Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary

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Abstract: Given the presumed importance of benthic and epibenthic estuarine habitats in Chinook salmon (*Oncorhynchus tshawytscha*) smolt growth and survival, resource managers would be well served by an improved understanding of how smolts use such habitats. A cabled acoustic positioning system was used to precisely track (<1 m resolution) the movement of seventeen 0-aged hatchery-reared fall Chinook smolts in a large (~4000 m^2) enclosure over a period of 10 days in Willapa Bay, Washington, USA. A hierarchical Bayesian state–space model of movement was subsequently developed to associate the behaviors of tagged salmon with characteristics of benthic habitat in the enclosure. Model results indicated that smolts had a strong preference for remaining in native eelgrass (*Zostera marina*). Conversely, no such preference existed for other structured benthic habitats such as oyster (*Crassostrea gigas*) beds, non-native eelgrass (*Zostera japonica*), and non-native smooth cordgrass (*Spartina alterniflora*). There was a positive relationship between individual survivorship in the enclosure and the strength of behavioral preference for native eelgrass, suggesting that predator avoidance may be the evolutionary mechanism driving behavioral responses of smolts to benthic habitats.

Résumé : Étant donné l’importance présumée des habitats estuariens benthiques et épibenthiques pour la croissance et la survie des saumoneaux du saumon chinook (*Oncorhynchus tshawytscha*), une meilleure compréhension de l’utilisation de ces habitats par les saumoneaux serait utile aux gestionnaires des ressources. Nous avons utilisé un système de positionnement acoustique avec câbles pour suivre avec précision (résolution de <1 m) les déplacements de 17 saumoneaux chinook d’automne de pisciculture d’âge 0 dans un grand (~4000 m^2) enclos pendant 10 jours dans la baie de Willapa, état de Washington, É.-U. Nous avons ensuite mis au point un modèle bayésien état–espace des déplacements afin d’associer les comportements des saumons marqués à des caractéristiques de l’habitat benthique dans l’enclos. Les résultats de la modélisation indiquent que les saumoneaux montrent une forte préférence pour demeurer dans les herbiers à zostères (*Zostera marina*) indigènes. À l’inverse, il n’existe pas de telle préférence pour les autres habitats benthiques structurés, les bancs d’huîtres (*Crassostrea gigas*), les herbiers de zostères (*Zostera japonica*) non indigènes et les herbiers de spartines (*Spartina alterniflora*) non indigènes. Il existe une corrélation positive entre la survie d’un individu dans l’enclos et l’intensité de sa préférence comportementale pour la zostère indigène, ce qui fait croire que l’évitement des prédateurs peut être le mécanisme évolutif qui explique les réactions comportementales des saumoneaux aux habitats benthiques.

[Traduit par la Rédaction]

Introduction

Estuarine residence is a critical life history stage for most salmonids. The interface between fresh and salt water aids in the physiological changes of smoltification (Simenstad et al. 1982; MacDonald et al. 1987; Thorpe 1994), the abundance of food in the nearshore environment allows for rapid growth (Congleton et al. 1982), and the habitat components of the estuarine environment provide ample cover from a potentially large predator base (Wood 1987). Estuaries all along the US west coast have suffered major anthropogenic impacts such as dredging and channelization, shoreline armoring, overwater structures, water quality degradation, and the introduction of invasive species (Kennedy 1982; Bottom et al. 2005; Lotze et al. 2006). These changes have undoubtedly impacted the growth and survivorship of Pacific salmon in general, and Chinook salmon (*Oncorhynchus tshawytscha*) in particular, given that the species characteristically resides in estuaries longer than other Pacific salmonids (typically around 1 month, although as long as 6 months in larger estuary systems such as Willapa Bay, Washington) (Healey 1982*b*; Simenstad et al. 1982; Thorpe 1994).

Pacific salmon stocks have endured persistent long-term declines in habitat quality and availability over the last century and in many cases steep population declines over the last few decades (Nehlsen et al. 1991; Bottom et al. 2005). To date, 27 distinct populations of salmonids along the Pacific coast of the United States have been listed as threat-

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ened or endangered under the Endangered Species Act. Given the ongoing anthropogenic impacts to Pacific coast estuaries and the recent Endangered Species Act listing of salmonid stocks, management and recovery efforts would be well served by an improved understanding of what characteristics of the estuarine habitat are important for growth and survival. Kareiva et al. (2000) used a demographic matrix model to demonstrate that even modest reductions in estuarine mortality would reverse current population declines in Snake River spring–summer Chinook salmon. Where should resource managers focus restoration efforts to reduce mortality in the estuary? Answering this question requires an improved understanding of how salmon use estuarine habitat.

Bottom et al. (2005) identified three general prey production–foraging habitat types important for juvenile Chinook salmon in the estuary: terrestrial–riparian, shallow benthic–epibenthic, and pelagic. To date, most studies of juvenile salmon habitat use have focused on terrestrial–riparian habitats such as river mouth emergent marsh areas (e.g., Fresh et al. 1981; Healey 1982*a*; Simenstad et al. 1982). Similarly, considerable research effort has focused on characterizing estuary-wide distribution patterns coincident with tidal cycles (Healey 1982*b*; Levy and Northcote 1982; Moser et al. 1991) and salinity gradients (Simenstad et al. 2000). Conversely, relatively few studies have investigated the distributions and relative abundances of salmon in relation to nearshore benthic–epibenthic estuarine habitats (an exception is Murphy et al. 2000). Benthic–epibenthic habitats in Pacific coast estuaries are important in the context of salmon management because they are a potentially productive source of prey (Bottom et al. 2005) and a source of physical structure (Murphy et al. 2000; Shaffer 2004). Additionally, these habitats are often modified extensively through aquaculture practices such as oyster culture (Dumbauld et al. 2001; Rumrill and Poulton 2004). An improved understanding of the behavioral ecology of Pacific salmon in relation to benthic–epibenthic habitats would undoubtedly aid in the effective multiple-use management of West Coast estuaries.

In this study, the fine-scale (<1 m resolution) movements of acoustically tagged juvenile Chinook salmon were monitored in a large (~4000 m^2) enclosure in Willapa Bay, Washington, USA, using a cabled acoustic positioning system (O'Dor et al. 1998; Ehrenberg and Steig 2003). The enclosure site was chosen to encompass representative patches of the principal benthic habitat components in Willapa Bay, native eelgrass (*Zostera marina*), non-native eelgrass (*Zostera japonica*), and oyster (*Crassostrea gigas*) beds and open substrate (e.g., mud flats), as well as an area of emergent vegetation composed of non-native smooth cordgrass (*Spartina alterniflora*). Following data collection, benthic habitat patches were digitized and subsequently linked to the positions recorded for each fish. These linked data sets were then used to model the influence of habitat on individual- and population-level behaviors.

Materials and methods

The work described in this study was carried out at the northern end of Nahcotta Harbor, Nahcotta, Washington. Fieldwork was conducted during July 2002 in cooperation with the Washington Department of Fish and Wildlife Shellfish Lab and the Port of Nahcotta. During the course of the study, the water temperature at the study site averaged 19.2 °C (SD = 1.6 °C). At the beginning and end of the experiment, the salinity of the water at the study site was measured at 24 and 26 PSU, respectively, at high tide. The Forks Creek Hatchery (Raymond, Washington) provided the juvenile Chinook salmon (Willapa stock, 0-aged fall Chinook smolts) for tagging under an agreement with the Washington Department of Fish and Wildlife. Two days prior to the initiation of the study, the subject fish were transported to Nahcotta Harbor using a transport container provided by Forks Creek Hatchery and subsequently placed in holding pens off the harbor dock. The transport container and holding pens were constantly aerated using oxygen cylinders and aeration stones.

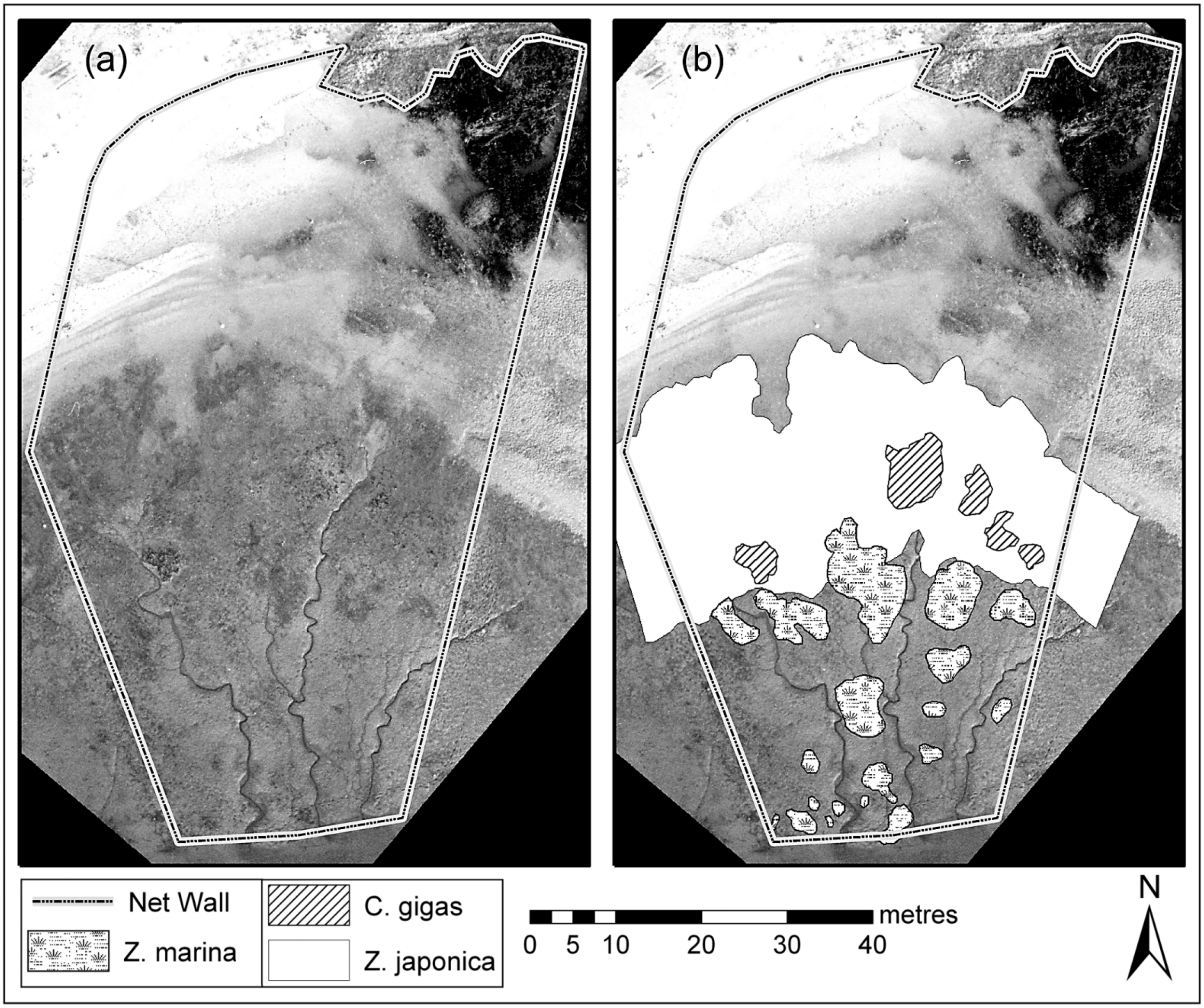
Enclosure setup

The enclosure (Fig. 1) was constructed during a period of high tidal flux so that during the lowest tides, the enclosure site completely dewatered. The tidal timing of the experiment was such that the enclosure never completely dewatered while fish behavior was being monitored. The enclosure was constructed with 2 cm stretched mesh netting and 6.4 m 17-gauge galvanized tubing posts. Posts were placed every 5 m along the enclosure edge. A coated steel line was then attached along the top of the posts, and each end of the line was secured to the substrate above the high-tide line. The top of the net wall was subsequently attached to the top line with zip ties and secured to the substrate by laying polyvinyl chloride poles along the bottom of the net and staking them down. At the deepest part of the enclosure, the net wall was 3.5 m in height. The walls of the enclosure ran up onto shore beyond the intertidal zone. The enclosure bathymetry ranged along an even grade from ~1 m above mean high tide to 3 m below mean high tide. The total area of the enclosure from the deepest wall to mean high tide was ~4000 m^2. In July 2000 (~1 year prior to conducting the study), the existing oyster habitat at the enclosure site was augmented by creating a ~3 m × 3 m patch of oysters by relocating oysters from a nearby oyster reef.

Acoustic tracking

Tracking was performed using an acoustic tag tracking system (model 290; Hydroacoustic Technology, Inc., Seattle, Wash.). The tag receiver gathers acoustic signals on up to 16 separate channels and stores them on a computer hard-drive connected by serial port to the receiver. A total of nine hydrophones were used in this study. Hydrophone wires were run along the enclosure net wall up into a truck bed that housed the tag receiver. The relative positions of each hydrophone were determined by measuring the pair-wise distances between all nine hydrophones. The arrival times of pulses from acoustic tags at each hydrophone were used to triangulate the locations of the tagged individuals using Hydroacoustic Technologies Incorporated proprietary software. Differences in pulse rates between tags were used to identify and track individual tags. Although the system is capable of tracking in three dimensions, this study did not

Fig. 1. (*a*) Orthorectified aerial photograph of the enclosure benthos taken during a low tide. (*b*) Photograph in (*a*) was used to digitize benthic habitat features in the enclosure. Non-native cordgrass habitat (dark area at the top right of the enclosure) was not digitized because no tagged fish swam into the area during the study. The high intertidal occupied by the cordgrass was submerged 2–3 h·day^{-1} during the study, with a maximum depth of ~0.75 m.



have enough vertical separation in the hydrophone array to resolve tag depth.

To evaluate error in two-dimensional (east–west and north–south) positioning, a single tag was placed consecutively at each of 11 known locations throughout the enclosure for a period of 5 min per location. These locations were specifically chosen to represent areas within the enclosure believed to have the poorest positional accuracy based on hydrophone geometry. Additionally, this error evaluation procedure was carried out when the tide was outgoing and the water was less than 1 m deep at the shallowest of the evaluated locations under the expectation that changes in water temperature, salinity, and noise interference would collectively contribute the most to position error. By taking this “worst-case” approach to error checking the tracking system, one could reasonably assume that error is no worse than, and perhaps generally better than, the assessed error. On average, system estimates of tag positions were less than 1 m from the true tag positions (mean = 0.69 m, SD = 0.39 m).

Fish tagging

Nineteen juvenile Chinook salmon were surgically implanted using microacoustic tags (model 795A; Hydroacoustic Technology, Inc.) weighing ~0.9 g in air (7 mm diameter, 17 mm length). Two of the implanted tags failed to activate properly, leaving 17 fish with active tags for the study (Table 1). Fish with the failed tags were released just outside the enclosure following recovery from surgery. Surgical procedures outlined in Adams et al. (1998) were used for implanting the acoustic tags in the gut cavity of fish. All implements and tags were bathed in antiseptic before each

Table 1. Lengths and weights of tagged fish and mean posterior values for each of the fish-specific parameters used to characterize movement rates based on both day and night positions.

Length (mm)	Weight (g)	$\bar{s}_i$	$\bar{n}_i$	$\bar{m}_i$	$\bar{o}_i$	$\bar{q}_i$	$\bar{p}_i$
119	19.4	5.15	–0.92	1.47	–0.30	–0.0157	–0.0764
119	19.6	5.58	0.86	0.04	1.32	0.0036	–0.1200
116	18.3	4.78	–0.92	0.16	–0.03	–0.0379	–0.1115
126	21.5	5.70	0.43	0.21	1.94	–0.0098	–0.1045
114	17.1	4.58	2.14	–0.60	1.72	–0.0115	–0.0912
115	18.1	5.05	–1.78	–0.39	0.52	–0.0191	–0.0239
113	15.6	5.09	–3.05	0.20	–0.73	–0.0205	–0.1177
118	19.2	2.01	–0.86	0.59	–0.30	–0.0450	–0.0522
114	16.2	5.81	–2.88	–0.82	–1.82	–0.0294	–0.1116
110	16.9	4.51	–0.95	0.24	–1.51	–0.0355	–0.1138
112	15.6	3.09	–0.99	0.22	2.62	–0.0172	–0.0880
112	15.3	4.75	–0.50	1.17	0.74	–0.0041	–0.0555
110	15.7	3.66	–1.03	1.54	–0.81	–0.0360	–0.1491
112	15.6	3.44	–0.53	–0.41	2.78	–0.0093	–0.0857
114	17.1	4.78	–2.31	–0.97	1.41	–0.0169	–0.0717
110	14.1	4.39	–2.91	0.20	0.52	–0.0166	–0.1462
114	16.1	2.58	–0.54	0.72	0.63	–0.0456	–0.0758
—	—	**4.41**	**–0.99**	**0.23**	**0.53**	**–0.0215**	**–0.0940**

Note: The units of $\bar{s}_i$ (base rate of movement), $\bar{n}_i$ (rate adjustment for native eelgrass), $\bar{m}_i$ (rate adjustment for non-native eelgrass), and $\bar{o}_i$ (rate adjustment for oysters) are metres moved per 30 s period. Values for $\bar{q}_i$ and $\bar{p}_i$ represent exponential rates of change in movement as a function of net proximity and location depth, respectively. The final row (bold) gives the mean posterior hyperparameter values associated with each of the parameters.

surgery. Fish were anesthetized with tricainemethanesulfonate (MS 222) prior to surgery in a rapid anesthetic bath. Once a fish lost motor function and did not respond to being bent at midbody, its weight and fork length were measured, and then it was placed ventral side up in a plastic cradle. Each fish was supplied reduced anesthetic over its gills through plastic surgical tubing inserted in the mouth during surgery. A small incision was made to open the abdominal cavity, the tag was inserted, and then the incision was sutured and covered with triple-antibiotic ointment. Approximately three-quarters of the way through each surgery, the solution flowing over the gills of the fish was switched to salt water. Throughout the surgery, the opercular activity of the fish was monitored, and if any significant slowing was evident, the switch to water was made immediately. Following surgery, the fish were placed in a recovery bath with oxygen bubbling through it for 30 min and then transferred to a pen near the enclosure site where they were held for at least 12 h prior to release in the enclosure.

Habitat characterization

The enclosure habitat was digitized using a high-resolution aerial photograph of the enclosure location taken 1 month after the conclusion of the study at a time when the low tide exposed the entire enclosure site. Before the photograph was taken, orange cones were placed on each of the hydrophone positions. The aerial photograph was subsequently scanned and orthorectified to the hydrophone coordinate system in Arcview 3.2 (ESRI, Redlands, California) using the IMAGEWARP extension, with each of the orange cones as reference points in the image. Using the orthorectified image, mutually exclusive polygons were drawn around all patches of oysters, native eelgrass, and non-native eelgrass (Fig. 1). All salmon paths were then brought into the geodatabase and all positions within each path were subsequently assigned habitat values of 1 or 0 for each benthic habitat type depending on whether the position fell over the given habitat type. Additionally, for each position, the absolute depth (the height of the substrate relative to the bottom of the lowest part of the enclosure), the relative water depth (the depth of water over the position given the absolute depth and tide height at the time of the position), and net-wall proximity (closest straight-line distance between each position and the enclosure net wall) were calculated. The result was thus a matrix of positions for each fish that included *XY* coordinates, binary values indicating presence or absence each benthic habitat type, and continuous values describing depth and net-wall proximity.

Modeling

Markov chain Monte Carlo simulations were conducted using a hierarchical Bayesian state–space model of juvenile salmon movement to investigate the influence of habitat on behavior. Although state–space models are widely used in engineering for analyzing data in series, their utility in analyzing animal tracking data has only recently been demonstrated (Jonsen et al. 2003; Morales et al. 2004; Jonsen et al. 2005). State–space models are useful for animal tracking data because they can simultaneously account for (*i*) technology-based (measurement) error sources in the estimation of true locations, (*ii*) random variability in directional movement, and (*iii*) state variables that affect movement (in this case, characteristics of habitat in the enclosure). Moreover, state–space models address issues of serial autocorrelation in path data by explicitly dealing with transition probabilities between animal locations as a function of underlying location attributes. Using a state–space model within a meta-analytic framework allowed for integration across multiple individual animal tracks in the estimation of population-level behaviors.

The state–space model formulation used followed that of Jonsen et al. (2003). Using their conventions, the two model components are the transition and measurement equations (eqs. 1 and 2, respectively):

$$(1)\qquad \alpha_{i,t+1} = \alpha_{i,t} + \eta_{i,t}$$

$$(2)\qquad y_{i,t} = \alpha_{i,t} + \varepsilon_{i,t}$$

where α_i represents the matrix of unobserved true locations of each fish i in two-dimensional space (state variables), η_i represents the matrix of process noise, y_i represents the matrix of observed locations, and $\varepsilon_i \sim (0, \sigma_\varepsilon)$ represents the matrix of errors in observed locations. Here, $\eta_{i,t} \sim (0, \sigma_{i,t})$, where $\sigma^2_{i,t}$ is the variance in movement of fish i defined in part by the habitat characteristics of the location at time t. The model assumed equivalence in observation error in two dimensions to avoid multiplicatively increasing the parameter hypervolume of the full model and because there were insignificant differences in variance between dimensions (paired t test, $p = 0.17$). Akaike's information criterion values were used as a guide in constructing appropriate habitat components of σ. Because of the size of the data set, model-fitting tests were conducted on individual fish while excluding observation error rather than running separate models within the entire meta-analytic framework. At the outset, adjustments to σ associated with *Z. japonica*, *Z. marina*, and *C. gigas* were included because these benthic habitats are clearly important to estuarine resource management in Willapa Bay and elsewhere (Ruesink et al. 2006). Additional factors for absolute depth (hereafter referred to simply as depth) and distance to enclosure wall improved model fit for all fish. The addition of a linear time adjustment to σ marginally improved model fit for the two tagged individuals that survived the longest in the enclosure but did not improve the fit for the remainder of the tagged fish. The meta-analytic model therefore did not include a time factor. Variance in movement for each individual i at each location t was thus parameterized as follows:

$$(3)\qquad \sigma_{i,t} = (s_i + m_i \times \mathrm{japonica}_{i,t} + n_i \times \mathrm{marina}_{i,t} + o_i \times \mathrm{gigas}_{i,t}) \times \mathrm{e}^{-p_i \times \mathrm{depth}_{i,t}} \times \mathrm{e}^{-q_1 \times \mathrm{net}_{i,t}}$$

By default, s_i reflects variance in movement over open substrate. Because values of *Z. japonica*, *Z. marina*, and *C. gigas* are binary in the data matrix, they act as dummy variables for the parameters m_i, n_i, and o_i, respectively. These parameters represent additive adjustments to s_i associated with the different benthic habitat components. The parameters p_i and q_i determine how rapidly the distance moved at each time step changes as an individual moves shallower in the enclosure or farther away from the net wall, respectively. In the meta-analytic formulation of the model outlined by eqs. 1 and 2 above, each parameter describing $\sigma_{i,t}$ is drawn from an associated normal distribution defined by hypermean parameters ($\widehat{s}$, $\widehat{m}$, $\widehat{n}$, $\widehat{o}$, $\widehat{p}$, and $\widehat{q}$) and hypervariance parameters ($\sigma_{\widehat{s}}$, $\sigma_{\widehat{m}}$, $\sigma_{\widehat{n}}$, $\sigma_{\widehat{o}}$, $\sigma_{\widehat{p}}$, and $\sigma_{\widehat{q}}$). These hyperparameters define the population-level influence of habitat features on the fine-scale movements of Chinook salmon by combining information across all tagged individuals in my study.

To account for the possibility that fish behaved differently during the day than at night, three separate model runs were conducted using the following data sets: (*i*) only nighttime positions (all positions collected between 1 h after sunset and 1 h prior to sunrise), (*ii*) only daytime positions, and (*iii*) all daytime and nighttime positions. Each model run incorporated uninformative priors (mean = 0, variance = 1000) for all parameters and hyperparameters used in the formulation of $\eta_{i,t}$ and informative priors (mean = 0.695, variance = 0.478) for σ_ε (observation error) based on the error in position estimates for the test tags. R-CODA (convergence diagnosis and output analysis) convergence statistics were used to ensure appropriate posterior chain lengths and thinning.

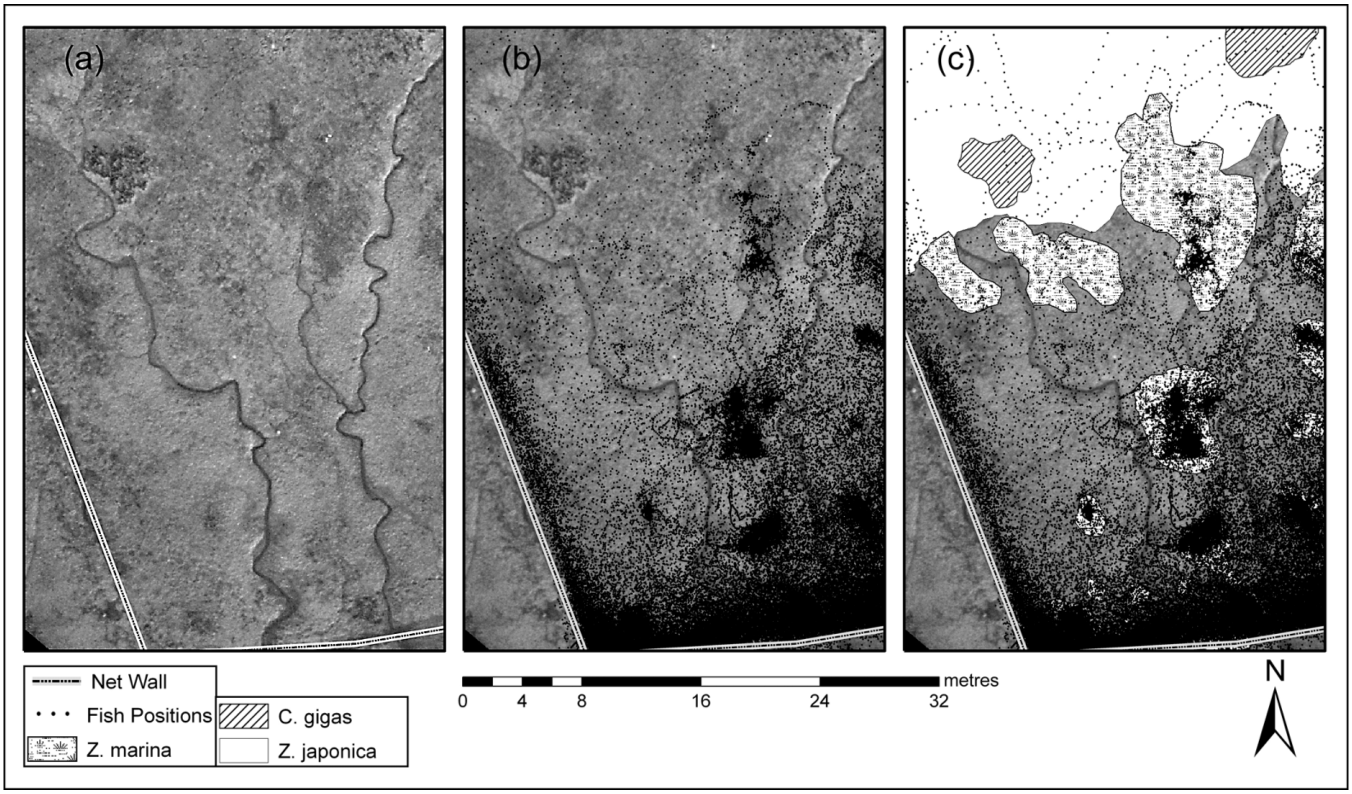
Results

All 17 tagged fish released into the enclosure were apparently killed by predators during the course of the study. Belted kingfisher (*Megaceryle alcyon*), great blue heron (*Ardea herodias*), and great egret (*Ardea alba*) were observed hunting in the enclosure. Caspian tern (*Sterna caspia*) probably also hunted in the enclosure, although they were not observed doing so. Because the enclosure net wall was put in place when the study site was completely dewatered, it is unlikely that tagged fish were killed by predatory fishes such as sculpin (Cottoidea). On average, fish survived ~60 h (2.5 days), with the fish that survived the longest spending nearly 7 days in the enclosure. Because the acoustic system updated fish locations approximately every 3 s, it was possible to determine where predation events took place in the enclosure. All 17 individuals were apparently preyed upon while over open substrate.

The plots of fish positions in the enclosure (Fig. 2) clearly showed high position densities above native eelgrass patches, near the net wall, and in the deeper parts of enclosure. The time-series paths of individuals appeared to show a periodic "resting" behavior over native eelgrass, where fish would stay virtually motionless for long periods, sometimes for an hour or more in eelgrass stands less than 2 m in diameter. These periods of rest did not appear to be correlated with tidal stage or time of day. The influence of non-native eelgrass and oysters on the behaviors of tagged individuals was not visually apparent based on plots of fish positions or by looking at the time-series paths of individuals. No tagged fish ever ventured into the non-native cordgrass habitat during the study period.

The state–space model results were in general agreement with the visual interpretation of the plotted fish positions. There were no marked differences between the posterior distributions of the model hyperparameters from the day and night data sets (Fig. 3). Considering the model run using all of the data (both day and night positions) (Fig. 3*c*; Table 1), the data provide strong support for a behavioral "slowdown" in smolts while over native eelgrass based on the posterior distribution of the hyperparameter $\widehat{n}$. Conversely, the model results show limited support for the notion that Chinook salmon speed up over native eelgrass. The posterior

Fig. 2. (*a*) Map of the lower-left (southwestern) corner of the enclosure. (*b*) Map including all of the recorded positions of the tagged individual that survived the longest during the study. (*c*) Map including an underlay of polygons representing the benthic habitats in the enclosure. Note that areas of increased position densities occur over patches of native eelgrass, near the net wall, and in the deeper (southern) area of the enclosure.



values for $\widehat{p}$ and $\widehat{q}$ were both nearly exclusively negative, demonstrating strong support for the notion that Chinook salmon slow down as they get deeper in the enclosure and closer to the net wall.

The loss of all tagged individuals due to predation during the study afforded the opportunity to investigate the relationship between behavioral responses to native eelgrass and survival times (Fig. 4). The software program WinBUGS (Lunn et al. 2000) was used to fit the following simple function (chosen based on Akaike information criterion model selection):

$$(4)\qquad \text{days}_i = \alpha \times \log(\bar{n}_i) + b$$

where days_i is the duration of time survived for each individual and $\bar{n}_i$ is the mean posterior value of n_i for each tagged individual. Uninformative priors for both the slope (*a*) and intercept (*b*) parameters were used. A plot is presented of the curve defined by the mean posterior intercept and slope values and a kernel density plot of the slope parameter posterior values (Fig. 3). The bulk of the posterior slope values were negative (Fig. 4*b*), supporting the hypothesis that fish that slowed down more in native eelgrass patches were less susceptible to predation during the study.

Discussion

Efforts to manage estuarine habitat to improve Pacific salmon growth and survival must be approached from a landscape perspective (Simenstad and Cordell 2000; Haggarty and Healey 2002; Bottom et al. 2005). Simenstad and Cordell (2000) proposed a conceptual framework for evaluating estuary habitat for Pacific salmon in terms of both opportunity (i.e., accessibility based on geography, oceanography, flow regimes, etc.) and capacity (i.e., opportunity for growth and survival based on biological interactions such as competition and predation). Ultimately, determining the opportunity and capacity afforded by an estuarine landscape requires both broad geographic information about the connectivity of habitat patches and an understanding of how the specific habitat components that comprise patches mediate biological interactions. Previously, studies addressing this latter information were limited by the tools available for collecting behavioral data at fine spatial and temporal scales in the estuary. The research presented here is the first to link benthic habitats with near-continuous fine-scale observations on multiple individuals over multiple days. Based simply on location point densities plotted over the benthic habitat of the enclosure, it appeared that tagged fish tended to stay deeper in the enclosure, near the net wall, and in patches of native eelgrass. The state–space modeling effort confirmed these relationships, expressed as adjustments to rates of movement.

Differences in position densities or rates of movement within a habitat type often, but not always, reflect differences in habitat quality (van Horne 1983; Winker et al. 1995). For instance, mobile animals may slow down over certain habitats owing simply to navigational hazards, regardless of habitat quality. The tagged fish in this study routinely re-

Fig. 3. Box plots of posterior values for the hyperparameters representing benthic habitat specific adjustments to population-level Chinook salmon (*Oncorhynchus tshawytscha*) movement rates using (*a*) daytime positions, (*b*) nighttime positions, and (*c*) both. For ease of interpretation, the posterior values for each benthic habitat hyperparameter are expressed as percent adjustments to the mean posterior value of the $\hat{s}$ hyperparameter (the base movement rate over open substrate). Negative values for a given habitat indicate that fish slow down; positive values indicate that fish speed up. Horizontal lines at zero on the *y* axes are provided to clarify the extent to which the posterior distributions are negative versus positive. The upper and lower ends of the boxes represent the 75th and 25th percentiles, respectively, and the whiskers depict the extent of the data.

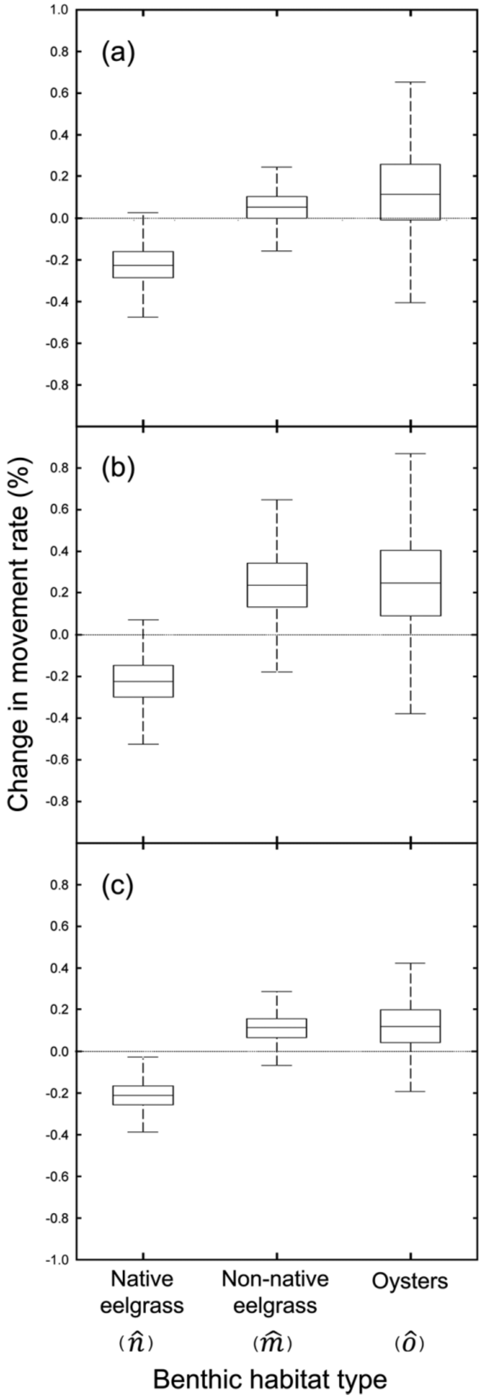
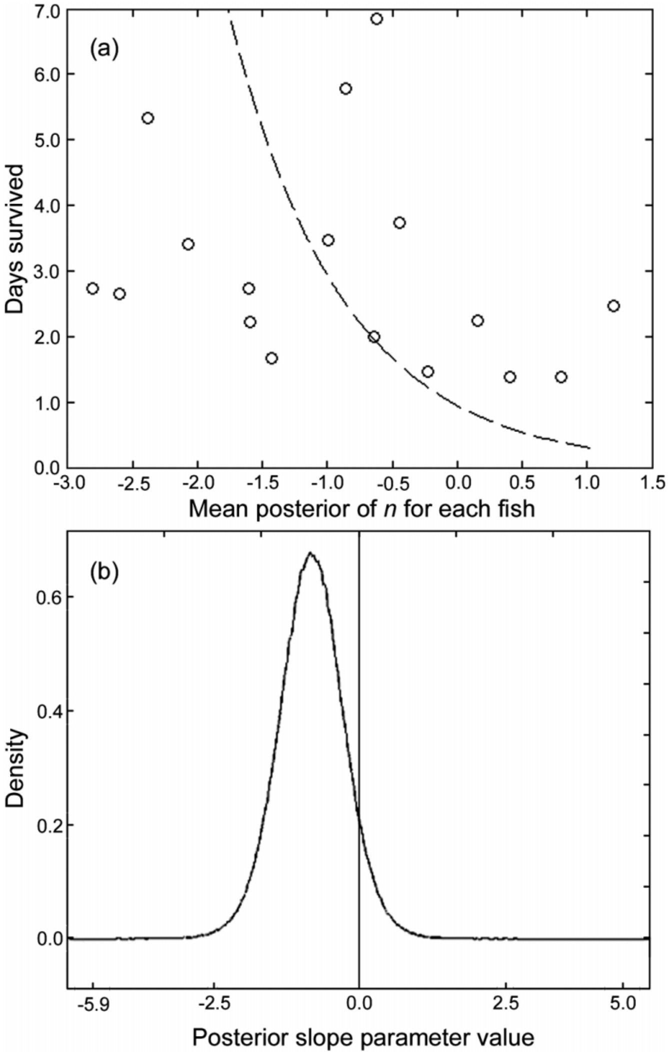


Fig. 4. (*a*) Scatterplot of the mean posterior values for $\bar{n}_i$, the adjustment to the rate of movement (metres per 30 s period) for each tagged individual while in native eelgrass, as a function of time (days) that each individual survived. The broken line represents the curve resulting from mean posterior values of the slope and intercept based on fitting the linear relationship between and log-transformed survival times (days). (*b*) Posterior distribution of the slope parameter. The plot includes a vertical line at zero on the *x* axis to demonstrate that most of the posterior density falls below zero.



mained in relatively small native eelgrass patches for long periods of time, suggesting a behavioral preference for the habitat rather than a simple mechanistic effect of habitat on movement. Ideally, the survival and production characteristics of habitats should be investigated to determine the extent to which habitat use or preference reflects habitat quality (van Horne 1983). Position densities, rates of movement, and patterns of survival in this study were all consistent with the hypothesis that native eelgrass is an important benthic habitat for juvenile Chinook salmon in the estuary.

The propensity of tagged individuals to remain in the deeper parts of the enclosure coincides with the results of previous large-scale netting studies that found that individuals of the size used in this study tended to be found in the deeper tidal channels of estuaries (Myers and Horton 1982; McCabe et al. 1986; MacDonald et al. 1987). Similarly, previous studies have demonstrated that fish of the size tagged move over much large areas than that encompassed by the enclosure on a daily basis (Levy and Northcote 1982). As such, it is not surprising that the tagged individuals spent a large proportion of their time along the net wall. The state–space model employed in this study explicitly accounted for and factored out the influence of depth and net-wall proximity in assessing the influence of benthic habitat on behavior. However, reducing habitat features such as depth to a single-parameter component of an equation describing movement may not capture the entirety of the complex and context-dependent influences of such habitat attributes. Given the lack of an obvious ecological explanation for the model support for increased movement rates in non-native eelgrass and oyster habitat and the fact that these habitats were specific to the mid-depth ranges of the enclosure, it is possible that the model results at least partially reflect an effect of depth not fully captured by the parameter q in the equation. In addition to the clear influence of the enclosure structure on the movement of fish, it is possible that the acoustic tags also modified fish behavior and susceptibility to predation (Bridger and Booth 2003). It seems unlikely, however, that the influence of the tags modified fish behavior to such a degree that responses to gross habitat features were substantially altered.

Juvenile Chinook salmon may slow down in native eelgrass because the habitat affords better foraging opportunities, better cover from predators, or both. Diet composition studies in both Willapa Bay (Dumbauld 2005) and Puget Sound (Brennan et al. 2004) suggest that Chinook salmon of the size used in this study feed predominantly on terrestrial insects, a food source that likely is not mediated by benthic habitat. Moreover, Hosack et al. (2006) found no difference between diversity and abundance of epibenthic fauna between eelgrass habitat and oyster habitat in Willapa Bay. These previous findings suggest that prey availability is probably not the principal reason that juvenile Chinook salmon slow down in native eelgrass habitat. On the other hand, the apparent relationship between native eelgrass use and the duration of survival in the enclosure suggests that native eelgrass plays an important role in predator avoidance. This is anecdotally supported by the fact that none of the tagged fish was preyed upon while in native eelgrass patches. Native eelgrass blades are taller and thicker than non-native eelgrass and therefore provide more vertical structure in the water column in which to hide. Additionally, native eelgrass tends to occur deeper in the intertidal than non-native eelgrass and may thus be ecologically more available as cover habitat given the proclivity for deeper water that Chinook salmon of the size tagged demonstrate.

Wild Chinook salmon smolts may not necessarily exhibit the same behavioral responses to habitat exhibited by the hatchery fish used in this study. Hatchery-reared salmonids tend to have lower survivorship than wild salmonids (Wales 1954; Kostow 2004). These differences have been attributed principally to the fact that hatchery fish have less well developed predator avoidance behaviors (Dickson and MacCrimmon 1982; Olla et al. 1998; Berejikian et al. 2003), tend to be more surface-oriented (Vincent 1960; Reinhardt 2001), and have elevated stress levels owing to handling (Olla and Davis 1989). This latter effect was unquestionably amplified in this study owing to transport, tagging, and introduction to a novel environment. Taken together, these hatchery-specific traits likely increased the susceptibility of the fish in this study to predation and may partially explain the high rate of mortality observed. Moreover, the fact that "naïve" smolts were used as subjects in this study may have masked even stronger behavioral responses to habitat (Healey and Reinhardt 1995).

Although a landscape perspective is critically important in the evaluation of habitat quality for Pacific salmon, it is difficult to enforce legislative rules aimed at preserving landscape features such as habitat matrices and connectivity. For this reason, management of estuarine habitats typically proceeds through the establishment and enforcement of simple conservation rules such as "no net loss of native eelgrass"; presumably, if well conceived, these rules scale across an estuary to approximate landscape management. An understanding of the relative importance of benthic habitat components for growth and survival will undoubtedly aid managers in the development of such scalable management actions. In other words, an assessment of the capacity and opportunity of benthic habitats requires an understanding of the ecological and physiological responses of juvenile salmon to habitat features. This is particularly true given that nearshore intertidal habitats in many Pacific coast estuaries are extensively used and manipulated by the aquaculture industry.

Aquaculture practices in Willapa Bay alter native eelgrass stands but do not exclude them. Approximately 10% of the total area of Willapa Bay is intensively cultured for bivalves (Feldman et al. 2000), and 10% of the Bay is covered by native eelgrass (Borde et al. 2003); the extent to which these benthic features overlap in the Bay is currently unknown. Even intensively cultivated areas of Willapa Bay have some coverage of native eelgrass (approximately one-third that of uncultivated sites; H.M. Tallis, Department of Biology, University of Washington, Seattle, WA 98195, USA, unpublished data), suggesting that the native eelgrass persists on cultivated intertidal areas, albeit with patchier distributions and lower percent cover. The overall mobility of Chinook salmon coupled with their ability to make use of relatively small stands of native eelgrass may allow for behavioral compensation in response to the reduction in native eelgrass resulting from cultivation. On the other hand, the extent to which compensatory behaviors can mitigate the impact of a reduction in habitat quality on growth and survival undoubtedly depends on the extent to which habitat quality is reduced. Future efforts to explicitly address differences in behavior across a gradient of habitat availability and quality may identify where such compensatory thresholds lie. The apparent similarity in habitat capacity provided by non-native eelgrass and oysters suggests that the common practice of assuming that native and non-native eelgrasses are ecologically equivalent may unduly burden the aquaculture industry during efforts to implement "salmon-friendly" management practices.

Life history traits specific to individuals or stocks play a fundamental role in the evaluation of habitat opportunity and capacity, as these traits dictate factors such as outmigration timing and estuarine residency (Bottom et al. 2005). Relatively large fish were used in this study because they were readily available from a nearby hatchery and because the size of the acoustic tags precluded the use of smaller fish. Although fish of the size used (<135 mm) are typically found in water shallower than 4 m (Dawley et al. 1981), they have a shorter estuarine residence than smaller subyearling migrants (Bottom et al. 2005) and are less dependent on shallow rearing habitats such as emergent marsh, tidal creeks, and associated dendritic channel networks (Levy and Northcote 1982; Gray et al. 2002). From a management perspective, it may therefore be tempting to downplay the importance of fine-scale benthic habitats in favor of larger-scale estuarine features such as deep tidal channels and salinity gradients for smolt-sized fish. However, the strong influence of benthic habitat on the behaviors of larger Chinook salmon juveniles identified in this study suggests that the benthic habitat plays an important role in survival during outmigration and should not be discounted in preservation and restoration actions aimed at conserving and recovering Chinook salmon stocks.

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