. This is likely related to the sizeable proportion of fish prey contributing to Pacific staghorn sculpin diets in this study (also see Whitney et al., 2017), possibly in relation to the large gape size of Pacific staghorn sculpin that allows them to consume larger prey (e.g., Gill and Hart, 1994). Crescent gunnel and starry flounder stable isotope values suggested that these species fed at similar trophic levels (similar δ^{15}N range), but crescent gunnel may be part of slightly different trophic pathways (different δ^{13}C ranges). Crescent gunnel are highly sedentary, often remaining within the estuarine intertidal, even with the 8-m tidal exchanges in the coastal Gulf of Alaska (Muench et al., 1978; Dean et al., 2000). As mentioned above, this strong site fidelity along the shoreline likely contributes to a more locally-sourced diet compared to other species that move beyond intertidal habitats. In crescent gunnel, this site fidelity may be reflected in diets that contain prey that could depend on terrestrially-sourced organic matter pathways (more negative δ^{13}C) (Peterson, 1999; Whitney et al., 2018; Possamai et al., 2020). Overall though, the terrestrial input into trophic pathways to fishes seemed relatively low, despite some ingestion of terrestrial plant material and insects, as benthic invertebrate species that serve as fish prey in these same estuarine systems did not rely significantly on terrestrial matter input (Schloemer et al., 2024). Contrary to the stomach content composition of the three fish species, their stable isotope values were more strongly influenced by a combination of dynamic and static environmental drivers. This likely reflects the more integrated view of stable isotope measures, which will be more reflective of the, at least part-time, overlap in glacial estuary use by the three fish species. It is possible that, in addition to the use of different coastal habitats, these fish species can select different sub-habitats in the glacial estuaries based on environmental conditions during the post-peak discharge period. This could explain the effects of turbidity on stable isotope composition, where the more mobile species may be able to move to areas of the glacial estuary that provide them with better foraging conditions.

5. Conclusion

A better understanding of fish trophic ecology in glacially influenced watersheds may inform management decision making in light of ongoing and accelerating climate warming at higher latitudes, and increasingly frequent marine and terrestrial heat waves (Frölicher et al., 2018; Harris et al., 2018; Perkins-Kirkpatrick and Lewis, 2020) causing significant loss of glacier mass (Larsen et al., 2015). The similar trophic structure across study sites indicated that the current range of conditions experienced in the glacially influenced estuaries have some influence on fish diet, but mostly through the seasonal progression associated with glacial discharge. It appears that the discharge periods created a wide range of environmental conditions at each site with more overlap in conditions among the sites than anticipated. Based on the environmental conditions in the downstream estuaries, major shifts in the habitat quality for estuarine fish with glacier loss seem unlikely. It must be noted, however, that our study period did not include abnormally warm or dry conditions (e.g., heatwaves or drought); therefore, we cannot rule out the possibility that glacial coverage and associated environmental variables might emerge as an important driver in more extreme climate years or with future conditions. We hypothesize that more nuanced watershed characteristics rather than a general percent glacial cover are better metrics in understanding nearshore fish diet. For example, total glacial cover area or total vegetation cover rather than proportional measures might be more informative. The specific inputs of nutrients from a combination of watershed characteristics such as vegetation, river length and slope of a watershed could be the focus of future studies to better understand the bottom-up drivers in these watersheds that can affect fish diet. Crescent gunnel may be an ideal focal estuarine fish species for such future studies due to their relatively sedentary lifestyle, making them good indicators of local conditions and variability.

CRediT authorship contribution statement

Lindsey Stadler: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Kristen Gorman:** Writing – review & editing, Supervision, Software, Methodology, Funding acquisition, Formal analysis. **Vanessa von Biela:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Conceptualization. **Andrew Seitz:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis. **Katrin Iken:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Link to open access data are provided within the manuscript. Where data are not pubised they are presented as part of the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2024.152022.

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