RESEARCH ARTICLE

Habitat associations and diet of young-of-the-year Pacific cod (*Gadus macrocephalus*) near Kodiak, Alaska

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Abstract The influence of environmental variables and habitat on growth and survival of juvenile gadoid species in the Atlantic has been clearly demonstrated; conversely, in the North Pacific little is known about the habitat and ecology of juvenile Pacific cod (*Gadus macrocephalus* Tilesius). The hypothesis that density of young-of-the-year (YOY) Pacific cod in nearshore habitats is predicted by shallow depth and the presence of eelgrass and macroalgae was tested in a variety of nearshore habitats adjacent to commercial fishing grounds near Kodiak Island, AK. From 10 to 22 August 2002, a beach seine and small-meshed beam trawl were used to capture YOY Pacific cod ($n = 254$) ranging from 42 to 110 mm fork length. Depth, water temperature, salinity, sediment grain size, and percent cover by emergent structure (i.e. tube-dwelling polychaetes, sea cucumber mounds, macroalgae) were measured prior to fishing. Density of YOY Pacific cod was highest in areas of moderate depth (15–20 m) and positively and linearly related to percent cover by sea cucumber mounds and to salinity. No previous studies have documented fish utilizing sea cucumber mounds as habitat. Furthermore, eelgrass and macroalgae were inconsequential to cod distribution. Diets consisted mainly of small calanoid copepods, mysids, and gammarid amphipods and were significantly related to cod length and depth. This work provides important information on previously undocumented factors that affect distribution and feeding of YOY Pacific cod, which ultimately influence growth and survival in this species.

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Introduction

Pacific cod (*Gadus macrocephalus*) support a valuable fishery in the Gulf of Alaska and regularly rank second in catch and product value in the Alaska groundfish fishery (see http://www.afsc.noaa.gov/species/Pacific_cod.htm); yet, surprisingly little is known about the ecology of its early life stages. Pacific cod spawn demersal and semi-adhesive eggs (Yamamoto 1939) and both incubation period and hatching success are temperature dependent (Forrester and Alderdice 1966). In laboratory studies with ambient water temperatures of 4.5–5.8°C from Chiniak Bay, AK, peak hatching occurred on day 21 (range 16–28 days; A. A. Abookire, unpublished data from March 2003). Larvae are pelagic and rise to the upper 45 m where they are transported toward shore (Rugen and Matarese 1988) and are generally observed between April and June around Kodiak (Dunn and Matarese 1987). By July, Pacific cod settle to the bottom and inhabit the demersal, shallow waters of coastal Alaska (Blackburn and Jackson 1982). Although large-scale distributions have been

described for adult Pacific cod (Shimada and Kimura 1994; Stepanenko 1995; Rovnina et al. 1997), no investigations have focused on nursery areas and habitat associations during the juvenile stage.

Knowledge of young-of-the-year (YOY) Pacific cod distribution and habitat associations is limited and is based on ancillary data from investigations on other species. In studies of juvenile groundfish in coastal Alaska, YOY Pacific cod were predominately captured at depths < 30 m (Blackburn and Jackson 1982; Laur and Haldorson 1996; Mueter and Norcross 1999; Abookire et al. 2000; Dean et al. 2000; Abookire et al. 2001). Young-of-the-year Pacific cod are closely associated with eelgrass in Prince William Sound, AK (Laur and Haldorson 1996; Dean et al. 2000, except see Rosenthal 1983) but not elsewhere in coastal Alaska (Murphy et al. 2000; Johnson et al. 2005). Clearly there is a need to identify and describe the habitats of YOY Pacific cod in relation to physical oceanographic properties, bottom type, and habitat complexity.

While information about YOY Pacific cod habitat is sparse, a number of studies have demonstrated the importance of substrate rugosity and complex nursery habitats for growth and survival of age-0 Atlantic cod, *Gadus morhua* (Keats et al. 1987; Lough et al. 1989; Gotceitas and Brown 1993; Tupper and Boutilier 1995; Lindholm et al. 1999). Furthermore, the availability of suitable nursery habitat may limit recruitment of Atlantic cod (Laurel et al. 2003b). Given that studies on Atlantic cod have demonstrated habitat-mediated growth and survival during the first year, it is appropriate to investigate the role of habitat in YOY Pacific cod growth, survival, and subsequent recruitment. However, before questions of habitat function and quality can be tested, the habitat associations of YOY Pacific cod must be defined.

The objective of this study was to determine habitat associations of YOY Pacific cod in Chiniak Bay, AK, located on the northeast side of Kodiak Island, where commercial fishing for Pacific cod is important and where juvenile Pacific cod have been captured previously (Mueter and Norcross 1999). Specifically, generalized additive models were used to relate the density of YOY Pacific cod to the following habitat variables: depth, temperature, salinity, sediment type, and percent cover by emergent structures (i.e. macroalgae, tube-dwelling polychaetes, and sea cucumber mounds). Additionally, diets were analyzed to identify prey consumed and examined for potential shifts related to size of Pacific cod and habitat. We tested the hypothesis that YOY Pacific cod would be distributed nearshore at shallow depths where eelgrass and macroalgae were present.

## Materials and methods

Field collections

From 10 to 22 August 2002, 66 stations were sampled along 10 transects in Chiniak Bay, AK, such that most transects had six stations (range = 4–13) at depths of < 5, 10, 15, 20, 25, and 30 m (Fig. 1). The transects covered approximately 32 km of coastline. Environmental variables were measured at each station: an underwater video camera with real-time video was used to measure habitat complexity (vertical relief, percent macroalgal cover, macroalgae species composition, percent cover of emergent structure), and either a beach seine or a small-meshed beam trawl was towed. All sampling was done from a 15.3-m commercial seine vessel during daylight hours.

Water temperature (°C), water salinity, and depth (m) were measured using a CTD (Seabird Electronics Inc, SBE-19 SEACAT profiler) at each station. Additionally, the top 3–7 cm of sediment was collected at each station with a 0.06-m^3 Ponar grab. Sediment samples were frozen and transported to the laboratory for grain-size analysis by sieving (Folk 1980). Substrate at a station was divided into four categories based on particle size: pebble (> 4 mm in diameter), gravel (2–4 mm in diameter), sand (0.07–1.68 mm in diameter), and mud (≤ 0.06 mm in diameter).

An underwater camera was used to classify percent cover of emergent structure and verify sediment type. At each station the camera, which was mounted on a vertical wing, was towed 1 m above the seafloor. The camera was towed parallel to the shoreline within ± 1 m of the targeted station depth at 1 kt for at least 6 min under ambient light conditions. In the field, real-time video was used to ensure a homogeneous habitat type along the station depth contour, and to confirm the beam trawl would not sample more than one habitat type. A trackline of the vessel's position was recorded and plotted throughout the camera tow and followed the same trackline with the bottom trawl. Beach seines were not as closely paired with real-time video from the underwater camera tow (see below). Video data were recorded and processed in the laboratory. Video data for each station were viewed at least once at normal speed and again at 1/3 speed. Each minute of video data was analyzed to estimate various measures of habitat complexity: emergent structure type and percent cover, bottom substrate type, and macroalga species and percent cover.

At stations ≤ 5 m depth, juvenile Pacific cod (*Gadus macrocephalus* Tilesius) were sampled with a beach seine. The beach seine was 43-m long, 4-m deep, and

Fig. 1 Study sites ($n = 66$) sampled in Chiniak Bay, on the northeast side of Kodiak Island, AK. Along 10 transect lines, *circles* denote sites sampled with a beach seine ($n = 11$) and *squares* denote sites sampled with a beam trawl ($n = 55$)
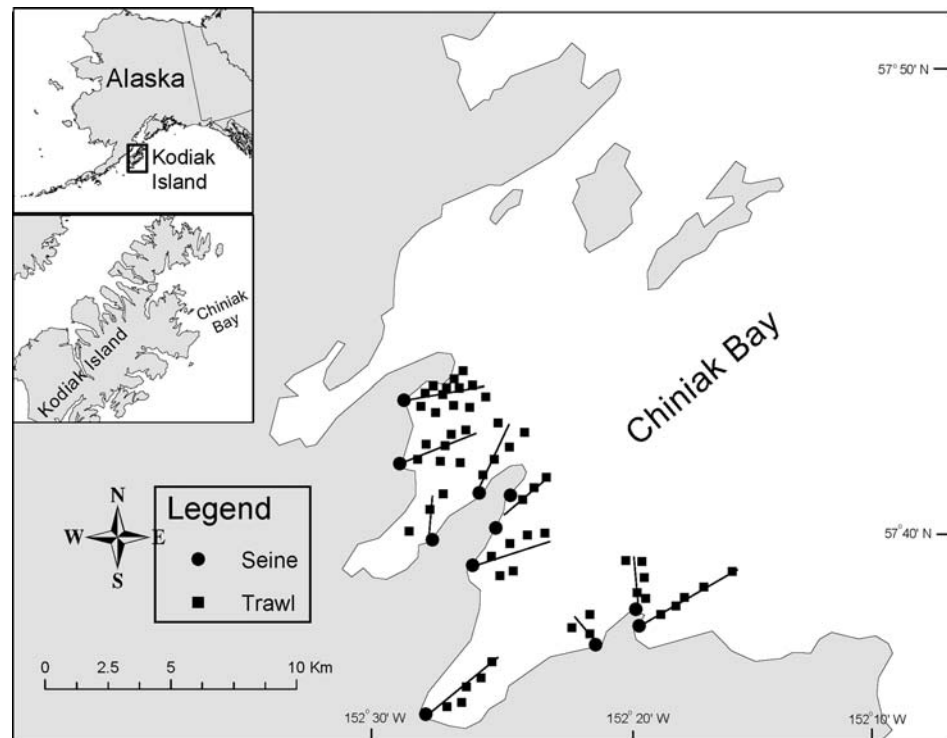
had a uniform mesh size of 13-mm. Twenty-five meters of line was attached to the wings for deployment. Using a skiff, the seine was set parallel to shore about 25 m from the beach and retrieved manually. All beach seines occurred within an hour of low tide, while the underwater camera was towed at either the preceding or following high tide to allow for the draft of the vessel. Due to indications that eelgrass (*Zostera marina*) may serve as habitat for YOY Pacific cod (Laur and Haldorson 1996; Dean et al. 2000), eelgrass beds, when present, were sampled with the beach seine.

At stations with depth 10–30 m, fish were sampled with a 3-m wide small-mesh beam trawl equipped with 10.2-cm disk groundgear (Abookire and Rose 2005). The net body was 7-mm square mesh with a 4-mm mesh codend liner, and the headrope height was approximately 80 cm. Standard tow duration was 5 min, and a towing speed of 1 kt (range 0.6–1.7 kts) was maintained with a trolling clutch. The scope ratio was 7:1 for depths ≤ 15 m and 5:1 for depths > 15 m (Abookire and Rose 2005). Fishing with the bottom trawl always followed the underwater camera tow; both were towed along the same trackline to ensure the habitat data were associated with the catch. The video and trawl tow directions were parallel to the shoreline to minimize microhabitat heterogeneity within a tow. Exact start and end positions of every fishing tow were measured with a global positioning system and used to

calculate the distance trawled. Trawl catches were standardized to catch-per-unit-effort (CPUE) for an area of 1,000 m². The area towed was calculated as the effective width of the net (2.1 m; Abookire and Rose 2005) multiplied by the distance trawled.

All fishes and invertebrates captured in beach seine and beam trawl tows were identified in the field to the lowest possible taxonomic level and counted. Fishes that could not be identified in the field were frozen and returned to the laboratory for identification. In the field, fork length (FL) of all non-gadid fishes was measured before they were released. However, if > 50 individuals of the same species were captured at a station, a random subsample of 50 individuals was measured. Gadids were frozen and returned to the laboratory for measurements of fork length (to the nearest 1 mm) and weight (to the nearest 0.1 g). Whole stomachs from the esophagus to the pyloric caeca were removed from freshly thawed Pacific cod and stored individually in a buffered 10% formalin-water mixture.

Preserved cod stomachs were blotted dry and weighed to the nearest 0.01 mg. Prey items were sorted and identified under a dissecting microscope to the lowest possible taxonomic level, counted, and weighed to the nearest 0.01 mg. Calanoid copepods were separated into two size classes: small calanoid copepods had prosome length < 2 mm and large calanoid copepods had prosome length ≥ 2 mm. Prey items were

categorized by condition using a relative scale of 1–4 ranging from total digestion to fresh prey, respectively. The overall condition of the entire stomach contents was also determined using this scale.

Statistical methods

A length-frequency histogram was plotted for Pacific cod, with FL grouped in increments of 5 mm according to fishing gear type. A *t* test was used to compare the mean FL of cod captured in beach seines and beam trawls.

Habitat

Generalized additive models (GAMs) were used to examine relationships between environmental variables and density of YOY Pacific cod. GAM analyses were initially conducted using binomial data (cod presence–absence) in response to bottom depth, bottom temperature, bottom salinity, sediment type (pebble/gravel, sand, or mud), percent tube worm cover, percent sea cucumber mound cover, and percent macroalgal cover. Percentage data were converted to decimal format and arcsine square root transformed to minimize heteroscedasticity. The sediment data were highly correlated and had significant interactions; therefore, a single sediment type categorical variable was created to avoid the problem of multicolinearity. GAMs were constructed using R software (see http://www.R-project.org) using a cubic spline smooth, the binomial family, the logit link function, and five degrees of freedom. Models were constructed in a reverse stepwise format, and terms were removed from the models such that each iteration removed the covariate that was least significant. The generalized cross validation (GCV) score was examined at each iteration to ensure that the smoothing parameter minimized the roughness penalty function.

The binomial GAM approach proved problematic as it appeared that the prevalence of zeros in the data set resulted in no significant effects of any tested environmental variables. To explore the data further, we used a subset of the data (collections made with trawls, 10–30 m) and used cod CPUE as the response variable. This approach also allowed us to utilize the greatest predictive power of the GAM analysis. In this case, CPUE was first transformed by fourth root transformation, and GAMs were constructed using the Gaussian family, the identity link function, and five degrees of freedom. Models were again constructed in a reverse stepwise format. The full model was the general form:

$$Y = \mu + \sum_{j=1}^{7} f_j(X_j) + \varepsilon,$$

where Y = the dependent variable, CPUE, μ = the intercept, j = the functions of X (depth, temperature, salinity, sediment type, tube worm cover, sea cucumber mound cover, and macroalgal cover), and ϵ = the error term.

A Burmann bootstrap procedure (a test for nonadditivity) confirmed that there were no significant factor interactions. The Burmann procedure was developed to check the additivity assumption of GAM models, essentially fitting the residuals of the GAM model with additive covariates to all possible interaction terms (Chan et al. 2003). Results were plotted with Bayesian 95% confidence intervals (see http://www.stats.gla.a-c.uk/~simon/simon/papers/pci.pdf) to graphically evaluate the effects of environmental parameters on Pacific cod density estimates. Because eelgrass was only present at beach seine stations (depth < 5 m), which were omitted from the GAM model, a separate analysis of variance (ANOVA) test was performed to investigate the effect of eelgrass on YOY cod density.

Diet composition

The index of relative importance (IRI) was used to determine the predominant prey items in YOY Pacific cod diet. It was calculated as IRI = (NC + GC) × FO, where NC is the percent numerical composition of prey items in a sample, GC is the percent biomass composition of prey items in a sample, and FO is the percent frequency of occurrence for that prey item (Hyslop 1980). IRI values from all prey items were summed to yield a grand total IRI value, from which the relative importance of each prey category was then expressed as a percentage (% IRI).

Non-metric multidimensional scaling (NMDS) was used to summarize patterns in prey composition of cod diets based on an ordination of pair-wise site dissimilarities following Field et al. (1982) and Mueter and Norcross (1999). NMDS was performed using R software (Venables and Ripley 2002, see http://www.R-project.org). Prey items were combined into larger taxonomic groups and considered in NMDS analyses if % IRI values were ≥ 0.010. Abiotic prey items such as sand were omitted from NMDS analysis, as were cod with empty stomachs ($n = 2$) or stomachs with mostly digested prey ($n = 1$). The dissimilarity in numerical composition (NC) of prey between each pair of cod ($n = 251$) was computed from fourth root-transformed prey data using the Bray-Curtis measure of

dissimilarity. This resulting Bray-Curtis site dissimilarity matrix was used as input for NMDS iterations.

The stress criterion (Kruskal 1964) was used to evaluate goodness of fit for the final NMDS model. The initial NMDS ordination was carried out in two dimensions, and the number of dimensions was increased until a Kruskal's stress value of about 15% was achieved (Kruskal 1964; Mueter and Norcross 1999). The orientation of axes derived from NMDS is arbitrary, and therefore the solution was rotated so the first axis corresponded to the axis of maximum variation (Field et al. 1982).

In the final NMDS configuration, station 'scores' which were derived from the Bray-Curtis dissimilarity matrix for each station along each axis, were used as indices of prey composition (hereafter referred to as diet-axes). Station scores were correlated with average numeric prey abundance along each of the rotated axes using Spearman rank correlation to interpret which prey items were represented by each diet-axis. Prey was associated with a diet-axis if the rank correlation was ± 0.30 or greater.

NMDS diet-axes were related to cod size (fork length) and environmental variables (depth, temperature, salinity, percent gravel, percent mud, percent tube worm cover, percent sea cucumber cover, and percent macroalgal cover) with multiple backward stepwise regression (BSR) models using SAS software, version 9.1 (SAS Institute Inc., 2004). Because multiple fish were caught from the same station the assumptions of independence needed for regression models is violated. Therefore, BSR analysis was used only to select the best models for input into randomization-tests (see below). To account for non-independence of cod size data, cod length was nested by station. Due to the inherent nature of colinearity among environmental parameters, principal component analysis (PCA) was first performed using SAS software (SAS Institute Inc., 2004) on the environmental variables. However, PCA results indicated that the first factor score only accounted for 19% of the variance among the environmental variables, and the combined variance explained by the first five factors was only 73%. Therefore, the actual environmental variables were used in BSR models. Each diet-axis was tested separately, and the partial R^2 value was calculated for all significant variables in the final regression models to determine the amount of variance explained by each variable. Significance for inclusion in these BSR models and for final overall model significance required $P < 0.05$.

Once final BSR models were selected, the significant variables from each final model were input into separate Monte Carlo randomization-tests using SAS

Software (SAS Institute Inc., 2004). Randomization-tests are valid even without random samples and they produce random probabilities (P^1 values) for variables that are free of assumptions of independence (Manley 1991). The randomization-test selected a random subset of 1,000 permutations based on the original dataset and calculated a P^1 value for each variable. The P values from the final BSR model were then compared with the P^1 values to examine the actual structure of the data compared with random rearrangements of the data. Significant P^1 values support the final regression model and yield valid significance despite the clear non-independence of the data (Manley 1991).

To determine if YOY Pacific cod size varied among habitats, average FL was examined in relation to environmental variables (depth, temperature, salinity, percent gravel, percent mud, percent tube worm cover, percent sea cucumber cover, and percent macroalgal cover) with BSR models (SAS Institute Inc., 2004) for all YOY cod combined. Significance for inclusion in these BSR models required $P = 0.10$, and overall model significance required $P < 0.05$.

Results

Microhabitat variables ranged widely among stations, with the exception of salinity, which differed by only one among stations (Table 1). Values of bottom temperature differed by 3.3°C. Substrate grain size compositions among stations ranged from 0 to > 90% pebble, gravel, sand, and/or mud. Habitat variables measured from the underwater camera video included percent cover of the following emergent structures: tube worms, sea cucumber mounds, and macroalgae. The emergent structure at a station ranged from 0 to 100% cover (Table 1). Tube worms formed dense mats resembling grass and were created by an unidentified species of polychaete worm (family Ampharetidae).

Table 1 Summary of habitat variables at 66 stations surveyed in Chiniak Bay, AK, in August 2002

Habitat variable	Mean	Minimum	Maximum
Depth (m)	17.4	5.0	32.0
Bottom temperature (°C)	9.7	8.1	11.4
Bottom salinity	32.1	31.7	32.7
Percent pebble (> 4 mm)	14.2	0.0	99.1
Percent gravel (2–4 mm)	8.1	0.0	64.8
Percent sand (0.07–1.68 mm)	46.4	0.3	98.4
Percent mud (≤ 0.06 mm)	31.3	0.0	90.7
Percent tube worms	15.1	0.0	80.0
Percent sea cucumber mounds	9.8	0.0	100.0
Percent macroalgae	14.5	0.0	80.0
Percent eelgrass	9.7	0.0	26.4

Sea cucumber mounds are conical structures created by the rat tail sea cucumber, *Paracaudina chilensis* (Lambert 1997). Over 15 species of algae were combined into the category 'macroalgae' for analyses. The most common macroalgae were *Desmarestia aculeata*, *Laminaria* sp., *Agarum clathratum*, *Ulva fenestrata*, and *Fucus gardneri*. Eelgrass (*Zostera marina*) was only present at depths < 5 m and occurred at 45% of the stations that were sampled with a beach seine. Eelgrass beds grew in small patches which measured approximately 3 m in diameter.

A total of 8,450 fishes representing 59 species were captured at 66 stations in Chiniak Bay, AK (Fig. 1). Due to the small meshes in the beach seine and beam trawl, the majority (91%) of fishes captured were < 150 mm FL. The most abundant species was northern rock sole (*Lepidopsetta polyxystra*). Pacific cod ranked seventh in abundance and were present at 41% of the stations sampled. Pacific cod (n = 254) ranged from 42 to 110 mm FL and, as estimated from their length-frequency distribution (Fig. 2), they were all considered to be YOY (Smith et al. 1984; Takatsu et al.1995; Abookire et al. 2001). Mean length of YOY Pacific cod was higher in beach seine than beam trawl catches (*t* test: t = 7.221, P < 0.001).

Habitat

Depth (P = 0.006), percent sea cucumber mound cover (P = 0.013), and salinity (P = 0.033) were all significant covariates affecting YOY Pacific cod density (GAM final model: n = 55, r^2 = 0.285, GCV = 0.617, P < 0.001; Table 2). These three covariates explained 35.5% of the variability in the distribution of YOY cod. Depth was non-linearly related to cod density with
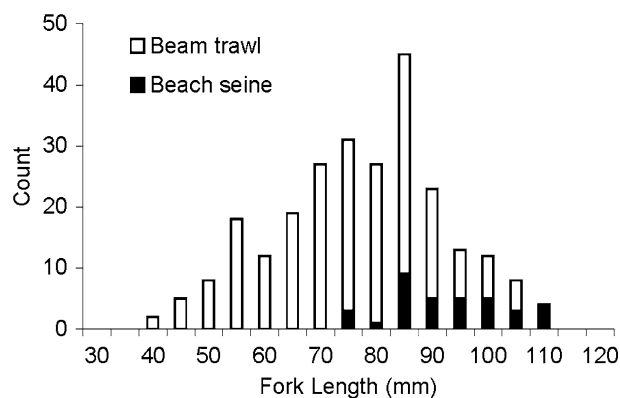
higher densities concentrated at moderate depths (15–20 m), declining at depths of 20–25 m, and increasing at depths > 25 m (Fig. 3). Percent sea cucumber mound cover and salinity were positively and linearly related to cod density (Fig. 3); however, due to the narrow range of salinity values among stations and the less significant P value, we considered the salinity result to be less robust than other significant variables affecting cod density. Beach seine catches of Pacific cod at stations ≤ 5 m (n = 11) were infrequent (18%) and were not related to the presence of eelgrass (ANOVA F = 1.32, df = 1, P = 0.2804).

Diet composition

Of the 254 cod stomachs analyzed, only 2 (0.8%) were empty. Most stomachs (66%) contained high quality prey which was less than half digested, suggesting that cod had fed recently. The predominant prey item in YOY cod diets was small calanoid copepods (Table 3). Other important prey groups were mysids and gammarid amphipods which, together with small calanoid copepods, accounted for 91% IRI.

The final NMDS ordination of species abundance considered 11 prey groups (Table 3) and had three dimensions (diet-axes) with a stress value of 16.4%. Each diet-axis represented a distinct group of prey items. Diet-axis 1 accounted for 64% of the overall variation in prey composition and had a strong positive rank correlation with mysids and strong negative rank correlations with small calanoid copepods, larval crabs,

Table 2 *Gadus macrocephalus*. Results of the full GAM model (GCV score = 0.683) and final GAM model (GCV score = 0.617) on the density of juvenile Pacific cod

Factor	P value
Full model	
Depth	0.019*
Temperature	0.406
Salinity	0.052*
Sediment category (pebble/gravel)	0.534
Sediment category (sand)	0.148
Sediment category (mud)	0.080
Worm tube cover	0.427
Sea cucumber mound cover	0.027*
Kelp and macroalgae cover	0.919
Final model	
Depth	0.006*
Salinity	0.033*
Sea cucumber mound cover	0.013*

Note that depth, salinity, and percent sea cucumber mound cover were significant factors in the full model (*), and removal of non-significant factors yielded increased significance of these parameters in the final model (GAM final model: n = 55, P < 0.001)

Fig. 2 *Gadus macrocephalus*. Length frequency histogram for Pacific cod (n = 254). Fork lengths ranged from 42 to 110 mm and were grouped in 5-mm intervals according to different fishing gears

larval barnacles, gammarid amphipods, and cladocerans (Fig. 4). Diet-axis 2 accounted for 24% of the overall variation in prey composition and had strong positive rank correlations with gammarid amphipods, annelid worms, isopods, and invertebrate tubes and strong negative rank correlations with larval barnacles and small calanoid copepods (Fig. 4). Diet-axis 3 accounted for 12% of the overall variation in prey composition and had strong positive rank correlation with small calanoid copepods and strong negative rank correlations with larval barnacles and larval crabs, a prey group consisting of planktonic zoeae and megalopae (Table 3). Amphipods and shrimp did not correspond with any of the three axes (Fig. 4), thus the variability in their distribution was not captured by the final NMDS configuration.

Backward stepwise regression models combined with randomization-tests were used to test for effects of cod size and habitat on diet composition (summarized by NMDS diet-axes). The final model for diet-axis 1 indicated a significantly positive effect of cod size on prey composition (BSR final model $R^2 = 53.8\%$, $n = 251$, $F = 47.42_{[6,244]}$, $P < 0.0001$); other variables such as tube worms, temperature, sea cucumber mounds, and macroalgal cover had a significant negative effect on diet-axis 1 but based on partial R^2 values cod size was the variable with the largest effect on diet-axis 1, explaining 21% of the variability in the model (Table 4). The final model for diet-axis 2 indicated a significantly positive effect of cod size and a significantly negative effect of depth on prey composition (BSR final model $R^2 = 38.9\%$, $n = 251$, $F = 25.91_{[6,244]}$, $P < 0.0001$); other variables such as salinity, temperature, and sea cucumber mounds had a significant negative effect on diet-axis 2 but to a lesser degree (Table 4). The final model for diet-axis 3 indicated a significantly positive effect of macroalgal cover, depth, mud, and temperature on prey composition (BSR final model $R^2 = 27.71\%$, $n = 251$, $F = 23.57_{[4,246]}$, $P < 0.0001$), with macroalgal cover explaining 21% of the variability in the model. In all cases the randomization-tests yielded significant P^1 values and confirmed the significance of variables selected in the BSR final models (Table 4).

The overall model for diet-axis 1 was more robust than the models for diet-axes 2 and 3. Cod size had a larger effect on the diet of YOY cod than habitat; although depth, macroalgal cover, and mud were also significant in several models (Table 4). Hence, diet-axis 1 increased positively with cod size such that larger YOY cod diets had more mysids; whereas smaller YOY cod predominately preyed on small calanoid copepods, larval cr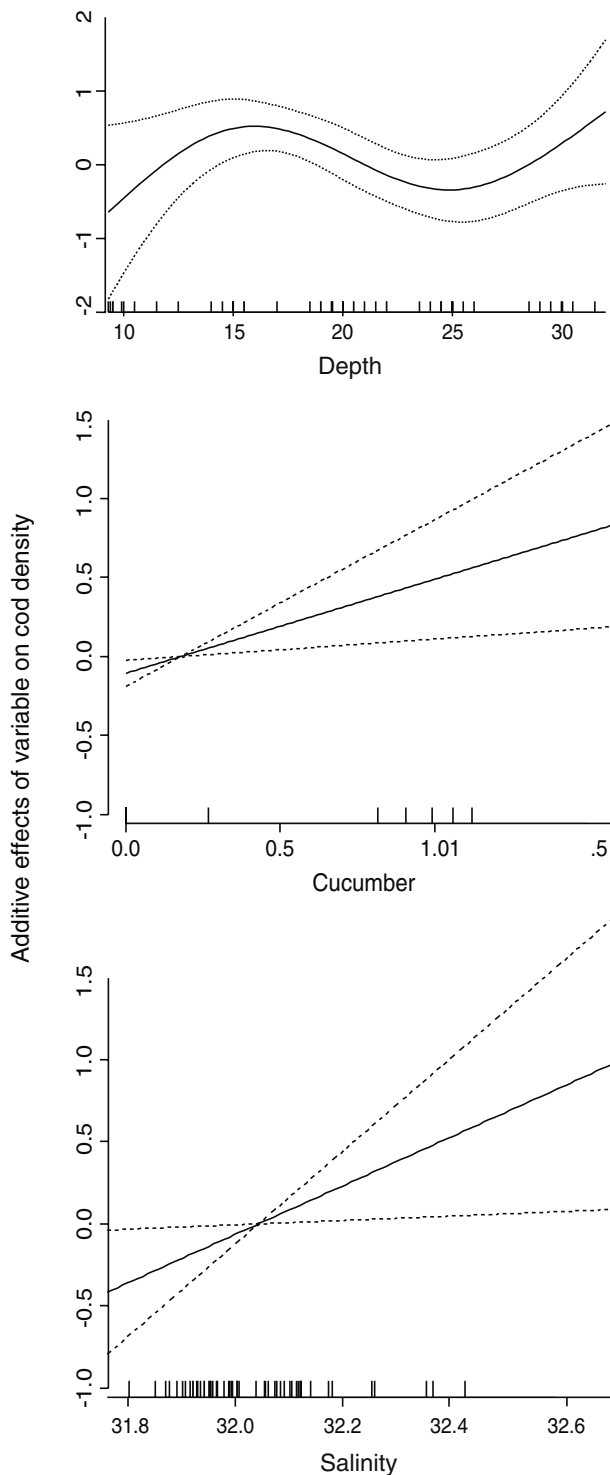abs, larval barnacles, gammarid amphipods, and cladocerans (Fig. 4). Likewise, diet-axis 2 was positively related to cod size and negatively related to depth which indicated that larger YOY cod present in shallower habitats had diets of gammarid amphipods, annelid worms, isopods, and invertebrate tubes and diets of smaller YOY cod in deeper stations consumed larval barnacles and small calanoid copepods (Fig. 4). The positive effect of macroalgae on diet-axis 3 suggests that YOY cod in high macroalgal cover have diets consisting more of small calanoid copepods and less of larval barnacles and larval crabs (Fig. 4). Generally, prey composition shifted with cod size such that smaller YOY cod predominately preyed on small calanoid copepods and larger YOY cod expanded their diets to include mysids and benthic prey items (Fig. 5).

Cod length was significantly positively related to percent gravel and percent tube worm cover (BSR final model $R^2 = 31.11\%$, $n = 27$, $F = 5.42_{[2,24]}$, $P = 0.0114$). These results suggest that larger YOY cod may utilize habitats with higher percent gravel sediment and higher percent tube worm cover (Table 5).

Discussion

The a priori hypothesis about YOY Pacific cod habitat, based on ancillary data from studies in coastal Alaska and research on juvenile Atlantic cod, was that they would be distributed nearshore at shallow depths where eelgrass and macroalgae were present. Instead, we found YOY Pacific cod density to be highest at depths of 15–20 m and positively linearly related to percent cover by sea cucumber mounds. Although salinity was statistically significant in the final GAM model (albeit less robust than depth or percent sea cucumber mound cover), the extremely narrow range of salinity values among stations suggested that salinity was not a biologically significant variable. Furthermore, eelgrass and macroalgae were apparently not related to YOY cod habitat. Previous studies in coastal Alaska have concluded that YOY Pacific cod were mainly distributed in waters < 30 m, but were occasionally captured as deep as 70 m (Smith et al. 1984; Mueter and Norcross 1999; Abookire et al. 2001). This finer-scale investigation of depths ≤ 30 m in August determined that cod density was highest at moderate depths (15–20 m), with some cod present outside this narrow depth range.

To our knowledge, sea cucumber mounds have not been known to provide habitat for any fish species. The sea cucumber, *Paracaudina chilensis*, which makes conical sediment mounds in Chiniak Bay, is widely

sediment surface (Lambert 1997). As the sea cucumber ingests sand, it forms a depression; after the organic particles are digested the excreted sand forms a conical mound, which is susceptible to perturbation and may be leveled in a severe storm (Yamanouchi 1926). However, because *Paracaudina chilensis* can process up to 8 g/h of sand (Lambert 1997), disturbed mounds can be reformed in hours to days (Yamanouchi 1926). Hence, while sea cucumber mounds are quickly re-formed, their presence as structured habitat is somewhat dynamic and may vary seasonally with storm frequency and severity. Given that YOY cod density was positively linearly related to sea cucumber mounds, these structures appear to be important habitat for YOY Pacific cod in Chiniak Bay; however, due to the limited spatial and temporal coverage of this study, we cannot predict the overall importance or function of sea cucumber mounds as habitat for YOY Pacific cod.

Because of the shallow depth range where eelgrass was present, we were unable to sample eelgrass habitats with the beam trawl due to vessel restrictions. Therefore, all eelgrass sites were sampled with a beach seine, which may have introduced bias in our results. Only Pacific cod ≥ 71 mm FL were caught in beach seines and the lack of smaller cod in seine catches may be attributed to mesh size and gear selectivity rather than habitat preference. Although smaller (44–55 mm FL) sculpins (*Myoxocephalus polyacanthocephalus* and *Blepsias cirrhosus*), flatfish (*Lepidopsetta polyxystra*), and Pacific sand lance (*Ammodytes hexapterus*) were captured regularly in our beach seine, variable-mesh beach seines used in southeast Alaska have sporadically captured smaller (21–67 mm FL) YOY Pacific cod (Johnson and Thedinga 2005). Regardless, since only YOY cod caught with the small-meshed beam trawl were analyzed in the GAM model, our habitat results are not influenced by this possible gear bias. The small-meshed beam trawl captured the full range of YOY cod lengths with the exception of the four largest fish measuring 106–110 mm. We are unable to report if larger YOY cod avoided the trawl, but it does

distributed along the entire Pacific Rim (Lambert 1997). From video analysis, *Paracaudina chilensis* mounds appear to be aggregated and measure 25–35 cm vertically (Spencer et al. 2005). *Paracaudina chilensis* grows to 20 cm in length, and lives with its head deep in the sand and the tail just below the

Table 3 *Gadus macrocephalus*. Stomach contents of juvenile cod listed by numerical composition (NC), mass (g) composition (GC), frequency of occurrence (FO), and percent index of relative importance (% IRI)

Prey name	NMDS prey group	NC	GC	FO	% IRI
Small calanoid copepods	Sm calanoid copepods	83.80	8.05	61.42	59.09
Mysidacea	Mysids	1.96	23.26	68.11	17.99
Gammarid amphipod	Gammarid amphipods	3.04	22.14	50.00	13.19
Pacifiacanthomysis nephrophthalma	Mysids	0.81	14.66	33.07	5.36
Unidentified	NA	0.32	4.23	42.13	1.18
Sand	NA	3.07	0.76	17.72	0.71
Larval crab unidentified	Larval crabs	0.98	0.92	24.02	0.48
Barnacle cypris and nauplii	Larval barnacles	1.26	0.09	33.46	0.47
Neomysis kadiakensis	Mysids	0.08	4.58	6.30	0.31
Larval mysid	Mysids	1.03	0.39	19.69	0.29
Polychaete	Annelid worms	0.12	1.74	7.09	0.14
Calliopius sp.	Gammarid amphipods	0.10	4.04	3.15	0.14
Cladocerans	Cladocerans	0.62	0.07	15.35	0.11
Idotea fewkesi	Isopods	0.13	1.61	5.51	0.10
Exacanthomysis alaskensis	Mysids	0.05	1.51	5.12	0.08
Valvifera	Isopods	0.07	1.37	3.15	0.05
Caprellidea	Gammarid amphipods	0.10	0.85	3.54	0.04
Flabellifera	Isopods	0.04	0.83	3.15	0.03
Amphipod unidentified	Amphipod unident	0.15	0.48	4.33	0.03
Isopod unidentified	Isopods	0.06	1.33	1.97	0.03
Invertebrate tube	Invertebrate tubes	0.24	0.20	5.91	0.03
Ampithoidae	Gammarid amphipods	0.03	0.92	2.76	0.03
Worms unidentified	Annelid worms	0.05	0.38	3.94	0.02
Pinnotheridae zoeae	Larval crabs	0.39	0.08	3.54	0.02
Disacanthomysis dybowskii	Mysids	0.03	0.55	2.36	0.01
Monstrilloida sp.	Sm calanoid copepods	0.20	0.03	4.33	0.01
Ampharetidae	Annelid worms	0.07	0.26	2.76	0.01
Shrimp unidentified	Shrimp	0.03	0.42	1.97	0.01
Nereidae	Annelid worms	0.01	0.52	1.57	0.01
Harpacticoid copepod	NA	0.12	0.01	6.30	0.01
Eggs unidentified	NA	0.28	0.02	2.76	0.01
Nematode	NA	0.04	0.08	4.72	0.01
Fish unidentified	NA	0.02	1.02	0.79	0.00
Anomuran zoeae	Larval crabs	0.15	0.03	1.97	0.00
Gnorimosphaeroma spp.	Isopods	0.03	0.28	0.79	0.00
Crangon alaskensis	Shrimp	0.00	0.57	0.39	0.00
Large calanoid copepod	NA	0.03	0.04	2.76	0.00
Anomuran megalopae	Larval crabs	0.01	0.10	1.57	0.00
Crangonidae	Shrimp	0.01	0.21	0.79	0.00
Synidotea spp.	Isopods	0.00	0.37	0.39	0.00
Capitellidae	Annelid worms	0.02	0.17	0.79	0.00
Larvacea	NA	0.10	0.07	0.79	0.00
Marsupium	Mysids	0.11	0.02	0.79	0.00
Neomysis rayi	Mysids	0.00	0.26	0.39	0.00
Copepod eggs	NA	0.09	0.00	0.79	0.00
Lumbrineridae	Annelid worms	0.00	0.18	0.39	0.00
Alienacanthomysis macropsis	Mysids	0.00	0.10	0.39	*
Euphausiids	NA	0.01	0.02	1.18	*
Aquatic insect or tick	NA	0.02	0.00	1.18	*
Cumacean	NA	0.01	0.01	1.18	*
Pinnixa spp. megalopae	Larval crabs	0.00	0.04	0.39	*
Podon spp.	NA	0.04	0.00	0.39	*
Paguridae spp. megalopae	Larval crabs	0.00	0.03	0.39	*
Oligochaeta	Annelid worms	0.00	0.02	0.39	*
Hydroids	NA	0.00	0.02	0.39	*
Hyperid amphipod	NA	0.00	0.01	0.39	*
Pteropod	NA	0.01	0.00	0.79	*
Pagurus ochotensis megalopae	Larval crabs	0.00	0.01	0.39	*

Table 3 continued

Prey name	NMDS prey group	NC	GC	FO	% IRI
Brachyuran zoeae	Larval crabs	0.01	0.00	0.39	*
Sipunculan	Annelid worms	0.00	0.01	0.39	*
Photis spp.	Gammarid amphipods	0.00	0.01	0.39	*

Prey groups not considered in NMDS analysis are signified with 'NA', and an asterisk (*) denotes a value < 0.001. Living and nonliving stomach contents are listed in order of decreasing % IRI

appear that the beam trawl is a more representative sampler of YOY cod than beach seines.

Eelgrass in Chiniak Bay was present at over a third of the stations shallower than 5 m, but was not associated with cod distribution. In Prince William Sound (PWS), AK, YOY Pacific cod were the most abundant fish in
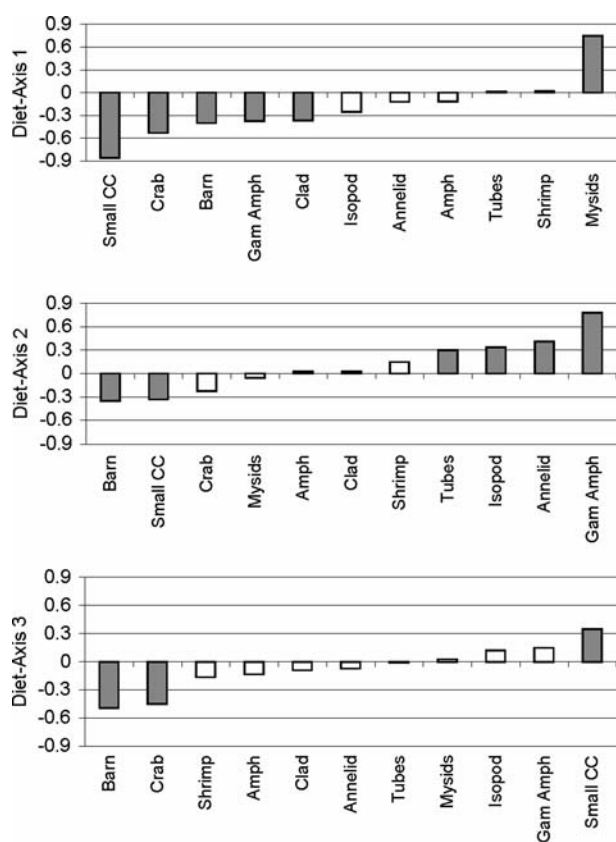
Fig. 4 Spearman rank correlation coefficients of final non-metric dimensional scaling (NMDS) scores correlated with 11 prey groups: small calanoid copepods (small CC), larval crabs (Crabs), larval barnacles (Barn), gammarid amphipods (Gam Amph), cladocerans (Clad), isopods, annelid worms (Annelid), unidentified amphipods (Amph), invertebrate tubes (Tubes), shrimp, and mysids. Prey groups were associated with a diet-axis if the Spearman rank correlation was ± 0.30 or greater (*filled bars*). Prey groups not associated with a diet-axis are shown with *unfilled bars*. Unidentified amphipods and shrimp did not correspond with any of the three axes. Note different order of prey groups along the *x*-axes

eelgrass beds from late May to early August (Laur and Haldorson 1996; Dean et al. 2000). However, in the late 1970s, YOY Pacific cod were mostly absent from eelgrass beds year-round in PWS (Rosenthal 1983). Additionally, in southeast Alaska, YOY Pacific cod were rare in eelgrass habitats sampled with beach seines in summer months (Murphy et al. 2000; Johnson et al. 2005). Murphy et al. (2000) could not explain the difference between the low catch of YOY Pacific cod in eelgrass in their study and the high association of cod and eelgrass in PWS (Laur and Haldorson 1996; Dean et al. 2000). They suggested it might be related to a lack of predator interactions because the function of eelgrass for juvenile Atlantic cod is to provide refuge (Keats et al. 1987; Gotceitas et al. 1997; Laurel et al. 2003a). The studies cited above all sampled during summer months from May to August, so seasonality does not explain the differences observed in eelgrass use by YOY cod among these study areas in coastal Alaska. It is possible that differences in gear types account for a portion of the variation among studies as beach seines (Murphy et al. 2000; Johnson et al. 2005), SCUBA diver surveys (Laur and Haldorson 1996; Dean et al. 2000), and SCUBA diver surveys combined with gill-nets (Rosenthal 1983) were employed. Furthermore, the high interannual variance in catches of YOY cod (Abookire et al. 2001; Johnson and Thedinga 2005) can complicate spatial comparisons from different years.

Another possible explanation for the lack of association between YOY cod and eelgrass beds in Chiniak Bay is that not all eelgrass beds provide equal habitat quality. The effectiveness of eelgrass as refuge for juvenile Atlantic cod depends both on the density of stems present, as the fish utilize *Zostera marina* habitats as refuge only when blade density is > 720 stems/m^2 (Gotceitas et al. 1997), and the area of the eelgrass patch (Laurel et al. 2003a). Eelgrass beds in PWS, which are vast and extend for miles, likely function differently than the small patches of eelgrass (approximately 3 m in diameter) observed in Chiniak Bay which may have insufficient biomass, blade density, or spatial coverage to provide refuge for YOY Pacific cod. Additionally, the quality of eelgrass can vary

Table 4 *Gadus macrocephalus*. Summary of significant variables remaining in the final backward stepwise regression models which tested for effects of cod length and habitat variables (depth, temperature, salinity, percent gravel, percent mud, percent tube worm cover, percent sea cucumber cover, and percent macroalgal cover) on prey composition of cod diets (Diet-axes 1–3)

Variable	Parameter estimate	Standard error	Partial R^2 (%)	P^1 value
Diet-axis 1				
Fork length	0.012	0.0012	21.0	< 0.0001
Tube worm	–0.007	0.0012	6.0	< 0.0001
Temperature	–0.495	0.0894	5.8	< 0.0001
Sea cucumber	–0.004	0.0009	3.5	< 0.0001
Mud	0.006	0.0017	2.3	0.0010
Macroalgae	–0.003	0.0014	1.1	0.0200
Diet-axis 2				
Fork length	0.006	0.0008	14.1	< 0.0001
Depth	–0.014	0.0022	10.8	< 0.0001
Salinity	–0.289	0.0745	3.8	< 0.0001
Temperature	–0.215	0.0644	2.8	< 0.0001
Sea cucumber	–0.002	0.0007	1.8	0.0080
Mud	0.001	0.0007	1.2	0.0230
Diet-axis 3				
Macroalgae	0.007	0.0008	21.0	< 0.0001
Depth	0.020	0.0026	16.7	< 0.0001
Mud	0.003	0.0004	10.7	< 0.0001
Temperature	0.094	0.0282	3.3	0.0010

Prey items were first summarized with NMDS into three distinct diet-axes (Fig. 4). Each diet-axis was tested separately and significance for overall models (in all three models: $n = 251$, $P < 0.0001$) is listed in the results. Variables are listed in decreasing order according to the partial R^2 value, which is the amount of variance in the model explained by the variable. The randomization probability value (P^1 value) is listed for each variable

interannually and spatially, as demonstrated in southeast Alaska where the mean area of an eelgrass patch varied from –13 to + 27 % between years and the eelgrass shoot density more than doubled between eelgrass beds < 25 km apart (Johnson and Thedinga 2005).
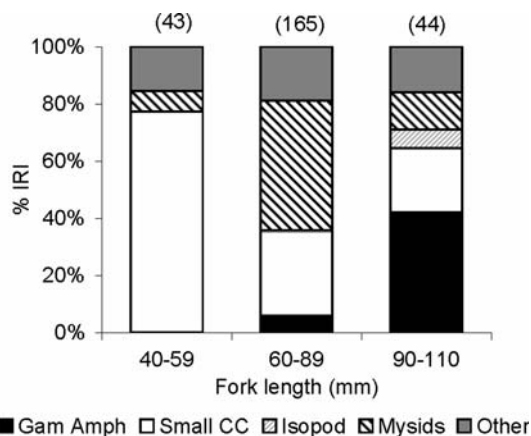
Fig. 5 *Gadus macrocephalus*. Juvenile cod diet by size group (fork length, *FL*) according to the prey groups gammarid amphipods (Gam Amph), small calanoid copepods (small CC), isopods, mysids, and other. Percent index of relative importance (% IRI) considers both numerical count and gravimetric weight of prey items (see Materials and Methods). The number of stomachs examined in each size group is listed in *parentheses above the bar*. All cod diet data are represented, except the two fish (FL = 70–79 mm) with empty stomachs

The role of fleshy macroalgae was also inconsequential for YOY Pacific cod habitat in Chiniak Bay. Juvenile Pacific cod were observed infrequently by SCUBA divers in kelp beds in Kachemak Bay, AK (Hamilton and Konar 2006), but this observation is complicated by the attraction of cod to the divers (J. Hamilton, personal communication). In other parts of coastal Alaska, YOY cod were absent in kelp and macroalgae (Murphy et al. 2000), occasionally present in kelp (Johnson et al. 2005), and negatively associated with the macroalga *Laminaria bongardiana* (Dean et al. 2000).

Habitat use by juvenile Atlantic cod shifts ontogenetically such that juvenile cod ≥ age-1 are found in greater density over coarse sediments like gravel, cobble, and boulder habitats that reduce vulnerability to predation (Gotceitas and Brown 1993; Fraser et al. 1996; Gotceitas et al. 1997; Cote et al. 2004). Larger juvenile Atlantic cod (10–12 cm) frequent gravel substrates rather than habitats with macroalgal cover (Gregory and Anderson 1997), and use of structurally complex habitats by older juvenile cod varies diurnally and seasonally (Cote et al. 2003). Correspondingly, as YOY Pacific cod increased in length they were found over habitats with higher percent gravel substrate and higher percent tube worm cover. Invertebrate tubes (from either polychaetes and/or amphipods) were a

Table 5 *Gadus macrocephalus*. Summary of significant variables remaining in the final backward stepwise regression model ($R^2 = 31.11\%$, $n = 27$, $P = 0.0114$) which tested if variability in cod length was related to habitat variables (depth, temperature, salinity, percent gravel, percent mud, percent tube worm cover, percent sea cucumber cover, and percent macroalgal cover)

Variable	Parameter estimate	Standard error	F value	P value
Percent gravel	0.534	0.221	5.84	0.0237
Percent tube worm cover	0.213	0.076	7.89	0.0097

main prey item for cod, and tube worm habitat may have provided important foraging opportunities for cod to prey either directly on the invertebrate tubes or on the crab megalopae that often associate with them (Stevens 2003). It is a fair assumption that several of the relevant biotic and abiotic factors that have strong habitat associations with Pacific cod in the study area may vary markedly at seasonal scales; however, despite the sampling occurring only in August we observed significant differences in habitat of YOY cod according to size.

Nearly 20% of cod stomachs from Chiniak Bay contained sand, but other studies (Takatsu et al. 1995; Laur and Haldorson 1996) did not mention the presence of sand or other sediment in cod stomachs. The appreciable sand content in YOY cod stomachs suggests that cod around Kodiak eat more benthic invertebrates and their feeding is closely tied to sediment. Because the residence time for cod within a microhabitat and the prey field at each site are unknown, the stomach contents may or may not represent the habitat where cod were captured. However, considering that fewer than 1% of cod stomachs were empty, most (66%) stomach contents contained high quality, undigested prey at capture, and most (73%) cod stomachs containing invertebrate tubes were captured in habitats with > 60% worm tube cover, there is a strong indication that cod were feeding at the capture location.

Young-of-the-year Pacific cod diets in Chiniak Bay were unusual in the large number of mysids and isopods consumed. In Japan (Takatsu et al. 1995) and in PWS, Alaska (Laur and Haldorson 1996), cod of similar size foraged mainly on calanoid copepods and gammarid amphipods. While larval crustacean decapods (specifically crabs) were also prey for cod in Japan (Takatsu et al. 1995), there was a notable absence of larval crabs in cod stomachs from PWS (Laur and Haldorson 1996). In Mutsu Bay, off the eastern coast of central Japan, Takatsu et al. (1995) documented a seasonal change in the diet of juvenile Pacific cod corresponding to increased length. Between April and June, cod (30–70 mm total length, TL) mainly consumed calanoid copepods along with larval crustacean decapods,

gammarid amphipods, larval gastropods, and cladocerans, but in July juveniles were larger (> 70 mm TL) and consumed shrimp, small crabs, and fish (Takatsu et al. 1995). Prey composition of cod diets in Chiniak Bay expanded with cod size from predominately small calanoid copepods to benthic prey items; a trend that has been observed for other gadoids and attributed to an increase in mouth gape (Lomond et al. 1998). Given that we did not sample the prey available at each site, it is not possible to say whether the observed geographic differences in YOY cod diets are attributable to geographic differences in prey availability.

The present study identified novel habitat associations for YOY Pacific cod, near Kodiak, AK, in spite of the low numbers of fish caught. Much research remains to be done, including the need to investigate why emergent structures such as sea cucumber mounds and eelgrass beds apparently constitute prime habitat in some areas of coastal Alaska but not others. Additionally, as it is unknown what size juvenile Pacific cod begin schooling, we are unable to address potentially important consequences of behavior and density-dependent habitat use that pertain to juvenile gadoids in the Atlantic (Laurel et al. 2004).

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