Aquatic Invasions 2025 Volume 20, Issue 1: 153–173

Research Article

Consumption pressure in estuaries peaks at intermediate salinities

Catherine E. de Rivera[1], Amy A. Larson[1], Benjamin G. Rubinoff[2,3], Luna R. Soto[1], Seth L. Wright[1], Edwin D. Grosholz[2], Gregory M. Ruiz[4], Andrew L. Chang[4,5]

1 *Department of Environmental Science & Management, Portland State University, Portland, Oregon, USA*
2 *Department of Environmental Science and Policy, University of California, Davis, California, USA*
3 *Washington Department of Fish & Wildlife, 1111 Washington St. SE, Olympia, WA 98501, USA*
4 *Smithsonian Environmental Research Center, Edgewater, Maryland, USA*
5 *Estuary & Ocean Science Center, San Francisco State Romberg Tiburon Campus, 3150 Paradise Drive, Tiburon, CA 94920, USA*
Corresponding author: Catherine E. de Rivera (derivera@pdx.edu)

OPEN ACCESS

Academic editor: Amy Fowler
Received: 20 January 2024
Accepted: 4 February 2025
Published: 15 April 2025

Co-Editors' Note: This study was first presented at the 11th International Conference on Marine Bioinvasions held in Baltimore, Maryland, USA, May 15–19, 2023 (http://www.marinebioinvasions.info). Since their inception in 1999, the ICMB meetings have provided a venue for the exchange of information on various aspects of biological invasions in marine ecosystems, including ecological research, education, management and policies tackling marine bioinvasions.

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Abstract

The nature and strength of biotic interactions change along stress gradients, but the importance of these interactions across estuarine gradients is under studied. Here, we examined how consumption varies across estuarine salinity gradients by deploying standardized baits ('squidpops') to measure consumption pressure along the gradients of five estuaries in Oregon, USA. The relationship between consumption and stress was nonlinear: consumption pressure peaked slightly at mid salinity and decreased at low salinity, especially as temperature increased, in the five estuaries studied. This finding does not support either of two existing models for consumption across gradients, including the Consumer Stress Model and a consumer extension of the Salinity Range Model. The pattern of consumption aligns better with the Prey Stress Model or the Invasion Stress Model, and the latter predicts that successful invasion by stress-tolerant predators extends consumption pressure further upstream along estuarine stress gradients than the Consumer Stress Model. Although these estuaries have been invaded by the crab *Carcinus maenas*, our catch data did not support the expected greater numbers of these invasive, stress-tolerant predators mid estuary or an expected relationship with native predators, as *C. maenas* was trapped in low abundance throughout each estuary. While our catch data did not directly support the Invasion Stress Model, we found that individual *C. maenas* ate more squid in lab experiments when at intermediate salinities than fresher salinities. Overall, our field and lab results suggest consumption peaked at mid estuary, at intermediate to high stress, in these temperate estuaries. The Invasion-Stress Model needs more testing to evaluate whether it, the Prey Stress Model, or a new model is best supported and can predict ecological impacts from changes in precipitation patterns and biological invasions, as well as other environmental stressors for estuarine food webs.

Key words: *Carcinus maenas*, consumer-stress relationship, estuarine gradient, invasion-stress hypothesis, salinity gradient, squidpops, stress gradient

Citation: de Rivera CE, Larson AA, Rubinoff BG, Soto LR, Wright SL, Grosholz ED, Ruiz GM, Chang AL (2025) Consumption pressure in estuaries peaks at intermediate salinities. In: Fowler A, Robinson T, Bortolus A, Canning-Clode J, Therriault T (Eds) Proceedings of the 11th International Conference on Marine Bioinvasions. Aquatic Invasions 20(1): 153–173. https://doi.org/10.3391/ai.2025.20.1.151447

Introduction

The strength and effects of biotic interactions change across a variety of stress gradients including elevation gradients (Preszler and Boecklin 1996; Callaway et al. 2002), latitudinal gradients (Pianka 1966; Rodemann and Brandl 2017; Musrri et al. 2019), and intertidal gradients (Connell 1961; Dayton 1971; Menge 1976). Higher-order consumers in particular are major modulators of species abundance, especially in aquatic communities (Sih et al. 1985; Shurin et al. 2002; Heck and Valentine 2007), and the strength of their effects changes with stress (Silliman and He 2018). Successful invasion and establishment by stress-tolerant species may change consumer-stress relationships and community structure along stress gradients, including in estuaries (Rubinoff and Grosholz 2022).

Estuaries are highly productive ecosystems with important foundational habitats such as salt marshes, mangroves, and eelgrass beds, as well as important human infrastructure such as ports, marinas and mariculture. Gradients of salinity, temperature, turbidity, and other variables characterize these dynamic systems and vary as a function of distance from freshwater and ocean sources (Pritchard 1967). Salinity and temperature are of particular ecological importance as they influence physiological functions and can vary drastically from the upper to the lower estuary. Because most organisms found in estuaries are marine in origin, upper reaches of estuaries near the freshwater source are the most stressful to the majority of (though not all) estuarine organisms, and the diversity nadir often falls around 5–8 PSU (Remane and Schlieper 1971). As a result, diversity is predicted to continuously decline from the marine and freshwater ends to mid-estuary, but this prediction does not consider possible changes resulting from species interactions or invasions by non-native species (Remane and Schlieper 1971; Attrill 2002).

Estuaries are some of the most invaded ecosystems in the world (Ruiz et al. 1997; Ruiz et al. 2000), and many of the successful introduced estuarine species are stress-tolerant (Crooks et al. 2011; Lenz et al. 2011; McKnight et al. 2021). Estuarine gradients can change the strength of species interactions such as predation, particularly where non-native predators are present (Kimbro and Grosholz 2006). Previous models such as the Consumer Stress Model suggest opposing effects between predation and physical or physiological stressors, whereby predators are more susceptible to stress than prey, so community structure is driven by physical processes in high stress environments versus consumer interaction in low stress environments (Menge and Sutherland 1987, Fig. 1A). This model suggests that consumption pressure would decrease with increasing stress. In contrast, the Prey Stress Model is an additive model in which predation is intensified across increased stress levels because prey are more affected by high stress than predators are (Menge and Olson 1990; Silliman and He 2018, Fig. 1B). This model suggests that consumption pressure would increase with increasing stress. The role of competition also can vary across ecosystems and at different trophic levels, but competition is thought to be of less importance in the soft bottom habitats of estuaries than in hard substrata communities (Seitz 1996; 2011).

One test of these models in estuaries favored the Consumer Stress Model. Sites further up estuary had lower trophic cascade strengths than ones toward the mouth due to decreased predator abundances in the higher stress, up-estuary sites (Cheng and Grosholz 2016). In contrast, in the same California estuary, a direct assessment of the effect of stress and predation, including non-native species, suggested a third model, hereafter called the Invasion Stress Model: Invasion by

stress-tolerant predators and prey can create a pattern that generally follows the Consumer Stress Model but expands the importance of predation much further along the estuarine gradient (Rubinoff and Grosholz 2022, Fig. 1C). The Invasion Stress Model further considers that (a) many invading species have relatively high stress tolerance (McKnight et al. 2021) and (b) introduced marine species are most common and diverse in estuaries than the outer coast (Chang 2009; Preisler et al. 2009; Ruiz et al. 2009; Zabin et al. 2018). A fourth explanatory model shows the variation in salinity as a driver of community diversity (Attrill 2002). If the physiological stress of high salinity variation reduces consumer abundance or consumption rates, then consumption pressure would decline to a nadir at the greatest range of salinities, which occurs mid-estuary (Fig. 1D).

We therefore set out to test in five Oregon (Pacific Northwest USA) estuaries whether consumption of standardized baits decreases along estuarine gradients in line with the Consumer Stress Model, whether there is a delayed decline with distance into an estuary aligned with the Invasion Stress Model, whether it increases along the gradient as predicted by the Prey Stress Model, or whether consumption dips mid estuary, where salinity fluctuations are greatest and diversity is lowest (Fig. 1). Given the invasion across these estuaries by the stress-tolerant predator *Carcinus maenas*, the European green crab or five-spine shore crab, we predicted the pattern of consumer pressure would follow the Invasion Stress Model in all estuaries. *Carcinus maenas* has invaded coastlines of several continents (Darling et al. 2008; Fofonoff et al. 2018). It tolerates a wide range of salinity and temperature values (Leignel et al. 2014), but often is common mid-estuary and in shallow estuarine areas along the west coast of North America. Its habitat use can be restricted due to predation at high salinities by the larger, native and more fully marine rock crabs *Cancer productus* and *Romaleon attenarium* (Hunt and Yamada 2003; Jensen et al. 2007). However, where it occurs, *C. maenas* can exert strong predation pressure on clams and crabs, impacting their populations (Grosholz et al. 2000, de Rivera et al. 2011). We therefore aimed to examine the relationship between consumption pressure and crab abundance, exploring if *C. maenas* extends further along the salinity gradient than the native predators in these estuaries. If stress tolerant *C. maenas* are responsible for a high consumption rate in the mesohaline (mid-salinity) parts of the estuary, we would expect at least one of the following three scenarios would be found: 1) its catch is predictive of consumption in statistical models; 2) *C. maenas* are found throughout salinities and eat more in mesohaline than marine or oligohaline conditions; or 3) *C. maenas* make up a larger portion of the consumer community in mesohaline waters. Finally, in addition to field-based measures of consumption and crab abundance along estuarine salinity gradients, we also conducted laboratory experiments to measure how consumption rate of individual *C. maenas* varied by salinity. This experimental approach provides a direct test of mechanism.

We used salinity (short term average and variation) rather than geographic location within the estuary to better compare consumer pressure to a biologically relevant environmental condition as well as to enable comparisons across estuaries and over time. This approach recognizes that the specific location of important shifts or threshold in biological interactions along estuarine gradients are likely to vary within an estuary across tidal cycles, seasons, and weather events. We also expect variation across estuaries based on freshwater inflow, depth, flushing rate. In this regard, salinity represents an important physiological stress as well as a proxy measure for other associated environmental variables.

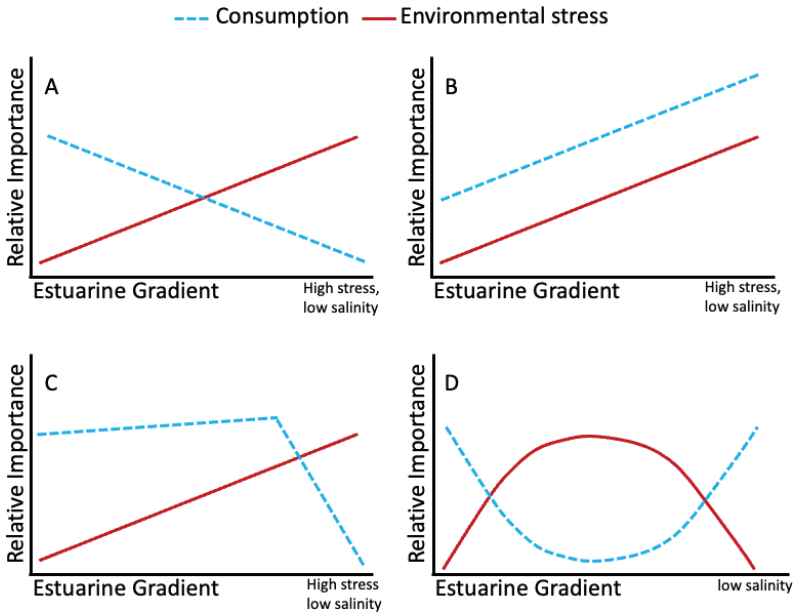

Figure 1. Theoretical predictions on the relative importance of consumption (blue dash) and environmental stress (red solid) in structuring communities, with increasing distance along estuarine gradients (standardized to % of estuarine length), translating to increased physiological stress for marine organisms **A** the Consumer Stress Model (CSM) proposed by Menge and Sutherland (1987) suggests that predation decreases with increasing stress **B** the Prey Stress Model (recreated from Silliman and He 2018, Menge and Olson 1990) suggests that consumption increases with stress **C** the proposed Invasion Stress Model (simplified from Rubinoff and Grosholz 2023) suggests that in systems with introduced species, the effect of consumption is extended further along estuarine stress gradients relative to the CSM (panel 'a') due to shifts from native to non-native predators, but eventually predation declines **D** the Salinity Range Model (Attrill 2002) predicts that areas with the greatest range in salinity, mid estuary, would have the least diversity, while the less variable stretches, near the estuary's mouth and head, would have more consumers.

Methods

We measured consumption pressure using standardized baits deployed across the salinity gradient of five estuaries, which varied in size and freshwater input along the coast of Oregon, USA (Table 1). From north to south these estuaries include Nehalem Bay, Netarts Bay, Salmon River Estuary, Siletz Bay, and Yaquina Bay (Fig. 2). The largest estuary we sampled was Yaquina Bay and the smallest was Salmon River Estuary (Table 1). The most marine dominated estuary was Netarts Bay whereas the others have less tidal exchange and more freshwater input.

We sampled 33 sites across the five estuaries, with 6 to 8 sites per estuary, spanning the estuarine gradient of each. The salinity of these estuaries varies over time and space. We compared across estuaries and time by comparing our survey values on consumer communities at specific salinity values. Towards the mouth, we selected the first access point near the mouth of each bay with stable-enough substrate to retain our sampling gear. Across bays, the average salinity during the sampling time at the sites closest to the mouths ranged from 19.8 to 27.5 PSU (Table 1). Towards the head of the estuary, we aimed for about 7 PSU; however, due to logistical constraints, variation in precipitation, and river flow, once we knew the salinity averages across the low and high tides we were sampling, we found the lows ranged from 3.3 to 11.4 PSU. Sites were each at least 0.5 km from their nearest neighbors, except one pair of sites in Salmon River which were 0.3 km apart.

We measured salinity and temperature just above the benthos using a Pro-2030 YSI (Xylem) handheld sampler or refractometer and thermometer at each visit to each site, taking a minimum of 3 measurements per site (at least a measurement near high tide and two around low tide). These measurements were taken across

Table 1. Study bays: The name, geographic coordinates, size, and range of salinities of the sites we used in each of the five study bays in Oregon, USA.

Location	Latitude, Longitude	Sample dates in main (and supplemental) analyses	Size, hectares[1]	Range of site average salinities, PSU (salinities at alternate dates)	Median (and spread) of salinity ranges of the sites	Distance to head of tide, km
Nehalem Bay	45.6959°N, 123.9144°W	19–21 Jun 2024 (13–15 Sep 2022)	1112.5	3.3–19.8 (16.7–32.7)	12.95 (7.5–22.6)	24.63
Netarts Bay	45.4028°N, 123.9484°W	4–6 May 2023 (5–7 July 2022; 21–23 Apr 2022)	1110.0	9.2–27.0 (20.2–31.2; 0.1–23.9)	25.3 (3.7–29.1)	10.77
Salmon River Estuary	45.0453°N, 124.0011°W	1–3 August 2023 (17–19 August 2022)	177.3	11.35–27 (17.3–30.0)	5.3 (1.3–30.4)	8.10
Siletz Bay	44.9036°N, 124.0083°W	17–19 September 2021 (15–17 August 2022)	591.2	6.1–24.8 (0.17–21.9)	16.4 (0.5–29.6)	39.82
Yaquina Bay	44.61.70°N, 124.0207°W	18–20 July 2022	1751.9	10.2–27.5	4.5 (0–6.1)	41.71

[1]Data on acreage from Oregon Coastal Atlas
[2]. Head of tide, the farthest point upstream where a river is affected by tidal fluctuations, was derived from Oregon Division of State Lands, Engineering March 1989, Heads of Tide for Coastal Streams in Oregon.

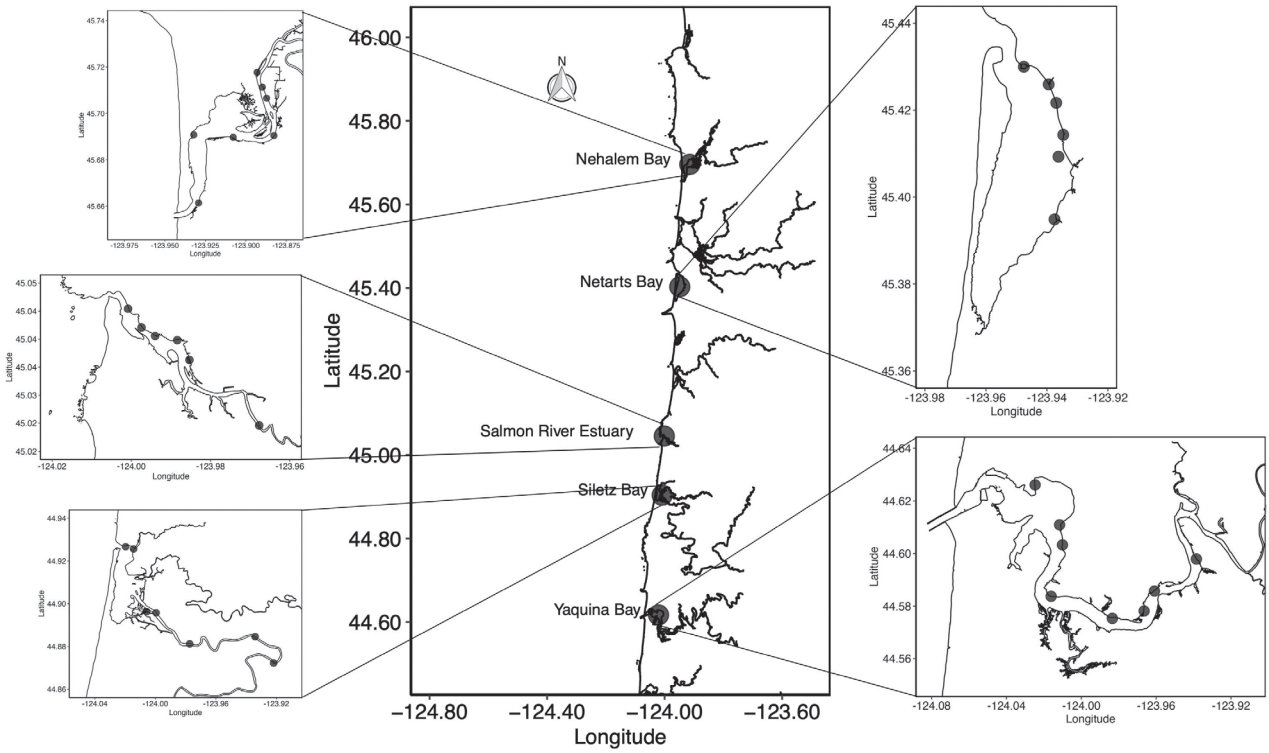

Figure 2. Map showing the five study bays in Oregon, USA and the sites along the bays.

the same 48 hrs in which we sampled the biotic community and consumption pressure. We averaged the readings per site to identify an estimate of the site's salinity at the time of sampling, and also used these readings to determine the variability of the salinity at the site during the 48 hrs of biological sampling.

We sampled from September 2021 through June 2024 in the dry season, late spring and summer (Table 1). We sampled all sites in summer (July 5-Sept 14) 2022, but many of those samplings did not meet our criteria of a salinity range that would allow us to evaluate how consumption varied across the salinity gradient. Our initial criteria included a range of at least 20 PSU, spanning an average high salinity 25–32 PSU through an average low of 5–10 PSU. Obtaining the full

range proved elusive so we settled for a broader set of lows and highs, and a range of at least 15 PSU as long as intermediate sites were dispersed along the gradient (Table 1). We visited sites by foot that were accessible from roads, limiting our access to all salinities of an estuary within a season. We therefore also sampled most of the bays again in late spring through summer in other years to ensure a broader salinity range if our 2022 sampling failed to capture it, and we visited Netarts Bay three times. The dataset with the best salinity spread per bay is described in Table 1.

Arrays of standardized baits provided estimates of relative consumption pressure at each site. Consumers we commonly trapped or saw at the sites included crabs (e.g., *C. maenas*, *Hemigrapsus oregonensis* and *H. nudus*, *Cancer productus*, *Metacarcinus magister*, *Pagurus granosimanus*, and *Pugettia producta*); small fishes (e.g., *Leptocottus armatus*, *Gasterosteus aculeatus*, *Cymatogaster aggregata*, *Pholis ornata* and *Platichthys stellatus*); and also larger predators like seals and sea and shore birds. We followed the published 'squidpops' protocols (Duffy et al. 2015), in which a 1.3 cm diameter round of dried squid mantle secured to a stake serves as a standardized bait. Each array consisted of 20 such squidpops deployed at each site, separated by at least 1 m from the nearest one. We deployed these stakes over open mudflat in the lower intertidal so the baits were just covered by water at the lowest tide and the bottom of the bait was just touching the substrata, allowing easy access to crabs and benthic-feeding fishes. Deploying the baits benthically is a deviation from Duffy et al. (2015), which we did because we were interested in consumption by crabs as well as fishes. In two bays, Netarts and Yaquina, we secured a second piece of squid to the top of each stake, 20 cm above the substrata, so we could compare consumption from bottom-feeders to those feeding a bit higher in the water column.

In all cases, we measured number of squid baits eaten per array after 24 hrs. Following Duffy et al. (2015), we categorized any squid piece that was at least ½ eaten as 'consumed', though > 95% of them were entirely eaten or entirely remaining and most of the rest had > 90% or < 10% consumed. In our initial survey, in Siletz Bay 2021, we checked the baits 1 hr after deployment, but we did not continue that 1 hr check because we recorded very little to no consumption in that timeframe at any of the sites along the bay, and due to logistical constraints especially the flooding tide and resulting greater water depth and turbidity. Since the sites had moderate to high usage by people and were easily accessible from the shore, the potential risk of theft was high, so we chose not to use cameras to film the baits even when the water was clear. However, we opportunistically made direct observations of consumers eating the baits.

In addition to measures of bait consumption, we deployed baited traps and made visual observations to census the crab and fish community across the estuarine gradient, at the same sites and time periods where we measured consumption pressure. We trapped the day before or the day after the consumption assay, with every other site trapped the day before and the other ones after. The standard trapping effort at each of the sites consisted of alternating three minnow traps with 1" openings with three larger Fukui-type collapsible fish traps (also called box traps), with traps separated by at least 20 m from the nearest trap and each separated by at least 40 m from the nearest trap of the same type (e.g., Grosholz et al. 2021; Turner et al. 2016). Traps were baited with sardines or smelt in perforated containers. We checked traps 24 hrs after deployment, identified each trapped individual to species, and recorded the number of individuals caught per species per trap. We also measured carapace width of the crabs. We returned all fish and native crabs immediately and retained *Carcinus maenas*, following Oregon state regulations.

We used laboratory trials conducted at Portland State University, Oregon, to examine the effect of salinity on feeding by comparing the amount of bait eaten by

C. maenas at different salinities. We brought crabs captured from Netarts Bay in May 2023 to lab and held them for a week under a 12 hr light: 12 hr dark cycle at 20 PSU, 15 °C. We fed the crabs and then after waiting 24 hours, we put an experimentally naïve single *C. maenas* (males and females 61.3 ± 13.5 mm CW (mean ± SD)), a piece of available squid, and a piece of squid in a bait box (procedural control) for two hours into each of five replicate 18.9 L tanks for each of three salinities. First, we used 34, 22, and 10 PSU. We then ran five more replicates per salinity, using 20, 15, and 10 PSU to hone in on the salinity where there was a decrease in feeding. All squid was weighed to the nearest 0.1 g before and after the feeding trial. For each assay, we subtracted the average amount of change in mass of the procedural controls (squid in containers) for each salinity from each experimental value.

Statistical analysis

To be able to test the alternate models adequately, we needed to have a range of salinities in each bay. Therefore, we focused our analysis on our sampling with the widest spread of salinities for each bay, even though these data come from different years. We present an analysis of data from all bays from just summer 2022 for a temporally controlled analysis, which suggests similar conclusions, in the Suppl. material 1: table S1).

Our overall approach was to use generalized linear models (GLMs) to assess effects of predictor variables on consumer pressure by adding terms sequentially and comparing the models with AIC, then running a segmented regression on the top model (Table 2), as described below. Consumer pressure was measured by comparing the proportion of the baits that were eaten in each array of 20 deployed baits for our response variable. We needed to test for both a linear and a non-linear relationship between consumption of the baits and salinity in order to examine whether the data aligned with the linear or the non-linear conceptual models we aimed to evaluate. Therefore, predictor variables in our global models included both average salinity (continuous) –key to the Consumer Stress and Prey Stress Models-- and the square of average salinity (continuous), which together allowed us to examine the non-linear relationships between baits eaten and salinity proposed by the Invasion Stress Model and a consumer-version of the Attrill Salinity Range Model. Other predictors in the models were salinity range (continuous), bay (nominal), average temperature (continuous), the interaction between temperature and average salinity, catch per unit effort (CPUE) of the introduced crab *Carcinus maenas* per pair of traps at the site (a box trap paired with a minnow trap; continuous), and also the CPUE of native consumers, i.e. all other trapped crabs and fish combined (continuous). We used catch per pair of traps rather than per individual trap because pairing reduces the zeroes in the data, and b) the two types of traps catch different sizes and species of crabs so are complementary rather than replicated. We used the generalized variance inflation factor (GVIF, as $GVIF^{(1/(2*df))}$ following Fox and Monette 1992) to verify that pairs of the predictor variables were not strongly correlated with each other, and the GVIF values were always < 10, usually < 5 in the models we used.

To explore the relationship between proportion of baits eaten and predictor variables, we used generalized linear models (GLM) with a gamma distribution and log link function (Table 2). We identified the global model and then followed a model selection process using AIC to identify the best fit models derived from it (Johnson and Omland 2004). We report the best fit model and all other models with AIC values within two of the models with the lowest AIC. We evaluated model fit to the data and checked uniformity and dispersion of residuals for the global model using simulation-based tools in the DHARMa package (Hartig 2023).

Table 2. Summary of the statistical tests conducted.

Question	Data subset	Statistical approach	Dependent variable	Independent variables
Do abiotic factors affect consumption across estuarine gradients?	The time period with benthic baits across the broadest salinity range for each bay (Appendix: data from summer 2022)	GLM with gamma distribution and log link, adding terms sequentially and comparing models with AIC	Proportion of baits eaten	Mean salinity; Square of mean salinity; Salinity range; Bay; Mean temperature; Mean temperature × Mean salinity; Catch per unit effort (CPUE) of *Carcinus maenas*; CPUE of native consumers.
Do abiotic factors affect consumption across estuarine gradients?	Time period with baits across the broadest salinity range for each bay	Segmented regression, gamma distribution with log link	Proportion of baits eaten	Mean salinity (specified as the segmented variable), Mean temperature, Bay
Does time period affect the relationship between salinity and consumption?	Netarts Bay only, benthic baits across three time periods	GLM with gamma distribution and log link, adding terms sequentially and comparing models with AIC	Proportion of baits eaten	Mean salinity; Square of mean salinity; Salinity range; Time period; Mean temperature; Mean temperature × Mean salinity; CPUE of *C. maenas*; CPUE of native consumers
Does bait height affect consumption?	Netarts and Yaquina Bays only, time periods with the greatest salinity ranges, baits available to benthos versus to species 20 cm above the bottom	GLM with gamma distribution and log link, adding terms sequentially and comparing models with AIC	Proportion of baits eaten	Height of bait; Bay; Mean salinity; Mean temperature; Square of mean salinity; Salinity range; Mean temperature × Mean salinity; CPUE of *C. maenas*; CPUE of native consumers
Does salinity affect *C. maenas* (invasive consumer) distribution along the estuarine gradient?	The time period with benthic baits across the broadest salinity range for each bay	GLM with gamma distribution and log link, adding terms sequentially and comparing models with AIC	Catch of *C. maenas* as a fraction of all predators; (Appendix: CPUE of *C. maenas*)	Mean salinity; Square of mean salinity; Salinity range; Bay; Mean temperature; Mean Temperature × Mean Salinity
Does salinity affect feeding rate of *C. maenas*?	Laboratory experimental data on 1) 10, 22, 34 PSU; or 2) 10, 15, 20 PSU	GLM with gamma distribution and log link	Change in bait mass	Salinity

Finally, we conducted a segmented regression using the predictors present in the best fit model following the steps in Muggeo (2008), including looking for the presence of thresholds in the relationships by estimating the break-points and slopes of multiple segmented relationships with the linear predictor (R package segmented, Muggeo 2008). We used the variables in the best fit model with the exception of salinity squared and salinity range. We excluded these two variables from the segmented regressions because they capture non-linear relationships with salinity and would be redundant with the goal of the segmented regression. For example, Attrill's data (2002) show that salinity variation peaks at mid (~20 PSU) average salinities. Therefore, the variation in range due to average salinity should be captured by specifying mean salinity as segmented. Similarly, including salinity squared in the main GLMs is the mechanism for the model to examine the possible nonlinear relationship between consumption and salinity. For best fit models that included salinity squared the nonlinear relationship was then directly tested by segmented regression without the quadratic term.

We then ran several models to better explore the system (Table 2). First, we examined the effect of time period on the conclusions for one bay, Netarts, which we sampled three times. We included time period (nominal) instead of Bay, but otherwise used the same suite of predictors as listed above for this GLM (Table 2). We also examined the effect of bait height on consumption with a GLM using the same variables as above and also height (benthic versus 20 cm above the bottom) and the interaction between bay (only Netarts and Yaquina Bays) and height

(Table 2). Finally, we examined the effect of salinity on consumer distribution with additional GLMs that included the CPUE of *C. maenas* and then also of the native consumers, as the response variables, and predictors of bay, salinity, the square of salinity, salinity range, and temperature, as above.

To determine the effect of salinity on *C. maenas* feeding rate, we used a GLM with a gamma distribution and log link. The dependent variable was the change in mass of the bait (also squid) through the experiment minus the average change in mass of the control pieces for that salinity (transformed by adding 0.5 to all values) so all values were positive, and the independent variable was salinity, which in this analysis was a categorical variable (levels; 10, 22, 34; then 10, 15, 20).

Results

Temporal variability

No statistical difference was found among the three sampling periods in Netarts Bay for consumption of baits; rather, the linear and polynomial terms of salinity were retained in all of the best fit models, and the best fit model also included temperature and its interaction with salinity (Fig. 3, Table 3). The third best model also included CPUE of native predators. The different time periods had different salinity ranges but had similar proportions of baits eaten where salinity measures overlapped (Fig. 3). Furthermore, the proportion of bait consumed from the combined sampling periods follows the same pattern as across estuaries (see below), peaking around 20 PSU, slightly lower at the marine-dominated mouth, and dropping off strongly at low salinity (Figs 3, 4).

Effects of salinity on consumption pressure

In the one best fit model, consumption of the tethered baits had a statistical relationship with both the linear and polynomial terms of salinity and also temperature and its interaction with salinity, but not salinity range (Table 4, Fig. 4). The consumption peak in the segmented regression model occurred at the low end of the mesohaline zone (~7 PSU) (Fig. 4A). The interaction between salinity and temperature was significant (Table 4). These findings held when we looked only

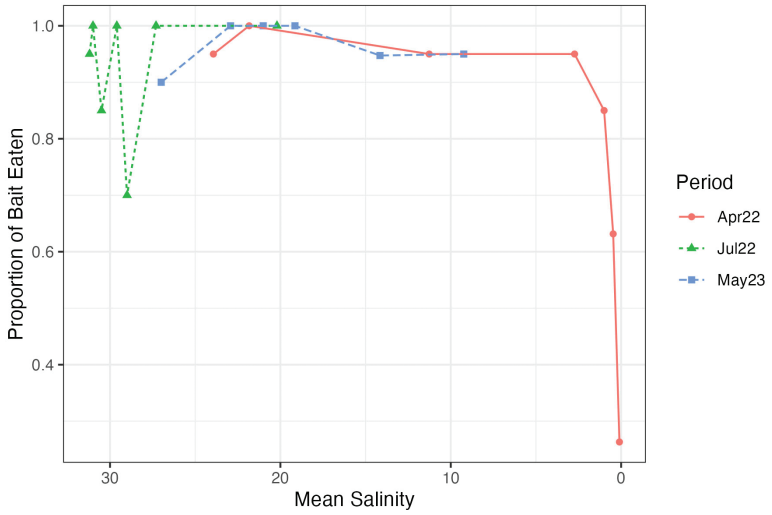

Figure 3. Line plot showing the proportion of baits eaten across salinities in Netarts Bay, Oregon, at three different sampling times: April 2022, (red) July 2022 (green), May 2023 (blue).

Table 3. Comparison of sampling periods within one bay: The best fit model GLM for the proportion of baits eaten across sampling periods in in Netarts Bay included as a function of the linear and quadratic relationship with average salinity, average temperature, and their interaction (reduced compared to global model). Sampling periods include April 2022, July 2022, and May 2023.

	Estimate	Standard error	t-value	Sig.
Intercept	-1.35	0.61	2.20	0.044
Salinity	-0.03	0.03	-0.88	0.395
Temperature	-0.12	0.04	-3.12	0.007
Salinity Squared	-0.001	<0.001	-2.84	0.012
Salinity × Temp	0.006	0.002	3.02	0.009

Table 4. Baits eaten along the salinity gradient: The results of the best fit Generalized Linear Model (GLM) for the proportion of baits eaten as a function of the linear and quadratic relationship with average salinity, and also average temperature, and the interaction between salinity and temperature. The original full model also included salinity range, bay, catch per unit effort (CPUE) of *C. maenas* crabs and, separately, of native predators (crabs and fish).

Source	Estimate	Standard Error	t-value	Sig.
(Intercept)	-0.28	1.17	-0.24	0.814
Salinity	0.26	0.08	3.12	0.004
Temperature	-0.24	0.06	-3.84	<0.001
Salinity Squared	-0.01	0.001	-5.25	<0.001
Salinity * Temperature	0.01	0.003	2.97	0.006

at data from summer 2022 (Suppl. material 1: table S1). Line graphs of the data show the bays varied in the amount of consumption pressure and the salinity at which consumption peaked, with peaks ranging from 13.4 to 26.7 PSU across bays (Fig. 4B). The peak in consumption predicted by the segmented regression occurred at a lower salinity than the peaks of these individual bays because high consumption persisted across a range of salinities, with one bay (Netarts) having high consumption through 7 PSU. Hence, consumption pressure was not highest in the highest or lowest stress area for marine organisms.

Despite our prediction and the logic of more baits being eaten when there were more predators, neither the *C. maenas* catch per unit effort (CPUE) nor the native predator CPUE had a statistical relationship with consumption pressure (Table 4).

In feeding experiments in the laboratory, however, salinity affected the amount consumed, with *C. maenas* eating less at 10 PSU than higher salinities (Fig. 5, Table 5). In the first experiment, which spanned from low to high salinity, crabs ate less at 10 PSU than 22 or 34 PSU. Similarly in the second experiment, which focused more on mesohaline salinities, crabs ate less at 10 PSU than 15 or 20 PSU.

Distribution of consumers

Introduced crabs, *C. maenas*, were caught across sites at which the measured average salinities ranged from 5.9 to 27.5 PSU in our main dataset (and from 2.7- 32.6 PSU across the summer 2022 data). Opposite of our prediction, the model with the lowest AIC suggests the proportion of our catch that was *C. maenas* decreased as a function of variation in salinity at each site; it also varied by bay (Table 6, Fig. 6). However, the second-best model highlighted the importance of average salinity and temperature instead of salinity range. Focusing on *C. maenas* catch

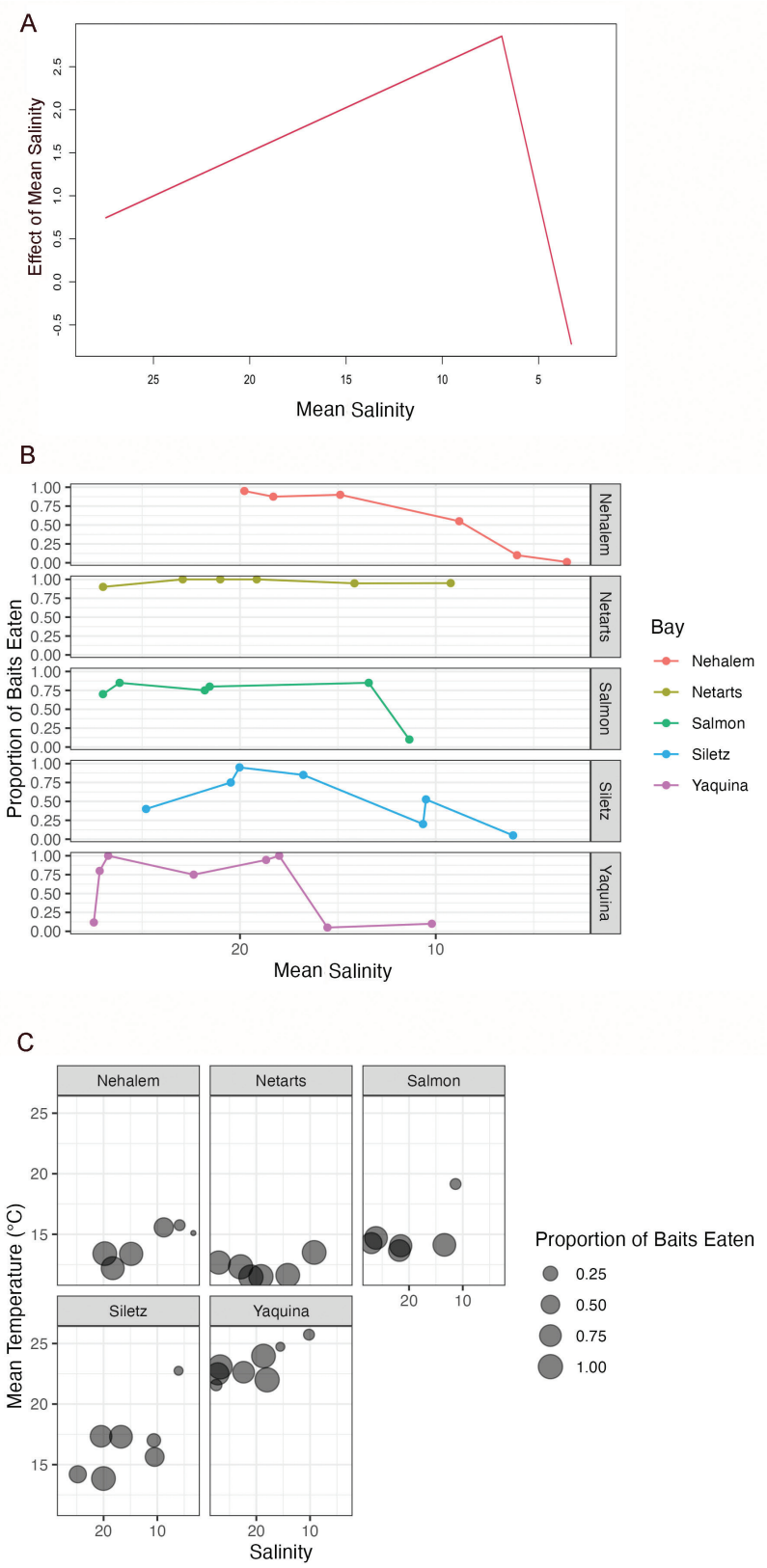

Figure 4. The effect of mean salinity on proportion of baits eaten shown by **A** Segmented regression plot for all bays combined and **B** line plots showing the values across salinities in each bay, and **C** bubble plots that also show the influence of temperature, with plots oriented with lower stress for marine organisms on the left and higher stress on the right.

Table 5. The effect of salinity on consumption rates in experiments. The results from GLM analysis of lab feeding assays of *C. maenas* at (A) 10, 22, and 34 PSU, and (B) 10, 15, and 20 PSU.

	Likelihood Ratio Chi-Square	df	Sig.
(A) Omnibus for 10–22-34 PSU	6.56	2	0.038
(Intercept)	7.10	1	0.008
Salinity	6.57	2	0.038
Parameter estimates			
10 PSU (vs. 34)	5.86	1	0.015
22 PSU (vs. 34)	0.11	1	0.741
(B) Omnibus for 10–15-20 PSU	7.46	2	0.024
(Intercept)	1.78	1	0.183
Salinity	7.46	2	0.024
Parameter estimates			
10 PSU (vs. 20)	9.25	1	0.002
15 PSU (vs. 20)	0.11	1	0.740

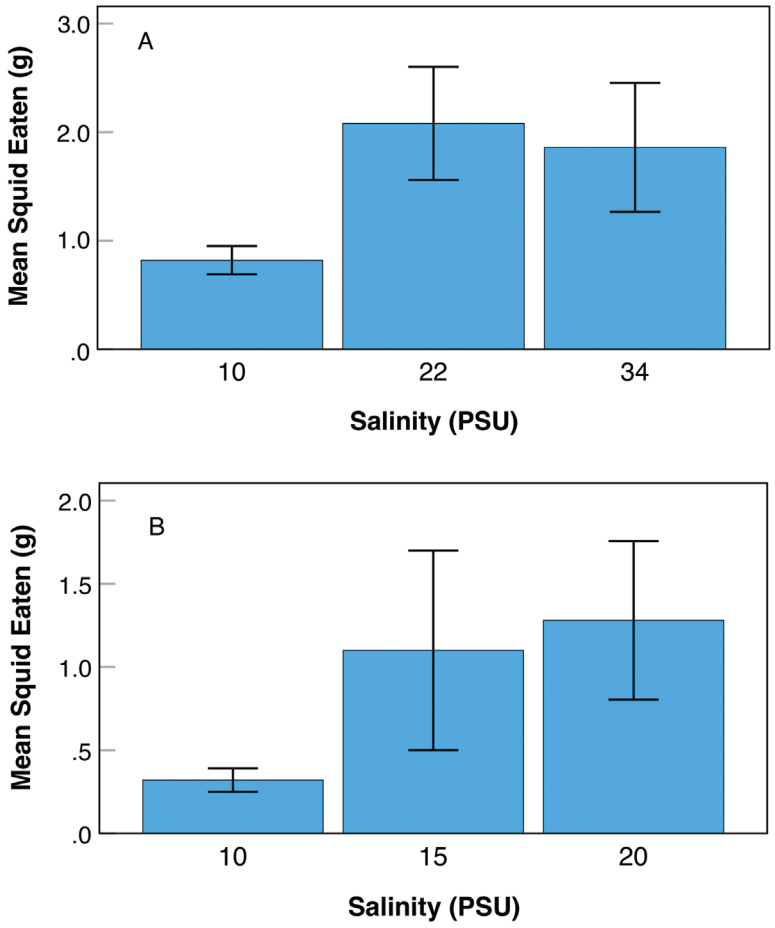

Figure 5. Bar charts showing the mean ± 1 SE of the amount of squid eaten (change in mass, grams) by 1 *C. maenas* per tank across 5 replicates of the three experimental salinities of **A** 10, 22, or 34 PSU, or **B** 10, 15, or 20 PSU.

alone, salinity did not predict green crab catch, though temperature did: within bays, fewer *C. maenas* were trapped in sites where the water temperature was warmer (Fig. 6A; Suppl. material 1: table S2). Similarly, salinity did not have a significant effect on catch of native predators (Fig. 6A, Suppl. material 1: table S3).

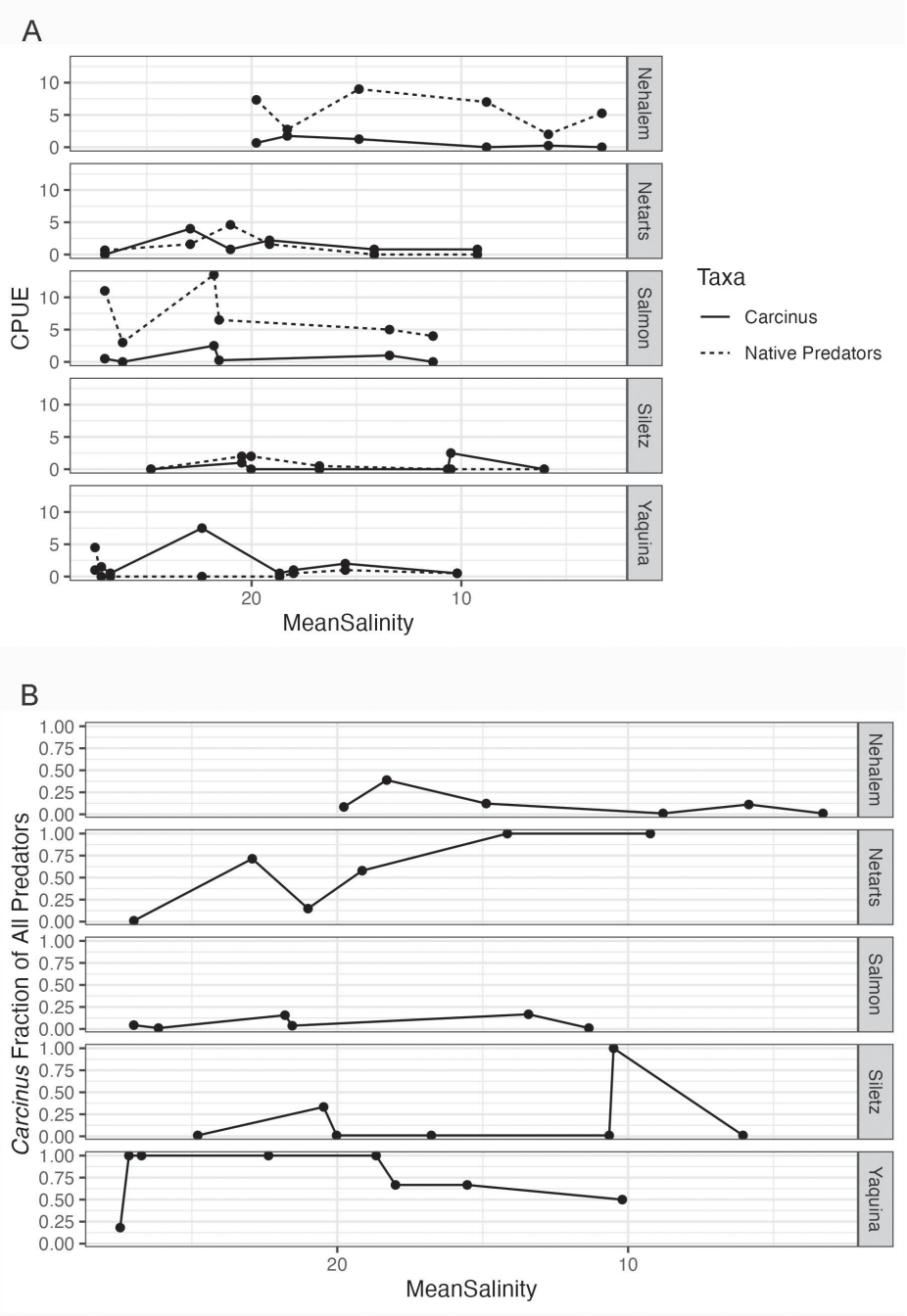

Figure 6. Line plots showing the relationship between mean salinity and **A** CPUE of *C. maenas* (solid line) and of all other trapped consumers (dashed line), which were all fishes and crabs native to the region, and **B** CPUE of *C. maenas* as a fraction of all trapped predators in each of the five bays.

Overall catch was low for both *C. maenas* and the native predators. We caught an average of 1.1 *C. maenas* per trap. Other observed predators in our traps included staghorn sculpin (*Leptocottus armatus*), small fish (3-spine stickleback *Gasterosteus aculeatus*, and saddleback gunnels *Pholis ornata*), Dungeness crabs (*Metacarcinus magister*), red rock crabs (*Cancer productus*), and hairy shore crabs *Hemigrapsus oregonensis*). Combined, these native predators averaged 2.9 individuals per trap; sculpin were the most abundant, averaging 1.8 individuals per trap. Other predators that were observed but not quantified by trapping, included seals, gulls and shorebirds, and some larger fish.

Table 6. Factors affecting Carcinus maenas distribution relative to other consumers within bays: GLM for the fraction of *C. maenas* relative to all predators, as a function of Bay (shown relative to Nehalem Bay), average temperature, and the quadratic relationship with average salinity.

Source	Estimate	Standard error	t-value	Sig.
intercept	-3.04	0.64	-4.76	<0.001
Bay Netarts	0.81	0.74	1.10	0.282
Salmon	-0.39	0.73	-0.54	0.596
Siletz	-0.23	0.69	-0.33	0.742
Yaquina	2.45	0.73	3.37	0.002
Salinity Range	0.08	0.03	2.82	0.009

Benthic versus pelagic predators

More bait was eaten when it was next to the bottom than when it was 20 cm above the bottom, suggesting consumption was largely from crabs and other benthic predators (Table 7, Fig. 7). In addition to bait height, the linear and quadratic salinity terms and temperature were all retained in the best fit model (Table 7) and the other models with similar AIC. The CPUE of native predators was retained in the best fit and third best model, and the third best model also included the interaction between salinity and temperature. Incidental observations of predators eating the baits provided insight into predator identity. One bait in Yaquina was pulled up in the mouth of a staghorn sculpin, *Leptocottus armatus*. We observed both the non-native *C. maenas* and the native *Metacarcinus magister* eating the bait six times across three bays (Salmon Estuary, Netarts Bay, and Nehalem Bay). Once, in Siletz Bay, we also observed many small fishes such as three-spine stickleback, *Gasterosteus aculeatus*, nibbling at the baits.

Discussion

Contrary to either the Consumer Stress Model (Menge and Sutherland 1987) or the Attrill Salinity Range Model (Attrill 2002), the observed relationship between stress and consumer pressure peaked mid-estuary. Although visual review suggests estuaries differed in the total amount of consumption and the salinities in which consumption pressure peaked, the estuaries consistently showed more consumption mid-estuary and less towards both the marine and especially the riverine extents. Therefore, the Invasion Stress Model from Rubinoff and Grosholz (2022), which suggests high consumption from the mouth through mid-estuary, or an extension of the Prey Stress Model (extended out until stress is too high for the predators as well) is better supported than either of the other two models considered (Fig. 1). The decline in consumption we observed at the upper, riverine edge of the estuary is consistent with findings that food web structure changes from the mid to the upper estuary (Vinagre and Costa 2014).

Although the Rubinoff and Grosholz (2022) findings that advanced the Invasion Stress Model were from a single California Bay that has much less freshwater input than four of our bays, our results suggest that a mid-salinity peak in consumption pressure may be robust across different types of eastern Pacific estuaries. We found high uniformity in the general pattern of consumption pressure peaking at intermediate to low salinities within each estuary.

The pattern of consumption within an individual estuary is likely linked to the salinities that characterize it. Our sampling of high through low salinities in multiple estuaries produced the consumption pressure curve shown in Fig. 4. Because of the convex shape of the response curve, the pattern of consumption from estuary-to-estuary or even in the same estuary across seasons may look different. Only capturing a small portion of a broader range of salinities might result in an erroneous claim that the

Table 7. Bait height affects consumption: Best fit GLM of consumption pressure (proportion of baits eaten) for Netarts and Yaquina Bays, as explained by bay, the height of the bait (benthic or 20 cm higher), their interaction, and the quadratic relationship with average salinity, average temperature , and the catch per unit effort of *C. maenas* and of native predators.

	Estimate	SE	t-value	Sig.
(Intercept)	-2.86	3.35	-0.854	0.4013
Native Predator CPUE	-0.28	0.11	-2.63	0.0148
Salinity	0.62	0.14	4.29	<0.001
Temperature	-0.25	0.12	-2.15	0.0419
Salinity Squared	-0.01	0.003	-4.24	<0.001
Bait Height	2.08	0.24	8.76	<0.001

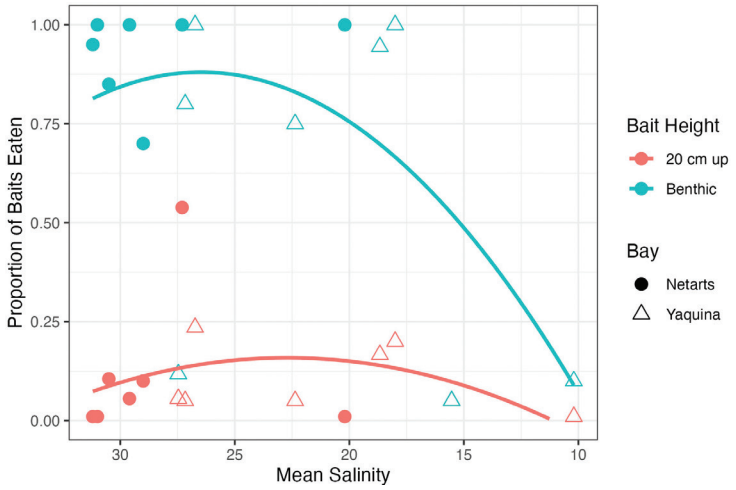

Figure 7. Scatterplot showing the quadratic relationship between proportion of baits eaten and salinity for two bait heights, benthic (blue) versus 20 cm above the bottom (red) for baits in Netarts (filled circles) and Yaquina (triangles) Bays, Oregon.

consumption pattern aligns with one of the other models. For example, an estuary that during sampling only has mid to high salinities could show consumption increasing with increasing stress (suggesting support for the Prey Stress Model), but an estuary with only low to mid salinity during sampling would show consumption decreasing with increasing stress (looking like support for the Consumer Stress Model). Many estuaries lack a broad range of salinities, at least for part of the year. Therefore, the direction and shape of the relationship between consumer pressure and salinity would be expected to vary among different times of year or estuaries that have a more limited gradient. The overall pattern we report here (mid estuary peak) can only be determined across the full gradient but often estuaries are studied across only a portion of the salinity gradient.

In addition, two other studies measuring consumption pressure along estuarine gradients in Virginia, USA and Queensland, Australia found consumption peaks nearer to the mouth of these estuaries and decreased further up the estuary (Duffy et al. 2015; Jones et al. 2021). The Duffy study spanned the salinity gradient of an estuary, from below 5 PSU near the freshwater head in June where predation was lowest, to full marine salinity towards the mouth and later in the summer, and consumption typically stayed high through 10 PSU except in September and October when it started dropping around 15 to 25 PSU, respectively (2015). A study across a greater range of estuaries and seasons would help identify the categories and drivers of patterns of consumption across estuaries and may produce a predictive relationship given different sets of conditions.

We had expected either a mid-estuary peak in predation or a continued plateau in predation with increased stress levels, and predicted it would be driven by invasion of stress tolerant species. When both predators and prey are stress tolerant and both groups are able to exist at lower salinities along the estuarine gradient, then habitat quality and nutrients may be more important in determining abundance and trophic interactions rather than tolerance of physical stress (Seitz 2011). If there is a shift to more stress-tolerant predators, as we expected would be the case with *C. maenas* now in many northeastern Pacific estuaries, there may be a marked shift in predation pressure for prey. Known to have broad salinity and thermal tolerances (McGaw and Naylor 1992; Cohen et al. 1995; Klassen and Locke 2007; Leignel et al. 2014; Tepolt and Somero 2014), *C. maenas* can reside in the mid to upper estuary and also up side channels, and has been shown to have greater abundance mid estuary than near the mouth (Hunt and Yamada 2003; Rewitz et al. 2004; Amaral et al. 2009). However, we did not detect a significant relationship between proportion of bait eaten and CPUE of *C. maenas*, which was the only introduced predator we caught, perhaps because of our low catch of this crab. We also note that a variety of smaller predators such as isopods and gastropods, including numerous introduced taxa, could be eating the baits while remaining undetected from our trapping.

We did find *C. maenas* along much of the salinity gradient of each of the sampled estuaries and at the full range of salinities except our most marine sites. In addition, we found that in lab experiments they consumed more in fully marine salinity and in salinities typical of mid estuarine areas (15–20 PSU) than at lower salinity (10 PSU). Their reduced numbers at marine salinities combined with their decreased foraging at lower salinities could together generate the observed pattern. However, more data, such as video documentation of the consumption or a clearer trend from trapping, would be needed to be able to conclude that the introduced, stress-tolerant *C. maenas* drove the observed trend in consumption pressure.

Instead, the Prey Stress Model may capture the data best. The Prey Stress Model suggests that an additive or synergistic pattern between stress and consumer pressure will occur when predators are more stress tolerant (or at least more mobile) than are prey. At some point, however, one would expect stress to limit the consumers as well. If stress-tolerant predators are introduced to an estuary, as happens with some, and perhaps many, marine invasions (Crooks et al. 2011; Lenz et al. 2011; McKnight et al. 2021), they could then create or contribute to the pattern predicted by the Prey Stress Model. Therefore, the Invasion Stress Model might be considered a special case of the Prey Stress Model. The effect of introduced consumers might explain part of why the pattern predicted by the Prey Stress Model is more common than the Predator Stress Model (Silliman and He 2018).

Evaluating the effect of *C. maenas* on the observed pattern presented challenges due to potential trapping artifacts, a predator community that was not fully represented in traps, and perhaps the effect of salinity on behavior as well as abundance. Despite extensive trapping experience and a general past trend of trapping reflecting abundance, our trapping did not seem to provide an effective estimate of *C. maenas* numbers or consumption pressure, perhaps due to variation in the abundance and diversity of alternate food resources in the bay for these crabs. We observed and sometimes hand-caught many green crabs from sites where few were caught by our traps. For example, we had a low catch of *C. maenas* (a total of six crabs in traps across three bouts of trapping: 4 caught in May 2023; 2 caught for July 2022 or 0 in April 2022) from a mid-salinity site in Netarts Bay where on multiple occasions we hand caught over 50 *C. maenas* in under 1 hr after finishing trapping. Twice we caught many females from under rocks in the intertidal at this site but the other times we caught a mixture of males and females that were walking about in the channel. Hence, although our trap data did not support

our predictions in this study, we also question how well CPUE reflected predator abundance in this case so further evaluation is needed. Video recording the baits, if possible given estuarine turbidity, or using multiple or improved methods of estimating green crab abundance and also abundance of other predators we may not have quantified would have helped resolve the driver of the observed consumption pattern. Additionally, there could be an ecological mismatch between *C. maenas* as predators and the squid baits used as prey in this study—*C. maenas* are shore crabs that are commonly found in estuaries, and squid could be a novel prey item to *C. maenas* in the field since offshore squid populations would rarely overlap with the preferred habitat of *C. maenas*.

In the two bays where we evaluated consumption pressure at different heights, we found many more benthic baits were eaten than baits suspended in the water column. Benthic consumers are therefore likely the main predators driving the trends in consumption pressure in the lower intertidal areas of these estuaries. Based on our observations and catch, we expect crabs were the major consumers on these baits, which is consistent with other work showing that consumption by crabs is more important at higher latitudes, which includes our study sites (Musrri et al. 2019). Future work should use cameras when water is clear enough and/or to also use natural baits to compare consumption of those to dried squid, which is easily available to all predators and scavengers, similar to methods used in other studies (Musrri et al. 2019; Yarnall and Fodrie 2020). Also, clearly the deployment height of the bait can greatly affect findings. Squidpops are typically deployed at the top of a stake 10 cm or more above the bottom (e.g., Duffy et al. 2015; Rodemann and Brandl 2017; Yarnall and Fodrie 2020), though are sometimes just above the benthos, like our main deployment (Ruesink et al. 2019). We recommend either targeting height to the typical feeding area of the predator community of interest or using multiple deployment heights.

Conclusions

Overall, we found a clear pattern of consumer pressure on benthic baits peaking in the lower mesohaline part of the estuary and, for the first time, examined this pattern across multiple estuaries, suggesting a robust finding across temperate estuaries with a broad salinity gradient. A shift to more stress-tolerant truly estuarine predators, including the invading crab *C. maenas*, could be contributing to this relationship. Although our catch data did not support this hypothesis, these data may not adequately reflect true consumer abundances, especially *C. maenas* abundance. Furthermore, our data from the lab studies indicated higher consumption rates as a function of salinity. Therefore, our abundance measure CPUE may not have captured the actual consumer pressure for this species. We also note that there are many aspects of the predator community that change across salinities, and it is challenging to evaluate the effect of a single predator in this context. Future research is needed to determine how the bait data translates to consumer pressure on estuarine prey communities and what drives the relationship. Knowing how stress and biological interactions shape local communities will help predict ecological impacts of climate change, biological invasions, and other environmental stressors.

Authors' Contribution:

CEDR: research conceptualization, sample design and methodology; investigation and data collection; data analysis and interpretation; ethics/permit approval; funding provision; and writing. AAL: sample design and methodology; investigation and data collection; ethics/permit approval; funding provision; writing: review & editing. BGR: research conceptualization, consultation on

data analysis and interpretation, original writing and editing. LRS: investigation and data collection; review. SLW: investigation and data collection; writing: review. EDG: research conceptualization review and editing. GMR: research conceptualization review and editing. ALC: research conceptualization; data analysis and interpretation; review and editing.

Funding Declaration

Funding was provided by Portland State University's Faculty Enhancement Grant program to CED and ALL. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Conflict of Interest, Declaration of Interests, Ethics and Permits

Authors had no conflict of interest, followed ethical guidelines for animal handling. It is understood that with submission of this article the authors have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects, and that we are willing to share the original data and materials if so requested. We conducted the research under scientific research permits from Oregon Department of Fish & Wildlife, permit ## 25871, 26478 and 27163, all entitled 'Impacts of estuarine gradients on predation intensity and associated research opportunities for undergraduate course

Acknowledgements

Thanks to many PSU students for their help in the field: Reagan Thomas, Peyton Priestman, Austin Holst, Emma Scott, Rodé Krige, Estrella Soto, Zosia Lynch, Kayla Neal, Mary Munt, Javier Mitchell, Trever Gelling, Stephanie Meikle, Nick Skinner, Patrick Gresh, Rowan Irene, Amanda Gannon, Jacob Rose, Ani Draper, Hannah Roy, Aaron DeLuca, Destiny Hazeri, Sebastian Pacheco, Deanna Michinski, and Kyle Swanson. Thanks too to the organizations that allowed us shore-side access: Jetty Fishery Marina, Kelly's Brighton Marina, Paradise Cove, Whisky Creek Hatchery, Coyote Rock Marina, & Sunset Marina.

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Supplementary material 1

Additional information

Authors: Catherine E. de Rivera, Amy A. Larson, Benjamin G. Rubinoff, Luna R. Soto, Seth L. Wright, Edwin D. Grosholz, Gregory M. Ruiz, Andrew L. Chang

Data type: pdf

Explanation note: **table S1.** Baits eaten along the salinity gradient in Summer 2022: Generalized Linear Model using data from summer 2022 only, for the proportion of baits eaten as a function of bay, the quadratic relationship with average salinity. **table S2.** Factors affecting Carcinus maenas distribution: GLM for the catch per unit effort of *C. maenas* as a function of bay, the quadratic relationship with average salinity, salinity range, and average temperature. **table S3.** No effect of salinity on native predator distribution within bays. Generalized Linear Model for the catch per unit effort of native predators as a function of bay, the quadratic relationship with average salinity, and average temperature.

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Link: https://doi.org/10.3391/ai.2025.20.1.151447.suppl1