Abstract.–Juveniles of four species of pleuronectid flatfishes were abundant in bays and nearshore areas around Kodiak Island, Alaska, during August 1991 and 1992. The four most abundant species of juvenile (age-0 or age-1) flatfishes were rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), Pacific halibut (*Hippoglossus stenolepis*), and yellowfin sole (*Pleuronectes asper*). These species appeared to share nursery areas; however, physical characteristics of the nursery areas occupied by each species limited the amount of true overlap among species. Tree-based regression of catch-per-unit-of-effort data on physical parameters was used to refine conceptual models of species distribution, which were originally based only on 1991 data.

Threshold values of the physical parameters were specified that best discriminated among stations with different abundances. Highest abundances of age-0 rock sole were found on sand or muddy sand at temperatures greater than 8.7°C, as well as on other mixed sand stations less than 28 m deep. Age-0 flathead sole were most abundant at temperatures less than 8.9°C and on mixed mud substrates. At warmer temperatures, abundances were high only if the depth was greater than 48 m, regardless of sediment type. Age-0 Pacific halibut were most abundant in depths less than 40 m at sites more than 2.9 km outside the mouths of bays. Inside bays, halibut were found in lower abundances in water over 9.0°C and on sediments containing both sand and mud. Age-1 yellowfin sole were always found in depths less than 28 m on mixed mud substrates. They were usually found within bays, with highest abundances at heads of large bays more than 32 km from the bay mouth. These four most abundant flatfishes therefore appeared to partition the available habitat in ways that minimized resource competition.

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Habitat models for juvenile pleuronectids around Kodiak Island, Alaska*

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In the Gulf of Alaska, there are directed fisheries for deep-water and shallow-water complexes of fishes. The deep-water complex is made up of rex sole (*Errex zachirus*), Dover sole (*Microstomus pacificus*), Greenland halibut (*Reinhardtius hippoglossoides*), arrowtooth flounder (*Atherestes stomias*), and rockfishes (*Sebastes* spp.). The shallow water complex incorporates all other flatfishes found in the area, including rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), yellowfin sole (*Pleuronectes asper*), English sole (*Pleuronectes vetulus*), starry flounder (*Platichthys stellatus*), Alaska plaice (*Pleuronectes quadrituberculatus*), butter sole (*Pleuronectes isolepis*), and sand sole (*Psettichthys melanostictus*), in addition to Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Theragra chalcogramma*). The groundfish harvest from the Gulf of Alaska has been over 190,000 metric tons (t) annually from 1990 through 1995, for a total of 1,320,000 t, not including Pacific halibut (*Hippoglossus stenolepis*) or discards. Of that, in 1995, 716,000 t were landed in Kodiak, Alaska, for a value of $34 million (NMFS, Fisheries Management Div., P.O. Box 21668, Juneau, AK 99802-1668). When Pacific halibut, a species regulated separately from other groundfishes, is included, the total landed at Kodiak in 1995 was 75,000 t at $49 million. Although rockfishes (Carlson and Straty, 1981; Krieger, 1992, 1993), cod (Wespestad et al., 1986; Dunn and Matarese, 1987), and pollock (Janusz, 1986; Dunn and Matarese, 1987; Kendall et al., 1994; Müter and Norcross, 1994; Swartzman et al., 1994) have been studied in the Gulf of Alaska, very little is known about flatfishes (Parker, 1989; Moles and Norcross, 1995). The large abundance and value of these commercially important flatfishes and lack of knowledge of their early life history led us to investigate distribution of juvenile flatfishes around Kodiak Island.

In general, recently metamorphosed flatfishes recruit to shallow, nearshore nursery areas with fine-grained sediments (Edwards and Steele, 1968; Gibson, 1973; Toole, 1980; Hogue and Carey, 1982; de Ben et al., 1990). Intertidal zones, estuaries, and shallow protected bays are nursery areas for flatfishes in the continental United States (Krygier and Pearcy, 1986; Allen, 1988; Rogers et al., 1988; Wyanski, 1990), Canada (Tyler, 1971), Europe

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(McIntyre and Eleftheriou, 1968; Gibson, 1973; Lockwood, 1974; Poxton et al., 1982; Poxton and Nasir, 1985; van der Veer and Bergman, 1986), and Japan (Tanaka et al., 1989). Abundance and size distributions have been related to water depth (Edwards and Steele, 1968; McIntyre and Eleftheriou, 1968; Lockwood, 1974; Riley et al., 1981; Poxton et al., 1982; Wyanski, 1990), sediment size (Poxton et al., 1982; Poxton and Nasir, 1985; Wyanski, 1990; Jager et al., 1993; Keefe and Able, 1994; Moles and Norcross, 1995), and food availability (McIntyre and Eleftheriou, 1968; Allen, 1988; Jager et al., 1993). The generally accepted rationale for juvenile recruitment to shallow, fine-grained nursery areas includes escape from predation, increased cover and food availability, and decreased intraspecific food competition (Toole, 1980; de Ben et al., 1990; Minami and Tanaka, 1992). The examination of diet diversity among a subset of the fishes in the present study showed a reduction of both interspecific and intraspecific dietary overlap when flatfishes coexisted in large abundances (Holladay and Norcross, 1995).

The coastline of Kodiak Island, Alaska, encompasses a variety of habitats from shallow, fine-grained tidal flats to deep and rocky areas. Kodiak Island is mountainous and cut by many fjords and open bays with shallow waters (<10 m) usually within 0.5 km of the beach. The tidal range is 3 to 4 m. The region is characterized by deep bays, rough bottom topography, strong currents, and bottom characteristics that change rapidly over relatively short distances. Around Kodiak Island, juvenile flatfishes occupy fine-grained sediments in bays and nearshore waters, as do flatfishes in other locations, but waters less than 10 m in depth are only a minor component of the area that is used (Norcross et al., 1995).

A nursery may be partitioned into areas dominated by individual species or intraspecific age groups (Edwards and Steele, 1968; Zhang, 1988; Harris and Hartt[1]; Smith et al.[2]). Habitats occupied by juvenile rock sole, flathead sole, Pacific halibut, and yellowfin sole collected on the east and south sides of Kodiak Island in August 1991 can be differentiated on the basis of depth, substrate, and within-bay distribution (Norcross et al., 1995).

We used linear discriminant functions to identify tentively the habitat characteristics of juvenile flatfishes with data collected in August 1991 along east and south Kodiak Island (Norcross et al., 1995). In this study, we repeated the linear discriminant function analysis with combined 1991–92 data to include observations from a much wider geographic area around the entire island of Kodiak collected in August 1992. We refined our previous habitat models by using tree-based regression methods (Venables and Ripley, 1994) on catch-per-unit-of-effort data.

Materials and methods

Sample collections

Two cruises were conducted in the nearshore waters of Kodiak Island, Alaska, during August 1992 (Fig. 1). These cruises were similar to, but covered more area than, two cruises conducted in August 1991 (Norcross et al., 1995; Norcross et al.[3]). Cruise KI9201 consisted of collections taken with a 7.3-m skiff from Kalsin, Middle, and Womens Bays near the town of Kodiak during 9–14 August 1992. Because these bays were sampled with a skiff, extremely shallow collections could be made. Collections ranged in depth from 1 to 60 m. Ten stations were occupied in Kalsin Bay, six stations in Middle Bay, and five stations were occupied within Womens Bay. Kalsin and Middle Bays were also sampled during August 1991.

Immediately following the sampling from the skiff, a counterclockwise circuit of Kodiak Island was completed aboard a 24.7-m chartered trawling vessel (FV *Big Valley*, cruise KI9202). Collections during KI9202 were made from 16 to 29 August 1992 and ranged in depth from 5 to 180 m. Areas sampled in 1992, but not sampled in 1991, included 52 stations in bays on the north and west sides of the island. Collections were also made at 41 stations off south Kodiak, Sitkalidak Strait, and in Ugak Bay, which were sampled during August 1991.

Sampling gears, vessels, and vessel operators were the same in both 1991 and 1992 (Norcross et al., 1995; Norcross et al.[3]; Norcross et al.[4]). At each station one sediment sample was collected with a 0.06-m^3 Ponar grab for analysis of grain size, and a portable conductivity, temperature, and depth (CTD) profiler was deployed to measure temperature and salinity. Fishes

[1] Harris, C. K., and A. C. Hartt. 1977. Assessment of pelagic and nearshore fish in three bays on the east and south coasts of Kodiak Island, Alaska: final report. *In* Volume 1: Environmental assessment of the Alaskan continental shelf, p. 483–688. U.S. Dep. Commer., and U.S. Dep. Interior Quarterly Reports of Principal Investigators, Anchorage, AK.

[2] Smith, R. L., A. C. Paulson, and J. R. Rose. 1976. Food and feeding relationships in the benthic and demersal fishes of the Gulf of Alaska and Bering Sea. *In* Volume 7: Environmental assessment of the Alaskan continental shelf, p. 471–508. Annual Report RU 0284.7. U.S. Dep. Commer. and U.S. Dep. Interior Environmental Research Laboratories, Boulder, CO.

[3] Norcross, B. L., B. A. Holladay, and M. Frandsen. 1993. Recruitment of juvenile flatfish in Alaska, phase 1. Final Contract Report, NOAA NA-16FD0216-01, 504 p.

[4] Norcross, B. L., B. A. Holladay, F.-J. Müter, and M. Frandsen. 1994. Recruitment of juvenile flatfish in Alaska, phase 2. Final Contract Report, NOAA NA-26FD0156-01, 653 p.

were collected on rising tides during daylight hours by using a modified 3.7-m plumb staff beam trawl with a double tickler chain (Gunderson and Ellis, 1986). Tows of 10-min duration were made at the approximate speed of 0.5–1.0 kn from both the skiff and the trawler.

Sample processing

Substrate type, water depth, bottom temperature, bottom salinity, and distance from the mouth of the nearest bay were evaluated for each station. Sediment samples were analyzed, as in 1991, by means

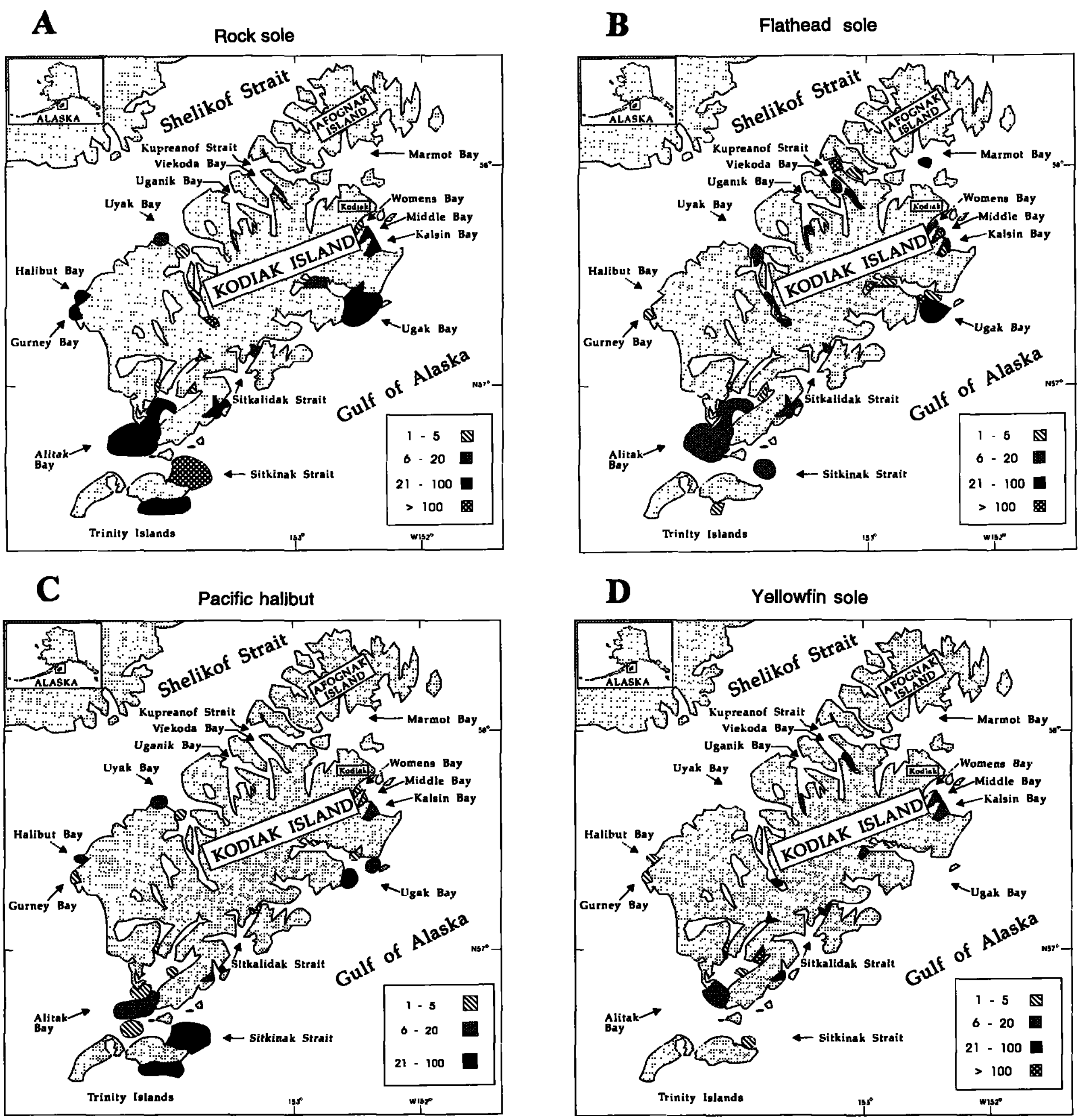

Figure 1

Distribution (CPUE) of (**A**) age-0 rock sole, (**B**) age-0 flathead sole, (**C**) age-0 Pacific halibut, and (**D**) age-1 yellowfin sole in August 1991 and 1992.

of a simplified sieve and pipette procedure to obtain the percents of gravel, sand, and mud (Norcross et al., 1995).

Distance from the mouth of the bay was used as a relative index of fish distribution with respect to station position within or outside the bay. Distance from each station to the nearest position at the mouth of a bay was calculated by drawing a line on a chart across the bay mouth between the two outermost capes. The shortest distance from the station to any position on this line was measured. Stations inside the mouth were designated as positive distances, and stations outside of bays were assigned negative distances. The narrowest point of Sitkinak Strait was considered the "mouth" of the bay; stations to the west of that point were considered within the bay and the exposed stations in the open ocean on the east side of Sitkinak Strait were considered outside the mouth.

Flatfishes were identified, and total length (mm) was measured in the field with a Limnoterra electronic, digital fish-measuring board. Ages of flatfishes captured in August 1992 were estimated with 1) length-frequency plots of fishes collected August 1992 (Norcross et al.[4]), 2) length-frequency plots (Norcross et al.[3]) and analysis of regional differences in total lengths (Norcross et al., 1995) of fish caught during August 1991, and 3) available literature (Southward, 1967; Best, 1974, 1977; Walters et al., 1985; Harris and Hartt[1]; Blackburn and Jackson[5]). Fish lengths were used to separate age classes of juvenile flatfishes. Catch per unit of effort (CPUE) based on a 10-min tow time was calculated for age-0 and age-1 individuals of each species. Habitat models were developed for the most abundant species and age-class combinations.

Statistical analyses

Linear discriminant function analysis of combined 1991–92 data included the broad range of conditions sampled around Kodiak Island. Canonical loadings of each variable and misclassification rates based on cross-validation were evaluated as outlined in Norcross et al. (1995) to test whether the same parameters had been selected as the best discriminators as those that had been selected solely on 1991 data. The magnitude of the canonical loading of each variable in the discriminant analysis is a measure of the importance of that variable in separating the stations with (presence) and without (absence) the fish species under consideration. The success of each combination of variables in assigning a new station to the presence or absence group can be evaluated by using misclassification rates from cross-validation.

The combined 1991 and 1992 data were further used to calculate Spearman's rank correlation (rho) between the abundance of each fish species and each physical parameter. The significance of rank correlations was evaluated at the 95% level. The nonparametric test with Spearman's rho was chosen because of non-normality of the CPUE data (even after transformation) and because of the high sensitivity of the parametric correlation coefficient (Pearson's r) to outliers. To maintain an overall confidence level of 95%, a Bonferroni-adjusted critical level of $\alpha = 0.025/28 = 0.001$ was used for the two-tailed test and for 28 comparisons (4 species × 7 variables).

To refine our previous habitat models, which were based primarily on presence or absence data (Norcross et al., 1995), we used regression trees to model CPUE as a function of habitat parameters. We used the same parameters as in the discriminant analysis, except instead of percentages of gravel, sand, and mud in the substrate, we used a categorical description of sediment type based on Folk (1980), i.e. sand (S), mud (M), gravel (G), and the modifiers of these substrates, such as sandy mud (sM), sandy gravelly mud (sgM), etc., 12 categories in all. This categorical classification avoided problems with high correlations among the three sediment variables. Both continuous and categorical predictor variables can easily be accommodated in regression trees.

The regression tree used the logarithm of CPUE (log(CPUE+1)) as the response variable and depth, distance from mouth of bay, bottom temperature, bottom salinity, and sediment type as predictor variables. A regression tree progressively splits stations on the basis of their values for one of the predictor variables until a leaf or terminal node is reached. Each leaf gives a predicted value of the response variable for the stations assigned to the leaf. The fit of the model is measured by the deviance, which is defined as

$$D = \Sigma_i (y_i - \mu_{[i]})^2,$$

or the sum of the squared differences between y_i = log(CPUE+1) at each station i and $\mu_{[i]}$ = the mean for all stations i at a leaf. The deviance is defined for the entire tree, as well as for each leaf, and is the analogue of the sum of squares in regression models. Each successive partitioning of the data reduces the deviance. For noisy data, the regression tree may overfit the data, resulting in an overly complex tree

[5] Blackburn, J. E., and P. B. Jackson. 1982. Seasonal composition and abundance of juvenile and adult marine finfish and crab species in the nearshore zone of Kodiak Island's east side during April 1978 through March 1979. *In* Outer continental shelf environmental assessment program, p. 377–570. U.S. Dep. Commer., Final Reports of Principal Investigators 54.

(Venables and Ripley, 1994). Therefore the initial tree was pruned to an optimum number of terminal nodes as determined by cross-validation.

Cross-validation as implemented in S-Plus (Venables and Ripley, 1994) uses 90% of the data as a training set to grow the tree and test it on the remaining 10%. This procedure is repeated 10 times with nonoverlapping test sets. Predictions on the test set are done for the initial tree as well as for trees pruned to smaller sizes. The resulting deviances are computed and plotted against tree size. Deviances typically are minimized at an intermediate tree size. We chose as optimum tree size the largest size before a marked increase in deviance occurred.

Results

Rock sole was the most abundant flatfish captured in our 1992 sampling (67% of flatfish), as in 1991 (51% of flatfish). In 1992, a total of 4,625 age-0 rock sole (17–60 mm TL) were collected across almost all locations, with the highest CPUE in the Sitkinak Strait region (Fig. 1A). Age-0 rock sole were found mainly near the mouths of bays ± 8–10 km, except for a single large catch at the head of Uyak Bay. Age-0 rock sole were somewhat more abundant with increasing depth between 0 and 30 m, and were collected in high numbers to 70 m, although they were also found deeper than 70 m. Age-0 rock sole were collected in large numbers between 7.5°C and 9.5°C and were most often found at salinities of 32.5–33.0 psu (Norcross et al.[4]). Rock sole were predominantly distributed on sand and mixed sand substrates. Although found at almost all combinations of depth and sand, rock sole were somewhat more concentrated in shallow, sandy locations (Fig. 2A). Spearman's rank correlation coefficients (Table 1) indicated that rock sole abundance was positively correlated with percent sand in the substrate and negatively correlated with depth, distance from mouth of bay, gravel, and mud. Rank correlation was highest with percent sand in the substrate.

Flathead sole increased from 12% of the 1991 catch to 18% of the 1992 catch. We captured 1,079 age-0 flathead sole (23–52 mm TL) during 1992. The distribution of flathead sole was more restricted than that for rock sole. Age-0 flathead sole were found almost everywhere around the island but were found in reduced numbers in Southeast Kodiak (Fig. 1B).

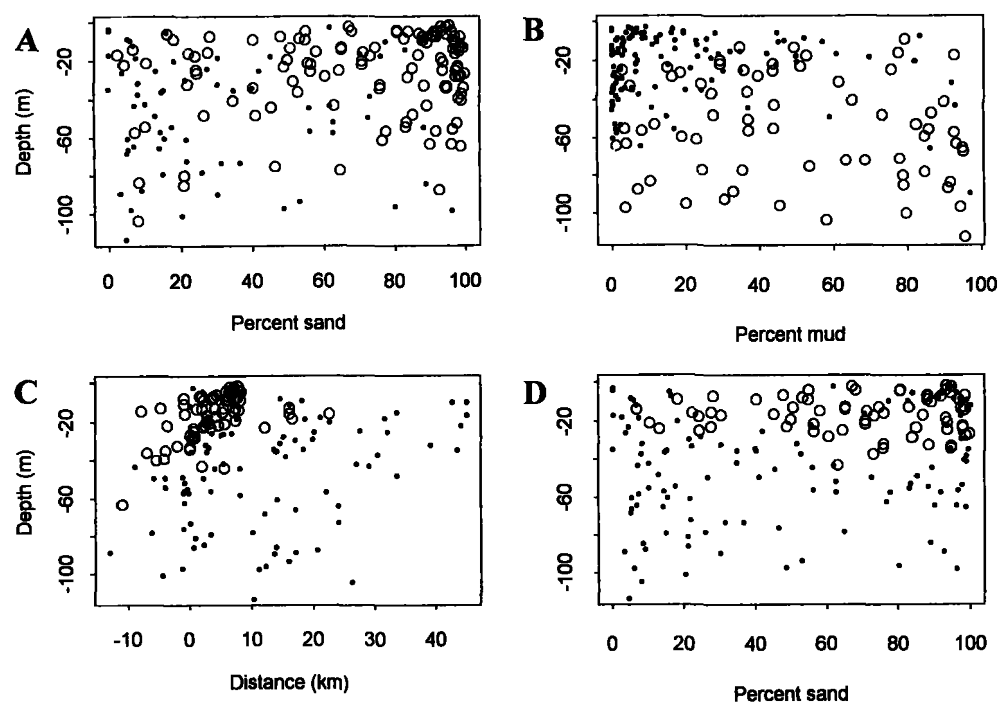

Figure 2

Presence (circles) and absence (dots) of (**A**) age-0 rock sole, (**B**) age-0 flathead sole, (**C**) age-0 Pacific halibut, and (**D**) age-1 yellowfin sole plotted against the two "best" discriminator variables. The depth axis is plotted with a 120-m limit, and data points occurring between 120 and 180 m are plotted at 120 m.

They were concentrated mainly in central, deep areas of bays at depths of 80–120 m, 6.0–9.0°C, 31.5–33.5 psu, on mud or mixed mud substrates (Norcross et al.[4]). High abundances of flathead sole were associated with deep stations, low temperatures, high salinities, low sand content, and high mud content; the highest rank correlations for flathead sole were obtained for depth and mud (Table 1). Flathead sole were predominantly collected in depths > 40 m, except on substrates with a high mud content (Fig. 2B).

Pacific halibut composed 5% of the catch in 1991 and 7% in 1992. During 1992, 627 age-0 halibut (22–84 mm TL) were found in exposed sites at all locations on the east and south sides of Kodiak Island (Fig. 1C). In northwestern Kodiak, halibut were collected only at the mouth of Uyak Bay. Age-0 halibut were found mainly at 10–70 m depth, 7.0–10.5°C, 32.0–33.0 psu, on mixed sand substrates, outside of or within 7 km of bay mouths (Norcross et al., 1995). Pacific halibut abundances were positively correlated with temperature and sand content and negatively correlated with depth, distance from mouth of bay, and mud content in the substrate. The highest rank correlations were with sand and mud (Table 1). Unlike rock sole, halibut were seldom found in water deeper than 50 m. Halibut juveniles, like rock sole, were concentrated most often in shallow waters with sandy substrate, near or outside mouths of bays (Fig. 2C).

Yellowfin sole was very abundant in 1991, composing 28% of captured flatfishes, but this species represented only 4% of the 1992 total catch. Unlike the other three species examined, in which age-0 fish predominated, age-1 yellowfin sole (41–105 mm TL) were analyzed in both 1991 and 1992 because of the small number (n=4) and size (15–20 mm TL) of age-0 yellowfin sole collected during the second year. During 1992, 268 age-1 yellowfin sole were collected at depths less than 40 m, mainly between 5 and 30 m. Age-1 yellowfin sole were found near the heads of bays, in warm (9.0–11.5°C) saline (31.0–33.5 psu) water (Norcross et al., 1995). They were collected on sandy mud, gravelly muddy sand, and muddy sand. Unlike rock sole and halibut, yellowfin sole were collected in the inner reaches of bays around Kodiak Island (Fig. 1D). The only significant correlation between yellowfin sole abundance and an environmental variable was a negative rank correlation with depth (Table 1). Yellowfin sole were never found deeper than 50 m and were always on mixed substrate, i.e. not predominantly on one grain size (Fig. 2D).

Linear discriminant function analysis for the combined 1991–92 data resulted in depth having the highest correlation with discriminant scores (canonical loadings) for flathead sole and yellowfin sole (Table 2). Sand was most highly correlated with the discriminant scores for rock sole and Pacific halibut. For all species, except flathead sole, the three highest canonical loadings were obtained for depth, temperature, and sand. In the case of flathead sole, mud was more highly correlated with the discriminant score than was sand.

Sand was clearly a good predictor for rock sole presence and was included in the habitat model for rock sole. Depth and temperature performed equally well in the discrimination owing to their high (negative) correlation. However, although rock sole abundance was significantly correlated with depth, the correlation with temperature was not significant. Therefore, sand and depth seemed to be the most important variables determining rock sole distribution (Fig. 2A).

The three best predictor variables for flathead sole were depth, gravel, and mud. Of these, depth and mud resulted in the lowest total error rates. Because

Table 1

Spearman's rank correlation coefficients between CPUE of four flatfish species and environmental parameters with 1991 and 1992 data combined. * indicates significance at an overall 5% confidence level.

Parameter	Rock sole	Flathead sole	Pacific halibut	Yellowfin sole
Depth	–0.258*	0.644*	–0.284*	–0.369*
Distance	–0.308*	–0.074	–0.314*	0.204
Temperature	0.193	–0.467*	0.346*	0.212
Salinity	–0.083	0.246*	–0.163	–0.192
Gravel	–0.240*	–0.219	–0.078	–0.168
Sand	0.583*	–0.219	0.449*	0.113
Mud	–0.310*	0.540*	–0.417*	0.188

Table 2

Canonical loadings from linear discriminant function analysis for combined 1991 and 1992 flatfish data.

Parameter	Rock sole	Flathead sole	Pacific halibut	Yellowfin sole
Depth	–0.557	–0.776	–0.620	–0.696
Distance	–0.379	–0.011	–0.501	0.234
Temperature	0.474	–0.597	0.647	0.545
Salinity	0.180	–0.225	–0.026	–0.005
Gravel	–0.453	0.321	–0.249	–0.377
Sand	0.783	0.220	0.655	0.406
Mud	–0.391	–0.624	–0.473	–0.099

these variables also had the largest rank correlations with abundance (Table 1), they were likely to be the most important parameters for flathead sole distribution. The error rates for predicting absence of flathead sole were consistently much lower than those for predicting presence.

Pacific halibut presence or absence could be most accurately predicted by using either depth or temperature with either distance or sand. Halibut abundance had a higher rank correlation with temperature than with depth and a higher correlation with sand than with distance from the mouth of the bay (Table 1). It is difficult to evaluate the relative importance of depth and temperature and of sand and distance owing to high correlations among these variables (Fig. 3). The depth-temperature factor explained most of the observed distribution. The error rates for predicting presence or absence changed significantly only if both depth and temperature were excluded. Error rates for stations where Pacific halibut were present were consistently much lower than those for stations where no halibut were found, thus this species appears to be strongly associated with specific habitat characteristics.

The three best predictors for yellowfin sole were depth and gravel combined with either sand or temperature. Of these, depth and gravel resulted in the lowest total error rates. Only depth was significantly correlated with yellowfin sole abundance (Table 1). The sediment parameters added very little information because yellowfin sole occurred over a wide range of substrate types. Error rates for stations where yellowfin sole were present were much lower than those for stations where this species was absent, reflecting the restricted depth range within which yellowfin sole were encountered. Presence and absence patterns for all four species are plotted against the two best discriminator variables (Fig. 2).

Regression trees were constructed by using CPUE for each species to refine our habitat models. The initial trees were allowed to grow, provided the number of stations in a node was five or greater. The resultant regression trees had sizes of 22 terminal nodes for rock sole, 16 for flathead sole, 19 for Pacific halibut, and 18 for yellowfin sole. The total deviances for the initial trees were 1.24, 0.57, 0.38, and 0.44 respectively, indicating that the model fitted for rock sole was much poorer than that for the other species and that the tree for Pacific halibut had the best fit.

The trees for all species seemed to overfit the data, as indicated by cross-validation. Plots of deviance against tree size (number of terminal nodes) for the four flatfish species indicated that deviance was usually at a minimum at very small tree sizes, consisting of only two or three nodes (Fig. 4). The deviance for each species tended to increase steeply at a tree size between 4 and 6 nodes, and we chose the largest size before a steep increase as optimum size for the tree. The initial tree was pruned to six terminal nodes for rock sole and halibut and to four terminal nodes for flathead sole and yellowfin sole.

The pruned regression tree for rock sole indicated that sediment, depth, and temperature were the best predictor variables for rock sole CPUE. The deviance of the pruned tree increased to 1.852 from 1.242 for the initial tree. This relatively poor fit may again be due to the widespread distribution of rock sole, a species that does not seem to be limited to any particular habitat type. Stations were first separated by sediment type into 89 stations on sand or muddy sand with a high mean CPUE (18 fish/10-min tow) and 80 stations on other sediment types that had a much lower mean CPUE (1.6 fish/10-min tow) (Fig. 5). The highest mean CPUE (25 fish/10-min tow) occurred at stations on sand or muddy sand which had a bottom temperature of more than 8.7°C. The colder stations on sand and muddy sand were separated into seven low salinity stations with low mean CPUE (0.58 fish/10-min tow) and 10 high salinity stations with medium to high CPUE (11 fish/10-min tow). Most stations on other sediment types, which included gravel, mud, gravelly mud, gravelly sand, gravelly muddy sand, gravelly sandy mud, muddy gravel, muddy sandy gravel, sandy gravel, and sandy mud, had low CPUE values except for a group in shallow water (<27.5 m) on gravelly muddy sand, sandy gravel, or sandy mud (13 fish/10-min tow). Thus, by combining results from the correlation analysis, presence and absence patterns, and regression trees, rock sole were found to be most common on sand or mixed sand substrates and most abundant in shallow and relatively warm water.

The regression tree for flathead sole indicated that temperature, sediment type, and depth were the best predictors of flathead sole abundance. The deviance of the pruned tree was 0.774 compared with 0.569 for the initial tree. Highest CPUE values tended to occur at stations where bottom temperature was less than 8.9°C (Fig. 6). At warmer stations, mean CPUE of flathead sole was very low (0.17 fish/10-min tow) if stations were less than 48 m deep, which was the case for the majority (n=109) of the stations. Mean CPUE at warm stations was higher, however, for the six stations located in water deeper than 48 m (4.6 fish/10-min tow). Stations with bottom temperatures below 8.9°C had a low flathead sole CPUE if the sediment was categorized as gravel, sand, muddy sandy gravel, or sandy gravel (1.6 fish/10-min tow). The CPUE was much higher on pure mud or mixed mud

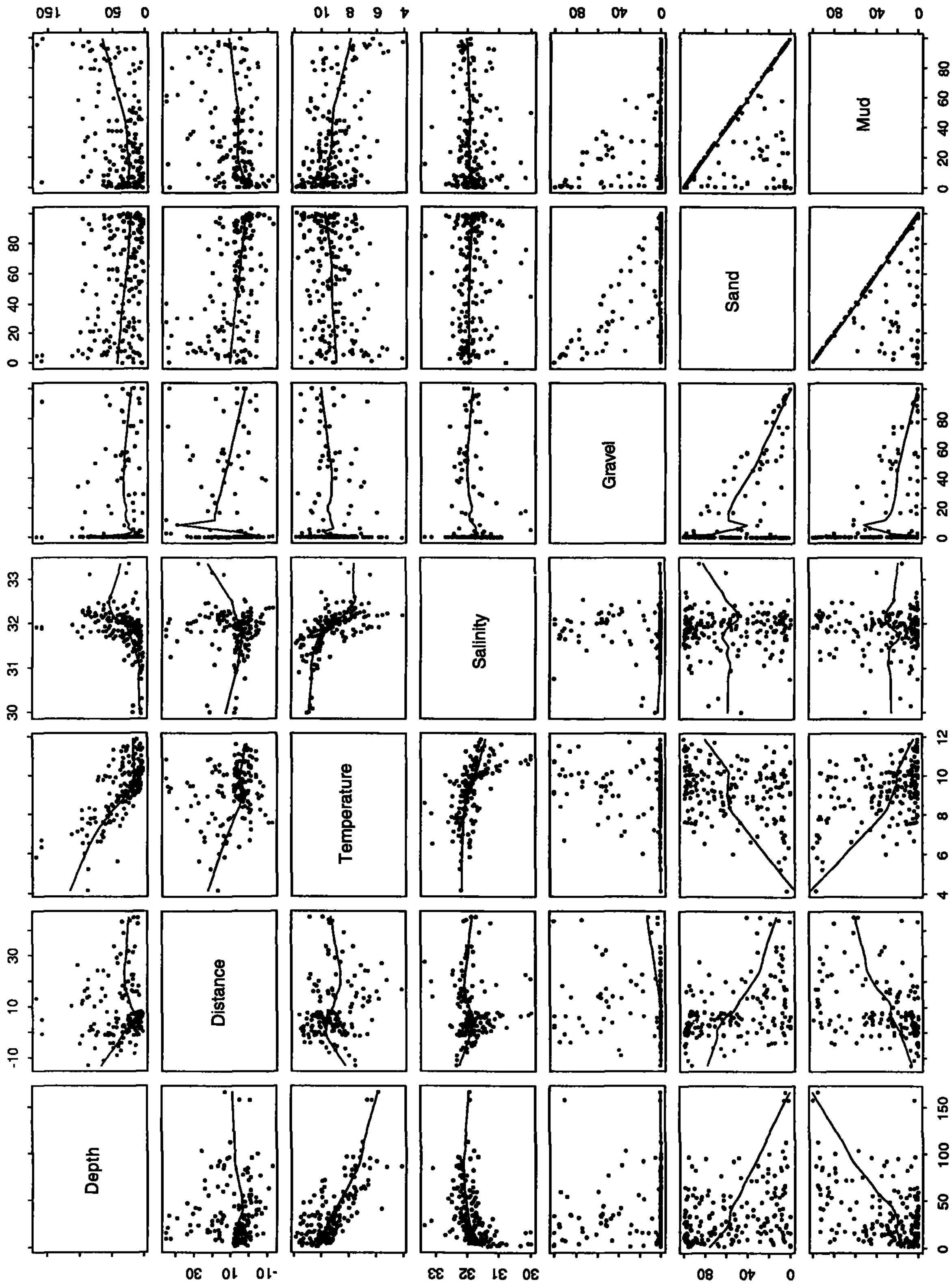

Figure 3

Scatterplot matrix of environmental variables with robust, locally linear fit (LOWESS).

sediments at low temperatures (8.0 fish/10-min tow). Thus, the highest CPUE values for flathead sole were on mixed mud sediments at stations with a bottom temperature of less than 8.9°C, as well as at warmer stations if they were deeper than 48 m. This suggests that temperature should be used in addition to

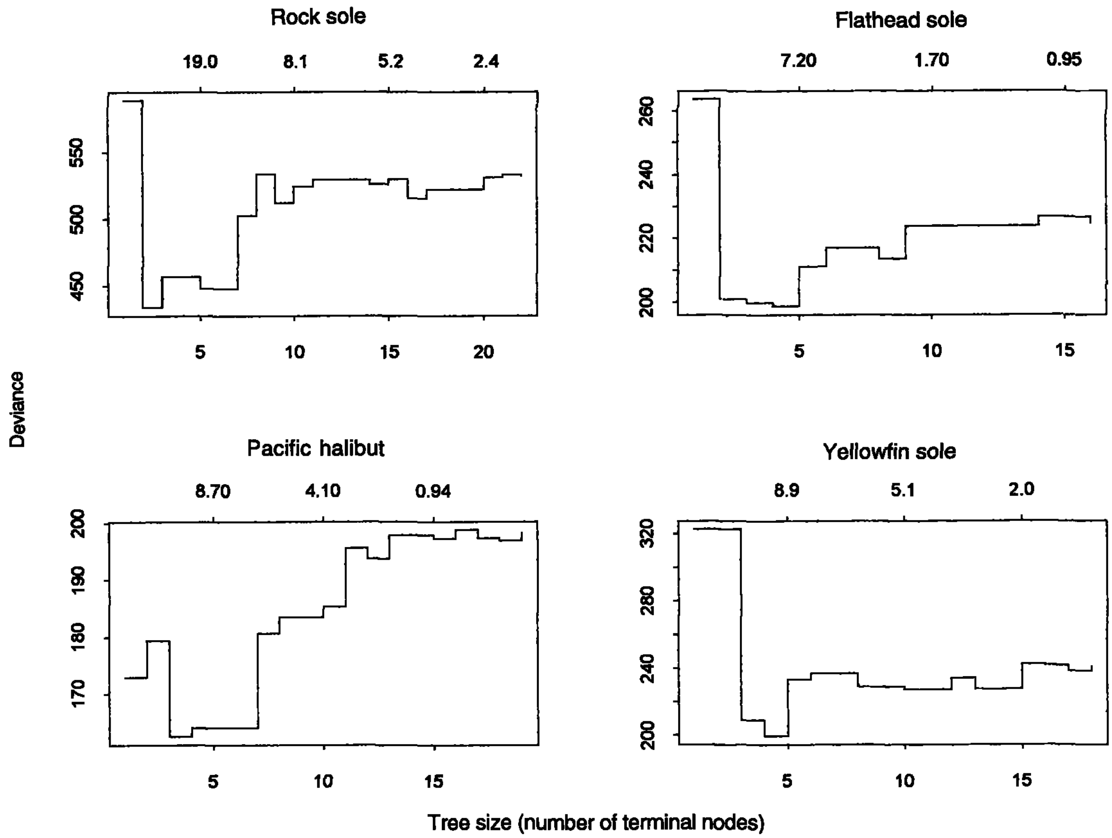

Figure 4

Cross-validation plots (deviance versus tree size) used to prune regression trees of catch per unit of effort on five habitat parameters. See text for further explanation.

sediment and depth selected by linear discriminant analysis as an important factor in determining the distribution of juvenile flathead sole.

Distance from the mouth of the bay and depth were the best predictors of halibut CPUE (Fig. 7) The deviance of the pruned tree was 0.587 compared with 0.384 for the initial tree. Highest CPUE values occurred at stations less than 40 m deep and more than 2.9 km outside the mouth of bays (10 fish/10-min tow). Very low abundances or no halibut were found at stations more than 7.9 km up the bay (0.13 fish/10-min tow). Intermediate CPUE values were found at 61 stations near the mouth of bays (–2.9 km to 7.9 km) which had high bottom temperature (>9.0°C) on sand or mixed sand substrates (2.9 fish/10-min tow). This confirmed our earlier finding that halibut tend to remain outside or near the mouth of bays in water less than 40 m deep on sandy substrates.

The most important variables used in predicting yellowfin sole abundance were depth, sediment, and distance. Deviance was increased from 0.442 for the initial tree to 0.895 for the pruned tree. The first split separated 100 stations less than 28 m deep from 69 stations deeper than 28 m (Fig. 8). The deeper stations had a very low mean CPUE (0.17 fish/10-min tow), and yellowfin sole were absent at 64 of the 69 stations that were deeper than 28 m. The shallow stations had a low mean CPUE (0.82 fish/10-min tow) if the substrate type was pure gravel, sand, or mud, or had mixed gravel sediment, whereas stations on mixed mud sediments had medium to high abundances of yellowfin sole (9.0 fish/10-min tow). The 53 shallow stations on mixed mud substrates were further split by distance, indicating that the highest CPUE values occurred near the heads of long bays. Thus yellowfin sole tended to be concentrated in very shallow locations on mixed mud sediments near the head of bays. This finding agreed with results of the linear discriminant function in its identification of depth and sediment as important factors, but further added distance from the bay mouth as a third important factor.

Discussion

Our results show that relations among flatfish distributions and habitats found within the geographic restrictions of eastern Kodiak Island in 1991 can be applied more broadly to other areas around Kodiak

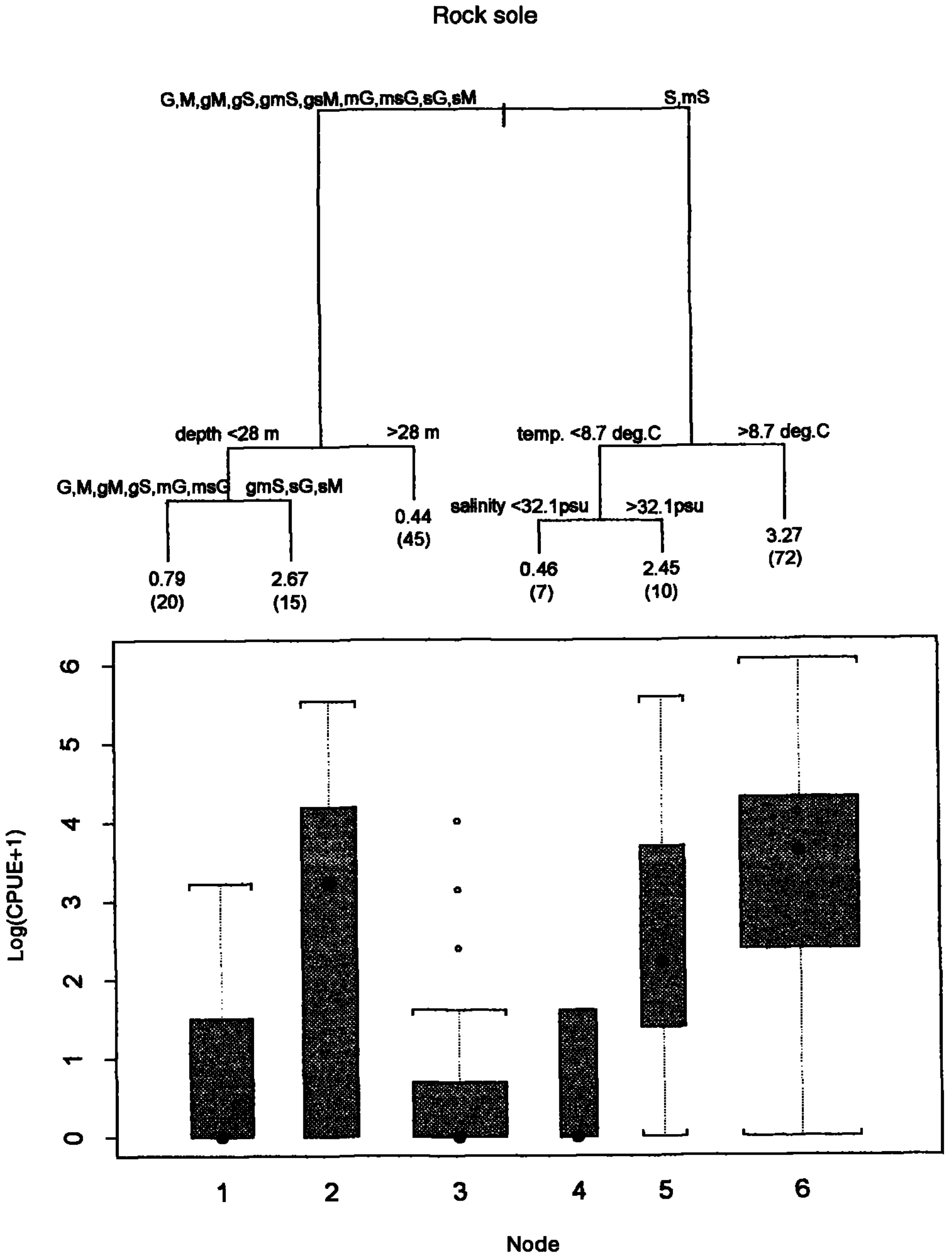

Figure 5

Pruned regression tree for age-0 rock sole with predictions of log(CPUE+1) at each terminal node, and number of stations in parentheses (top figure). Bottom figure contains box plots of log(CPUE+1) by terminal node. Each box plot summarizes distribution of CPUE at stations represented by the terminal node directly above it. Box plots indicate median (filled circle), interquartile range (box height), and outliers (open circles). Whiskers indicate upper quartile plus 1.5 times interquartile range and lower quartile minus 1.5 times interquartile range. Width of boxes is proportional to square root of number of stations at that node. See text for sediment abbreviations.

Island, i.e. to those areas sampled during 1992. Two groups of variables explain much of the observed distribution. These variables are substrate composition and a depth-temperature factor. The relative importance of depth and temperature or of gravel, sand, and mud is difficult to assess because each group is

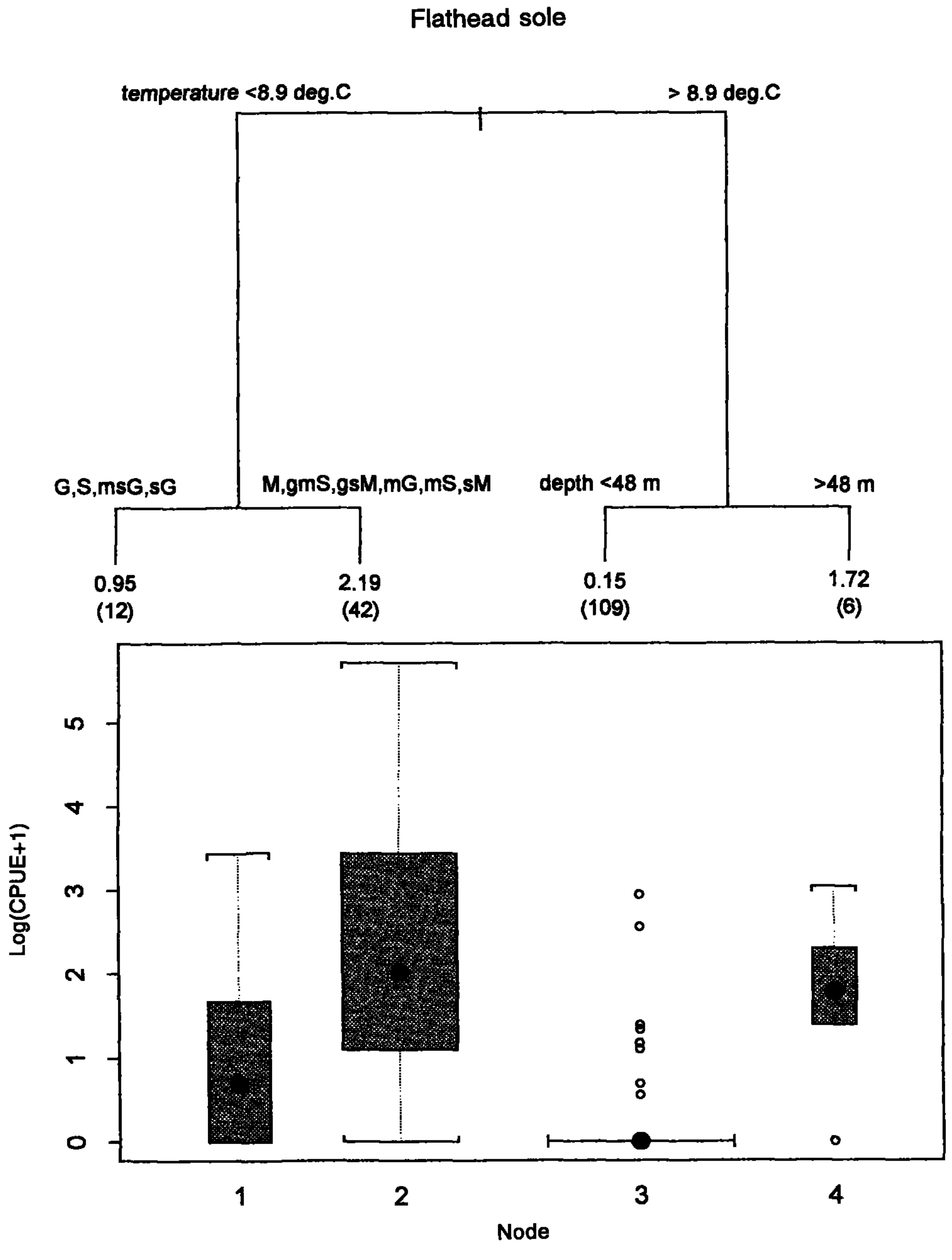

Figure 6

Pruned regression tree for age-0 flathead sole with predictions of log(CPUE+1) at each terminal node, and number of stations in parentheses (top figure). Bottom figure contains box plots of log(CPUE+1) by terminal node. Each box plot summarizes distribution of CPUE at stations represented by the terminal node directly above it. Box plots indicate median (filled circle), interquartile range (box height), and outliers (open circles). Whiskers indicate upper quartile plus 1.5 times interquartile range and lower quartile minus 1.5 times interquartile range. Width of boxes is proportional to square root of number of stations at that node. See text for sediment abbreviations.

highly intercorrelated (Norcross et al., 1995; Fig. 3). These parameters have been linked to the habitat quality of juvenile flatfishes in many other locations (Gibson, 1994). Larvae of many flatfish species are known to settle either in shallow water (Edwards and Steele, 1968; Lockwood, 1974) or offshore water

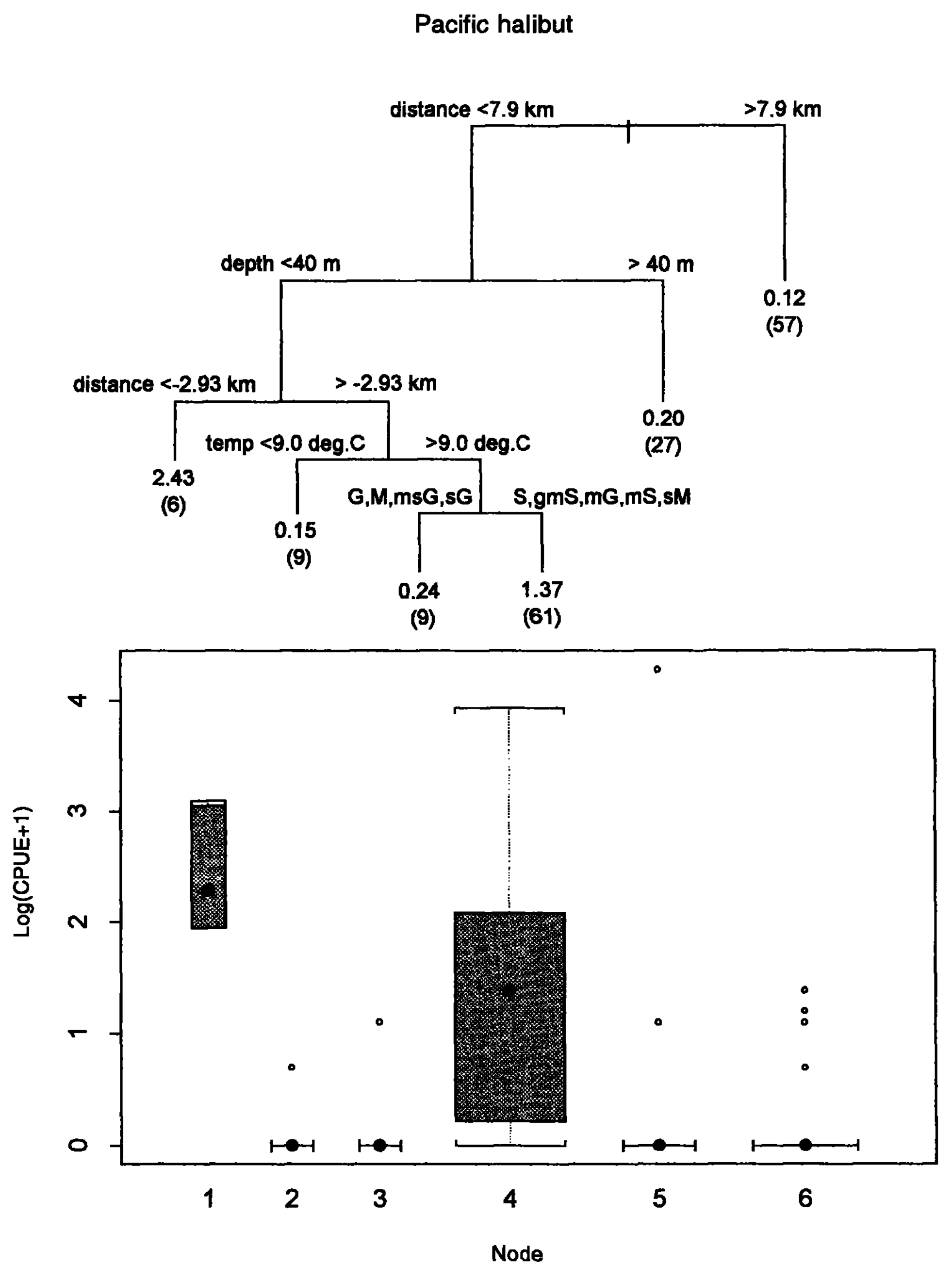

Figure 7

Pruned regression tree for age-0 Pacific halibut with predictions of log(CPUE+1) at each terminal node, and number of stations in parentheses (top figure). Bottom figure contains box plots of log(CPUE+1) by terminal node. Each box plot summarizes distribution of CPUE at stations represented by the terminal node directly above it. Box plots indicate median (filled circle), interquartile range (box height), and outliers (open circles). Whiskers indicate upper quartile plus 1.5 times interquartile range and lower quartile minus 1.5 times interquartile range. Width of boxes is proportional to square root of number of stations at that node. See text for sediment abbreviations.

and then to move into shallow water as age-0 juveniles (Gibson, 1973; Lockwood, 1974; Tanaka et al., 1989). In prior studies (Gibson, 1994) as well as this one, depth and its effect on water temperature may play an important part in determining distribution of juveniles. Water temperature affects growth and

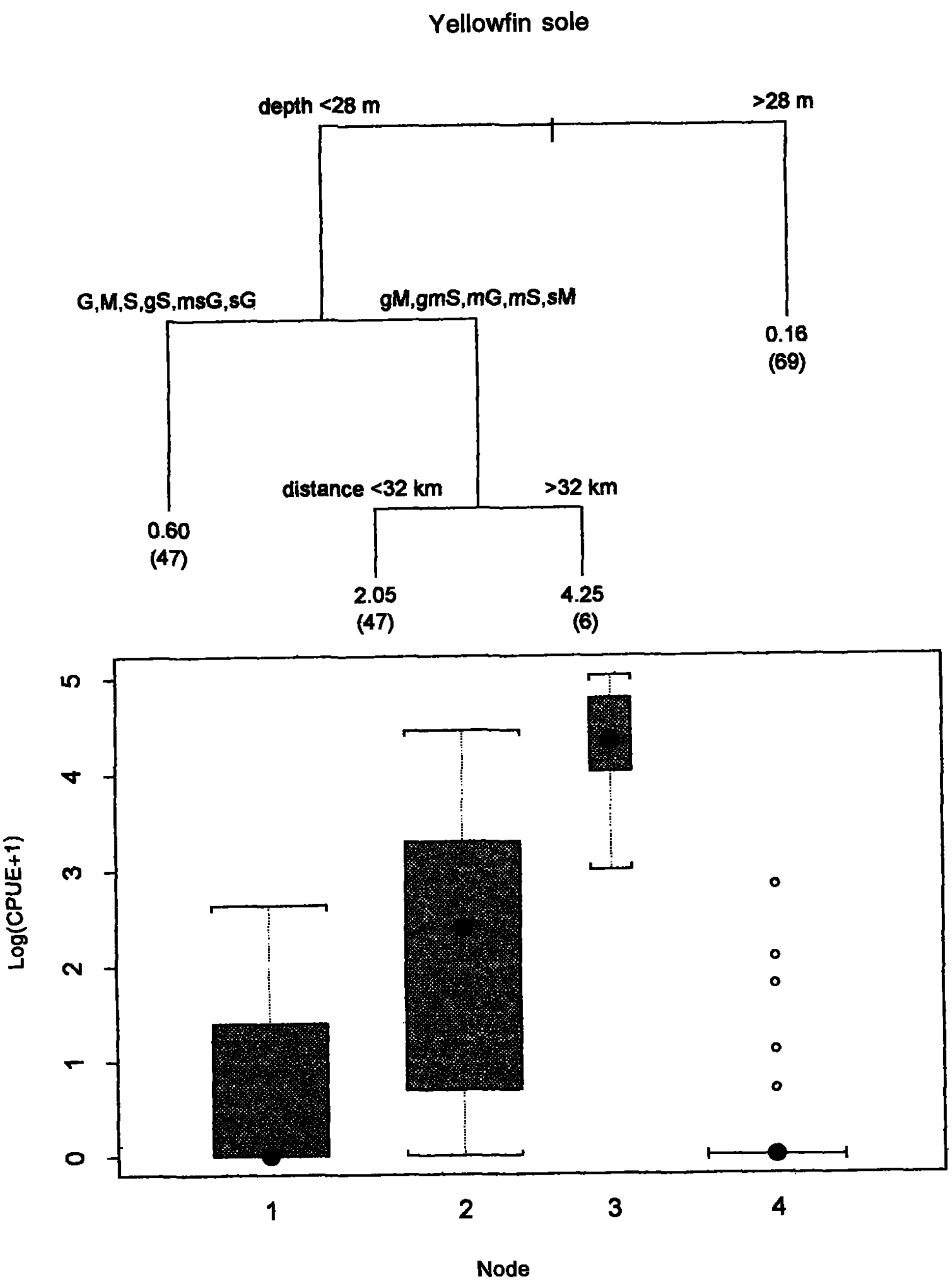

Figure 8

Pruned regression tree for age-1 yellowfin sole with predictions of log(CPUE+1) at each terminal node, and number of stations in parentheses (top figure). Bottom figure contains box plots of log(CPUE+1) by terminal node. Each box plot summarizes distribution of CPUE at stations represented by the terminal node directly above it. Box plots indicate median (filled circle), interquartile range (box height), and outliers (open circles). Whiskers indicate upper quartile plus 1.5 times interquartile range and lower quartile minus 1.5 times interquartile range. Width of boxes is proportional to square root of number of stations at that node. See text for sediment abbreviations.

feeding rates, and shallow, warm waters promote faster growth (Malloy and Targett, 1991; van der Veer et al., 1994).

Distribution of juvenile flatfishes has been linked to substrate type (Tanda, 1990; Kramer, 1991; Gibson and Robb, 1992). Juvenile flatfishes appear to avoid coarse sediments (Moles and Norcross, 1995) and choose fine-grained sediments (Rogers, 1992; Keefe and Able, 1994) which vary in size from mud (Wyanski, 1990; van der Veer et al., 1991) to sand (Jager et al., 1993). In laboratory tests, rock sole prefer sand and mixed sand substrates, halibut prefer a combination of mud and fine sand, and yellowfin sole prefer mud and mixed mud sediments (Moles and Norcross, 1995); these findings are in agreement with the classification and regression trees of our study. Choice of settlement location is affected by the ability of a fish to bury itself in the sediment (Gibson and Robb, 1992) as well as by the availability of prey in the substrate (Burke et al., 1991). When diets of juveniles of the four species were examined from the same collections in 1991 that were used in these models, it was found that epibenthic crustacean taxa composed most of the diets (Holladay and Norcross, 1995). Stomach contents were related to physical parameters of capture, including location, depth, and substrate. When distribution of juveniles overlapped, dietary overlap was sometimes reduced, in that one or more groups of flatfishes appeared to alter their feeding (Holladay and Norcross, 1995), i.e. preference for specific prey types did not appear to be a primary factor governing distribution of these species.

A discriminant analysis was employed in this study to test whether stations could be accurately classified into groups defined by the presence or absence of a given flatfish species. The classification based on the observed parameters resulted in relatively high error rates for all species; between one-sixth and one-third of the stations were incorrectly classified.

Although no discrimination method is able to predict perfectly the presence or absence of populations that have a gradation in abundance in marginal habitats, there are several possible reasons for the observed high error rates found in this study. For rock sole, halibut, and yellowfin sole, error rates for predicting presence were generally much lower than error rates for predicting absence. This finding may indicate that these species were mostly confined to relatively well-defined depth-substrate characteristics. The high misclassification rate for predicting absence of rock sole, halibut, and yellowfin sole suggests that many stations may offer suitable depth, temperature, and substrate conditions for these species but that the species are not collected there because their physical habitat preferences may be different. The situation is different for flathead sole; their presence is not as predictable as their absence. Flathead sole are generally absent from shallow areas with little mud, whereas they are usually, but not always, present in deep, muddy places.

The classification results suggest that although the seven environmental variables (%sand, %mud, %gravel, depth, temperature, salinity, and distance from bay mouth) used in our discriminant analysis do not account fully for observed flatfish distributions, they do provide a useful first step at defining juvenile flatfish habitat near Kodiak. The initial linear discriminant function models developed with the 1991 data (Norcross et al., 1995) are still applicable after incorporating 1992 data. Similar linear discriminant methods have been used to examine nursery grounds of *Solea solea* (Rogers, 1992).

Regression trees of CPUE for each species generally agree with the results of the linear discriminant analyses. They determine specific values of the physical parameters as related to the abundance of juvenile flatfishes and, as easily comprehensible diagrams, can be used to predict species abundance based on habitat parameters.

This detailed analysis, based on CPUE and incorporating both 1991 and 1992 data, does not disagree with the original models that we were testing (Norcross et al., 1995) but rather refines those models and incorporates actual abundances (CPUE) in the multivariate analysis. The previous models characterized nursery areas of age-0 rock sole, flathead sole, Pacific halibut, and age-1 yellowfin sole on the basis of correlations and discriminant analyses by using presence or absence for 1991 data. Depth and substrate were statistically significant variables previously, and a measure of distance in relation to mouth of the bay was included qualitatively for each species. Depth, temperature, sediment composition, and distance from bay mouth were all found to be important predictors of the abundance of juvenile pleuronectids with regression trees for the combined 1991 and 1992 data.

Additional factors influence the presence or absence of these flatfish species at any given site. Possible factors that were not included in this study are additional measures of location (such as position around the island or distance from shore), abundances of prey or predators, and a substrate or habitat parameter that would account for microhabitat features not reflected in sediment composition.

A location parameter may be a categorical variable that assigns each station to a well-defined geographical area. For example, we observed large differences in the abundance of halibut and rock sole between the east and west sides of Kodiak Island and among different bays. These differences possibly reflect oceanographic conditions that lead to variable levels of recruitment into different nearshore areas around Kodiak Island. Habitat models incorporating geographical and oceanographic information may help to reveal these mechanisms but would require larger sample sizes than are presently available.

The abundance of prey (McIntyre and Eleftheriou, 1968; Minami, 1986; Allen, 1988) and predators (van der Veer et al., 1991; Seikai et al., 1993) may influence the distribution and abundance of flatfish species but cannot be quantified without extensive surveys. Incorporating prey or predator abundance into a general habitat model is therefore probably of little practical use in applying the model to other areas. Postmetamorphic flatfishes in southeastern Alaska (Sturdevant, 1987) and juvenile flatfishes near Kodiak (Holladay and Norcross, 1995) feed primarily on small meiofaunal, benthic, and epibenthic crustaceans, including mysids, amphipods, cumaceans, and copepods. The diets of flathead sole, Pacific halibut, yellowfin sole, and rock sole were different in different capture sites, when region, depth, and substrate were the parameters used for the sites. This finding suggests that these species are opportunistic and feed on the prey available in their locale, rather than that they are discriminating, determining locale on the basis of prey availability.

Additional information is desirable to describe the microhabitat at each station more precisely. During our sampling, we obtained qualitative descriptions of the benthic flora and fauna that were collected at each station and a very broad quantification of the dominant invertebrates that were caught together with the fishes. In the future, we will attempt to consolidate this information into a categorical "community descriptor" for each station. This "community descriptor" can then be used as an additional explanatory variable in future models.

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