Journal of Fish Biology (2002) **61,** 540–559
doi:10.1006/jfbi.2002.2056, available online at http://www.idealibrary.com on IDEAL®

Sediment preferences and size-specific distribution of young-of-the-year Pacific halibut in an Alaska nursery

A. W. STONER*‡ AND A. A. ABOOKIRE†

**Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 2030 S. Marine Science Dr., Newport, Oregon 97365, U.S.A. and †Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 301 Research Court, Kodiak, Alaska 99615, U.S.A.*

(*Received 13 February 2002, Accepted 3 July 2002*)

A combination of laboratory experiments and field surveys was used to test the hypotheses that responses to sediments change with fish size and that sediment grain-size is the predominant environmental factor affecting small-scale distribution in young-of-the-year (yoy) Pacific halibut *Hippoglossus stenolepis*. Laboratory tests showed that the smallest fish (31–40 mm L_T) chose fine sediments (muddy and fine sands), fish 51–70 mm had high selectivity (primarily medium sand), and the largest fish (80–150 mm) were not selective although they avoided the largest grain-sizes (pebbles and granules). Sediment preferences were correlated with size-dependent burial capabilities. Beam trawl collections were made over a 6 year period in Kachemak Bay, Alaska, to examine the distribution of yoy Pacific halibut (14–120 mm L_T) using small size classes (e.g. 10 mm intervals). Canonical correlation analysis showed that the per cent of sand in the sediment was a highly significant variable for all but one size and date combination. Catch per unit of effort (CPUE) for newly settled fish (<30 mm L_T) was highest on very fine sand, fish 41–80 mm were most abundant on fine sand, and the largest yoy fish (81–120 mm) were abundant over a range of sediments from fine sand to mud. Except for the smallest fish, Pacific halibut in the field were associated with sediments somewhat finer than predicted from the laboratory experiments; however, virtually all were captured where they could bury easily. The ability of flatfish to bury and shelter in sediment is related to fish size; consequently, habitat associations shift rapidly during the first year of life. Habitat models for yoy flatfishes should consider size-dependent shifts in capabilities and preferences.

Key words: habitat selection; sediment; behaviour; distribution; Pacific halibut.

INTRODUCTION

There is increasing awareness of the important link between habitat and sustainable fisheries for demersal species (Langton *et al.*, 1996; Schmitten, 1999). In particular, the mechanisms that make certain locations or habitats important as nursery grounds need to be understood, and these nurseries need to be identified and protected (Beck *et al.*, 2001). The habitats of early post-settlement fishes are poorly understood in most cases, however, especially in high latitude species. Most information on flatfish habitat comes from field surveys and distribution-based models which incorporate primarily the environmental variables: depth, temperature and sediment type (Rogers, 1992; Swartzman *et al.*, 1992; Jager *et al.*, 1993; Abookire & Norcross, 1998; Norcross *et al.*, 1999; McConnaughey & Smith, 2000; Amezcua & Nash, 2001). Temperature

‡To whom correspondence should be addressed. Tel.: +1 541 867 0165; fax: +1 541 867 0136; email: al.stoner@noaa.gov

0022–1112/02/030540+20 $35.00/0

probably sets large-scale boundaries on distribution, but sediment (often linked closely with depth) should be a critical factor for determining fine-scale distributions of flatfishes because they live in direct association with the sediment and because sediment provides both food and shelter from predation (Gibson, 1994). In fact, sediment may be the first line of defense for flatfishes, and there is probably high selective pressure for habitat choices related to sediment that increase the survivorship of young flatfishes.

Relatively little is known about young-of-the-year (yoy) flatfishes because routine fishery-oriented surveys do not ordinarily collect these small fishes. Important insights, however, have been gained through studies targeting small flatfishes with fine-meshed trawls, particularly with plaice *Pleuronectes platessa* L. (Kuipers, 1977; Berghahn, 1986; Pihl & Van der Veer, 1992), and some other commercially important species in recent years (Abookire & Norcross, 1998; Norcross *et al.*, 1999; Van der Veer *et al.*, 2001; Goldberg *et al.*, 2002). In most cases, however, distributional analyses for flatfishes are conducted by year class or groups of year classes. Recent laboratory experiments with well-studied species such as plaice (Gibson & Robb, 2000) and winter flounder *Pseudopleuronectes americanus* (Walbaum) (Phelan *et al.*, 2001) reveal that there can be rapid shifts in sediment preferences within the first year of post-settlement life. These preferences can result in rapidly changing habitat associations, as well as changes in the locations and amount of suitable habitat (Stoner *et al.*, 2001). Because the amount of suitable habitat in the nursery grounds may limit recruitment of certain flatfishes (Rijnsdorp *et al.*, 1992; Manderson *et al.*, 2002), it is clear that more detailed information is needed for yoy fishes.

This investigation was conducted with Pacific halibut *Hippoglossus stenolepis* Schmidt, one of the most valuable fishery resource species in the North Pacific Ocean, yielding 30 000–60 000 t year^{-1} over the last decade (NMFS, 1999). While the fishery for this species extends from Russia and Alaska south to Oregon, the primary spawning and nursery grounds occur in the Gulf of Alaska and Bering Sea (IPHC, 1998). The International Pacific Halibut Commission conducted summer surveys for juveniles over a broad spatial scale (hundreds of kilometres) for nearly three decades (1961–1981) (Best & Hardman, 1982; Schmitt, 1985) but juveniles were considered to be any fish <65 cm total length (L_T), and no size-specific analysis of distribution or habitat association has been made. Since that time beam-trawl surveys for juvenile flatfishes have provided important new information on the diets (Holladay & Norcross, 1995) and distribution of yoy Pacific halibut in inshore waters of Kodiak Island (Norcross *et al.*, 1995, 1997, 1999) and Kachemak Bay, Alaska (Abookire *et al.*, 2001). To date, however, Pacific halibut ranging in size from 14 to >100 mm L_T have been grouped together for distribution analyses. In the only experimental analysis of yoy Pacific halibut that is known, Moles & Norcross (1995) examined sediment preferences in 50–80 mm Pacific halibut together with three other flatfish species.

The present investigation expanded upon earlier studies with juvenile Pacific halibut by examining relationships between sediment choices, burial capabilities and fish size through a combination of laboratory and field studies. It was hypothesized that sediment grain size is the predominant environmental factor affecting small-scale distribution in yoy Pacific halibut because the ability of flatfish to bury and shelter in sediment is determined by sediment type. It was hypothesized further that distribution is variable during the first year of life in the benthos because of changes in response to sediment type related to fish size. To test these hypotheses the following were used: (1) laboratory experiments to determine size-specific sediment preferences and burial capabilities in Pacific halibut ranging from 30–150 mm L_T, and (2) beam trawl surveys conducted over a 6 year period in Kachemak Bay, Alaska, to verify the importance of sediment grain size for Pacific halibut during their first months in the benthos.

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS

Young-of-the-year Pacific halibut for laboratory experiments were collected in Chiniak Bay on the eastern shore of Kodiak Island, Alaska (57°40′ N; 152°30′ W) in August 2000 and August 2001. Collections were made with a beam trawl (2 m wide, 3 mm mesh) towed at *c.* 1 m s^{-1}. The fish were held in flow-through seawater tanks at the Kodiak Laboratory of the Alaska Fisheries Science Center for 2 days prior to air transport to the Hatfield Marine Science Center in Newport, Oregon. Shipping generally took <30 h and temperatures remained near 10° C in insulated containers. No fish died in transport, and most fed within 24 h of arrival in Newport.

The Pacific halibut were maintained in multiple tanks 1·3 m in diameter, with 1 cm of sand on the bottom (combination of fine, medium and coarse), and supplied with flow-through sea water maintained at 9 ± 1° C (mean ± S.D.). The fish were fed to satiation 3 days per week on a diet of chopped frozen shrimp and dry pellet foods high in protein and lipid. Growth in the yoy fish were typically 0·25–0·50 mm day^{-1}.

Fish for sediment preference and burial experiments were tested in size classes: 31–40, 41–50, 51–60, 61–70, 71–80, 81–100 and 101–150 mm L_T. This size range includes fish somewhat larger than those considered in the field analysis (to 120 mm L_T); however, there was no difference in sediment preferences observed in the laboratory for fish in classes 101–125 and 126–150 mm and the results for these fish were combined to provide a larger number of replicates. The smallest increments of length were used for the smallest fish because their relationships with sediment changed more rapidly than in the larger fish. All fish were tested individually.

LABORATORY STUDIES

Sediment preference experiments

Gibson & Robb (2000) recommended that a knowledge of activity pattern in fishes is desirable when using point measurements in preference studies. Preliminary experiments and video recordings of young Pacific halibut revealed that their locomotory activity and diurnal rhythms were strongly affected by feeding history. Fish fed to satiation normally buried in the sediment and remained essentially motionless for 12–24 h. Fish transferred during mid-day to experimental tanks after 24 h starvation generally made a brief exploration of the tank, buried into one of the finer sediments, then remained motionless for several hours. Exploration of the tank resumed during hours of darkness, and choices appeared to be made during this time. By the time the light began to rise in the morning, the fish were buried again and with few exceptions they did not shift position between 0800 and 1200 hours. Observations made into the second day revealed that the choice of sediment remained stable after the first morning. Fish that were starved for longer periods swam almost continuously during the night and into the daytime in an apparent search for food.

Pacific halibut were tested for sediment preferences in circular tanks scaled to fish size: fish ≤50 mm were tested in 25 cm, fish 50–60 mm in 42 cm, fish 61–100 mm in 72 cm, and fish 101–150 mm in 110 cm tanks. Each experimental tank had seven sediment types (Table I) chosen to be as close as possible to those used in a study conducted by Moles & Norcross (1995) with Pacific halibut and three other flatfish species. The sediments

TABLE I. Sediments used in burial and substratum preference experiments with yoy Pacific halibut. DE, diatomaceous earth

Classification (screen)	Median grain-size (mm)	Approximate phi value	Composition
Pebble	*c.* 10	− 3·0	River gravel
Granule	2–4	− 1·0	River gravel
Coarse sand	1	0	(No. 16 silica sand)
Medium sand	0·5	1·0	(No. 30 silica sand)
Fine sand	0·2	2·25	(No. 70 silica sand)
Muddy sand	*c.* 0·1	3·25	70% fine sand + 30% DE
Sandy mud	*c.* 0·04	4·5	70% DE + 30% fine sand

were arranged in equal wedges 25–40 mm deep (depth increasing with fish size) such that wedges containing fine and coarse grains were interspersed. The same pattern was used in each of four tanks, but the tanks were rotated to different orientations to prevent any room or lighting effects. Each of the sediment sections were stirred between runs to keep them loose and aerobic. When the boundaries between sediment types became blurred after four or five runs, the sediments were replaced entirely.

Flow-through sea water was provided ($9 \pm 1^\circ$ C, mean ± S.D.) to a depth of 25 cm above the sediment, except for the smallest fish (<50 mm) which were tested in closed systems in a cold room. This was necessary because the experiments needed to be conducted while small fish were still in quarantine due to interstate transport regulations. All of the experiments were conducted in light-controlled spaces shielded from human traffic. Photoperiod was 12 L : 12 D (as in the holding areas), with a light level of 2 to 3×10^{-1} μEm^{-2} s^{-1}, equivalent to dim daylight. Illumination with dim red light (4 to 6×10^{-2} μEm^{-2} s^{-1}) allowed for overhead video recordings during night-time hours.

On the basis of preliminary observations, the following protocol was established for sediment preference experiments. Fish were fed in the afternoon prior to testing, and transferred to experimental tanks between 1300 and 1500 hours. One fish was released on a sector known to be avoided by young Pacific halibut (i.e. either pebbles or granules). Observations were made on the location and burial status (% covered) of the fish 1 min after release and at 1600 hours during the first day, and at 0800 and 1000 hours on the second day. Video tape recordings were made for every run during the last 15 min interval of every hour from midnight until the end of the run (1000 hours). This video tape was used to determine whether or not a sediment choice would be considered valid and for general observations on the behaviour of Pacific halibut relative to the different sediments. A run was considered valid when the individual had been active for 3–4 h prior to 0800 hours, it had encountered all seven of the sediment types at least once, and the fish remained essentially stationary on the substratum between 0800 and 1000 hours. Runs not meeting these specifications (13%) were eliminated from the analysis. Like Gibson & Robb (2000) Pacific habitat preference was scored during the quiescent phase. A log-likelihood test (*G*-test) (Sokal & Rohlf, 1969) was used to determine whether choices diverged significantly from a uniform distribution among the seven sediment types.

Burial experiments

Short-term tests of burial behaviour were conducted for Pacific halibut in size classes identical to those used in sediment choice experiments (Table I). Fish <40 mm L_T were tested in circular aquaria 16 cm in diameter (8 cm deep). Fish 40–60 mm were tested in aquaria 24 cm in diameter (10 cm deep) and fish >60 mm were tested in rectangular aquaria (25 cm wide, 50 cm long, 15 cm deep). As in sediment preference experiments sediment depth (25–40 mm) was scaled to fish size so that none could reach the bottom

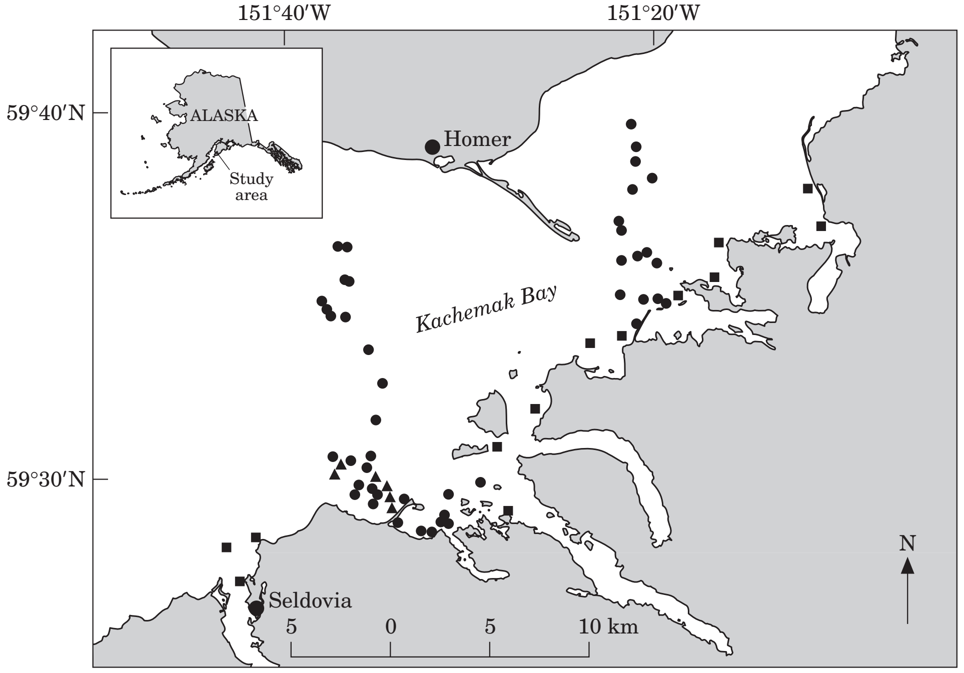

FIG. 1. Locations of beam trawl collections in Kachemak Bay, Alaska, 1994–99. ●, 45 stations sampled by Abookire & Norcross (1998); ▲, six stations sampled by Abookire *et al.* (2001); ■, 13 stations sampled by Abookire *et al.* (2000).

of the container. The seven sediment types were tested independently. All runs were made in static seawater systems in a cold room held at 9° C. Light levels on the bottoms of the test arena were 3–6 × 10^{-1} μEm^{-2} s^{-1}.

Pacific halibut were deprived of food for 24 h prior to testing, for reasons similar to those described above. The fish were measured for L_T and transferred from holding tanks to the experimental aquaria, one fish per aquarium. Trials were started between 0900 and 1300 hours, a period during which juvenile Pacific halibut are normally buried. Four different individuals in each size class were tested on each sediment type, except that fish <70 mm L_T were not tested on the largest grain size (pebbles) because no fish <100 mm was able to cover with this substratum type. Naïve fish were used in all of the burial trials. Recordings on fish behaviour and colouration were made during the first 30 s after transfer, and subsequently at 5, 15, 30, 60 and 120 min. Ordinarily the fish attempted to bury immediately upon transfer, and fish that could bury substantially did not move again during the 2 h run. Fish unable to bury or burying only partially made repeated attempts and shifts in position, and burial usually increased with time up to 60 min. Burial was scored as per cent of body covered with sediment, and time to maximum burial was evaluated using the time intervals specified above. Relationships between burial and fish size were examined with standard regression techniques.

FIELD STUDY

Surveys

Pacific halibut were surveyed in Kachemak Bay, Alaska, a deep estuary on the east side of lower Cook Inlet, at the west end of the Kenai Peninsula (Fig. 1). Data were compiled on yoy (<120 mm L_T) juvenile Pacific halibut from three different investigations made between 1994 and 1999 (Table II). The first was an investigation of juvenile flatfish habitat and distribution at 45 stations from 1994 to 1996 focused on flathead sole *Hippoglossoides elassodon* Jordan & Gilbert and rock sole *Pleuronectes bilineatus* (Ayres)

TABLE II. Summary of beam-trawl surveys in Kachemak Bay, Alaska, 1994–1999. The surveys were described by (1) Abookire & Norcross, 1998, (2) Abookire *et al.*, 2001, and (3) Abookire *et al.*, 2000

Sampling dates	Year	Reference	No. tows	Tow duration (min)
24–30 Sept	1994	1	20	10
3–11 May	1995	1	27	10
1–9 Aug	1995	1	44	10
21–31 May	1996	1	45	10
7–9 Aug	1996	3	10	5
10–17 Aug	1996	1	42	10
6–14 Aug	1997	3	13	5
17–18 Aug	1997	2	6	10
13–14 Aug	1998	3	13	5
15–16 Aug	1998	2	6	10
17, 20 Aug	1999	3	13	5
21 Aug	1999	2	6	10

(Abookire & Norcross, 1998). This study included stations ranging from 10 to 110 m depth arranged in three transects, two of which spanned the inner and outer bay. The second study involved the continued monitoring of six of the 45 stations in the outer bay from 1997 to 1999, in a depth range from 10 to 70 m (Abookire *et al.*, 2001). The third investigation included 13 beam trawl stations along the southern shore of Kachemak Bay (8–25 m) between Seldovia and the inner bay from 1996 to 1998 (Abookire *et al.*, 2000).

All field collections were made with a 3·05 m plumb-staff beam trawl equipped with a double tickler chain (Gunderson & Ellis, 1986). The net body was 7 mm square mesh with a 4 mm mesh codend liner. Standard tow duration was either 5 or 10 min (Table II), depending upon bathymetry. Stations sampled by Abookire *et al.* (2000) were all in relatively shallow depths (<25 m) and shorter tows were necessary to maintain survey depths at ± 2 m. From 1994 to 1997, the net was fished from a 9·3 m open boat, and from 1998 to 1999, the survey vessel was the 10 m R/V ' David Grey '. All tows were made in the same direction as the tidal current. The start and end positions for each tow were determined with a Global Positioning System (GPS) and used to calculate the distance travelled. The target towing speed was 50 cm s^{-1}. If a tow resulted in a twisted or torn net, a broken weak-link, or if the net was full beyond the codend, the station was resampled until a successful tow was made. All of the surveys were observed to ensure consistent towing speed and net efficiency (A. A. Abookire, pers. obs.). Before each net tow a CTD (Seabird Electronics, Inc., SBE-19 SEACAT profiler) was deployed to measure water temperature (° C), salinity (psu) and depth (m). These data were used for comparisons of bottom water temperature and salinity which were calculated by taking average values of data collected in 30 s within the deepest 5 m of the water column (*c.* 12 points). CTD data were available for all stations and dates except eight because of instrument malfunctions.

The top 3–7 cm of sediment was collected at most stations (all except 3) from 1994 to 1996 with a 0·06-m^{-2} Ponar grab (Abookire & Norcross, 1998). Samples were frozen and transported to the laboratory for grain-size analysis using a standard sieve and pipette procedure (Folk, 1980) to determine percentages of mud, sand, gravel and cobble. Sediments were then classified according to Folk's standard textural scheme (Folk, 1954). Sediment data were not collected in 1997–1999. Average sediment data were obtained for stations which were sampled continuously in August 1997–1999 (Abookire *et al.*, 2001) by taking the station's average sediment grain-size from previous August collections in

1994–1996 (Abookire & Norcross 1998). No sediment information is available from stations sampled between Seldovia and the inner bay from 1996 to 1999 (Abookire *et al.*, 2000). Thus, median grain-size was available for 193 station and date combinations; these were used for direct comparison with laboratory results.

Pacific halibut that could be identified in the field were counted and measured to the nearest mm (L_T). Newly settled flatfishes that could not be identified positively in the field were frozen and returned to the laboratory for identification and measurement. Fish data were standardized to catch-per-unit-effort (CPUE) for an area of 1000 m^2. The area towed was calculated as the effective width of the net (0·74 m, Gunderson & Ellis, 1986), multiplied by the width of the trawl (3·05 m) and the distance towed as determined from GPS data. Pacific halibut >120 mm L_T were omitted from the field analysis, as previous studies in coastal Alaska have shown this to be the maximum size for yoy fish in August (Norcross *et al.*, 1998).

Pacific halibut were grouped in length intervals of 10 mm, except for fish <30 and 81–120 mm which were relatively few in number. Only length groups that were >5% of the total Pacific halibut catch for each month were analysed. May collections yielded two length groups, <30 and 81–120 mm, and August collections provided data for six groups (31–40, 41–50, 51–60, 61–70, 71–80 and 81–120 mm). Few fish <30 mm were collected in August, and these fish were eliminated from the analysis.

Statistical analysis

Statistical analyses were performed separately by month using data from all years. Canonical correlation analysis (SAS, 1996) was used to examine presence and absence data for Pacific halibut in relation to depth, bottom temperature, bottom salinity, per cent sand and per cent mud. Separate analyses were made for each size class in May and August. Linear combinations of environmental variables were derived to produce canonical variables that summarized within-species variation in the data (Johnson & Wichern, 1992). Samples from different years were considered replicates. Environmental variables were correlated with the canonical variables to produce canonical correlation components, with the first canonical correlation accounting for the maximal multiple correlation. The (+) or (−) sign of the canonical coefficients within the canonical correlation resulted from the frequency and weight of presence and absence in the data. If presence was weighted heavier than absence, a positive coefficient was interpreted to mean that Pacific halibut abundance increased with increases in the variable being considered. The two highest canonical coefficients >0·7 were chosen from the first total sample canonical correlation to account for presence and absence of Pacific halibut. Alpha was set at 0·05 for all tests of significance.

RESULTS

LABORATORY STUDIES

Young-of-the-year Pacific halibut demonstrated distinct preferences for sediments of particular grain sizes which changed with fish size (Fig. 2). The smallest fish (31–40 and 41–50 mm L_T) were found on all of the sediments classified as medium sand or finer, while highest sediment specificity occurred in Pacific halibut 51–70 mm L_T. These medium-sized fish were associated with medium sand and were rarely observed on the finest and coarsest sediments. Pacific halibut in all of the classes <70 mm L_T showed a significant non-uniform distribution (*G*-test, $P<0·05$) among the sediment types. Fish 71–80 mm L_T were marginally selective for sediment type ($P<0·10$), with a mode of choice for fine sand but with a broad range of choices from sandy mud to coarse sand. Pacific halibut >80 mm L_T demonstrated no statistically significant preference for sediment type ($P>0·05$), although they avoided the largest grain sizes and only

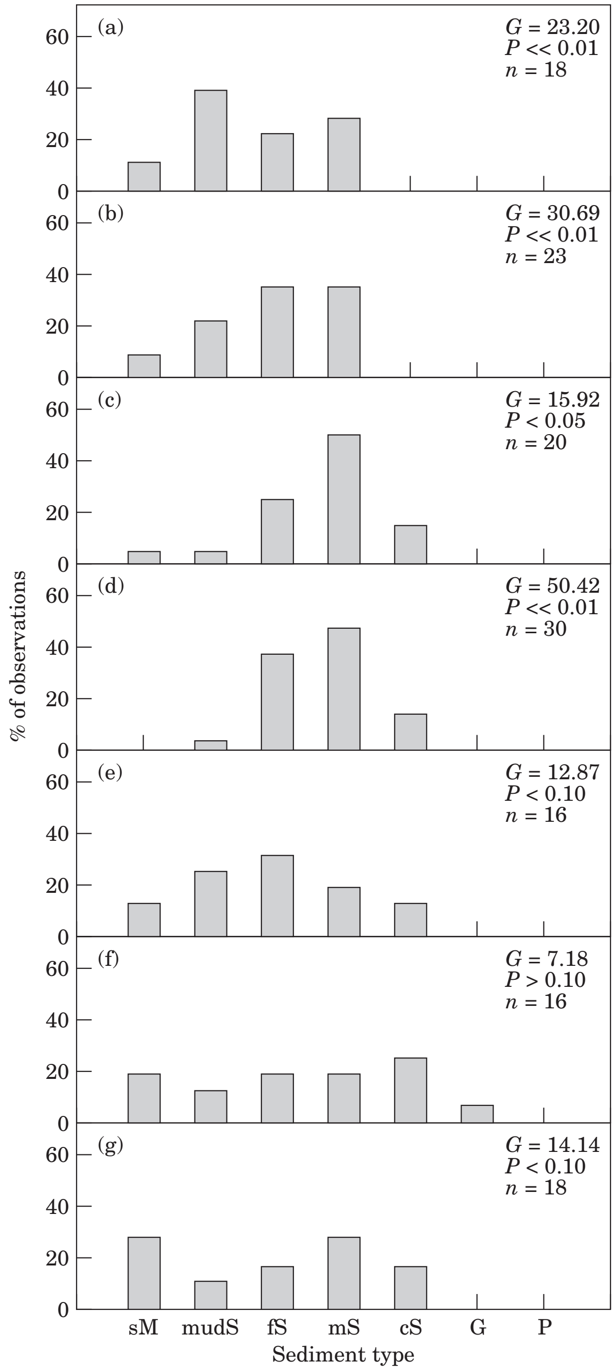

FIG. 2. Choices of sediment type made by yoy Pacific halibut in size classes (a) 31–40, (b) 41–50, (c) 51–60, (d) 61–70, (e) 71–80, (f) 81–100 and (g) 101–150 mm L_T. Values shown are per cent of total numbers (n) found on each sediment type when fish were tested as individuals. Results of the log-likelihood test (G-test) for even distribution among the seven sediments are reported for each size class. Sediment codes from finest to coarsest grains: sM, sandy mud; mudS, muddy sand; fS, fine sand; mS, medium sand; cS, coarse sand; G, granules; P, pebbles (see Table I).

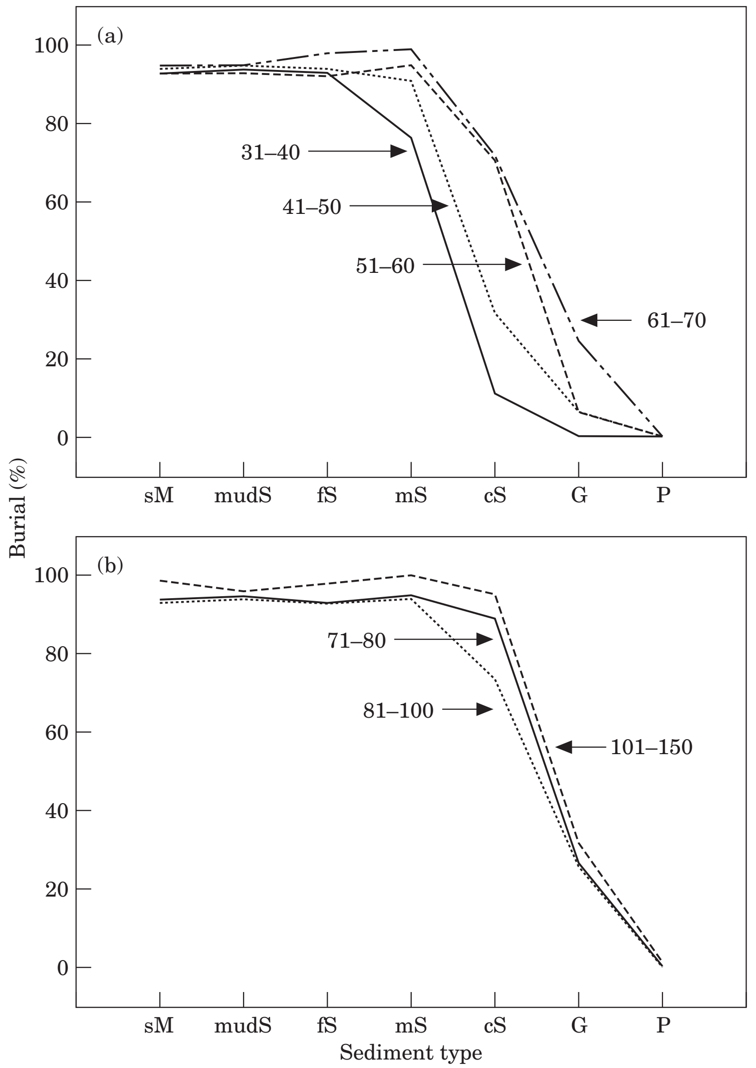

FIG. 3. Maximum burial (per cent coverage) of yoy Pacific halibut in seven different sediment types shown as a function of fish size class (a) 31–40, 41–50, 51–60, 61–70, (b) 71–80, 81–100 and 101–150 mm L_T. Sediment codes as in Fig. 2.

one Pacific halibut individual (>80 mm L_T) chose granules. These largest fish had a nearly even distribution over all of the sediments ranging from sandy mud to coarse sand.

Observation of the video recordings revealed that the scoring system for sediment choice was accurate. Time spent on less favoured substrata was short. For example, Pacific halibut rarely rested on pebbles or granules, nearly always moving quickly over those substrata to finer sediments. Similarly, medium-sized Pacific halibut moved rapidly over the sandy mud substratum, apparently avoiding that flocculent substratum.

Burial capabilities in Pacific halibut were strongly size dependent as expected (Fig. 3). Virtually all of the fish were able to bury substantially (>90%) in the

TABLE III. Summary of physical-chemical conditions at the stations surveyed in Kachemak Bay, Alaska, for each survey period

Month	Year	n	Bottom temperature (° C)			Bottom salinity (psu)		
			Mean	Min.	Max.	Mean	Min.	Max.
May	1995	27	4·3	3·8	4·8	31·7	30·4	33·8
	1996	38	5·6	5·0	7·1	31·9	30·8	32·3
August	1994	20	9·6	9·2	9·8	30·6	30·3	30·8
	1995	43	8·7	7·8	10·1	31·2	28·4	31·4
	1996	52	9·3	8·6	10·3	31·4	29·0	31·6
	1997	19	10·9	9·4	11·6	31·5	31·1	32·0
	1998	19	10·0	9·6	12·1	31·1	28·8	31·5
	1999	19	9·7	8·9	10·6	31·4	31·0	31·6

finest sediments (sandy mud, muddy sand and fine sand) and capabilities in coarser sands increased with fish size. Burial of >90% was also possible in medium sand for all of the fish except those 31–40 mm L_T (76%). Size effects were most evident in the coarser sediments. In coarse sand, mean burial increased significantly with the logarithm of L_T (r^2=0·805, P=0·006). Burial in granules was much lower than in coarse sand, ranging from 0 to 31%, however, mean burial was also significantly correlated with the logarithm of L_T (r^2=0·856, P=0·003).

Sediment choices made by Pacific halibut were related to burial capabilities in the different sediment types. Pacific halibut never selected sediments in which maximum burial was <25% and rarely chose sediments (≤15% of observations) where burial capability was <70%. The smallest Pacific halibut generally chose fine sediments where they buried quickly and easily.

FIELD STUDY

A broad range of depth (8–110 m) and sediment conditions (mud to gravel) were surveyed for fishes in Kachemak Bay, but relatively narrow ranges of temperature and salinity were surveyed (Table III). Temperature spanned just 1° C in May 1995 and 2° C in 1996, and in August temperature never ranged >2·5° C. Average salinity over the stations sampled was remarkably constant *c.* 31·5 psu, with a range of <5·5 psu for the entire study period.

A total of 1099 juvenile Pacific halibut were captured in 245 tows in Kachemak Bay. The majority (88%) of Pacific halibut collected in May were newly settled fish ranging in size from 14–30 mm L_T, and most of the rest (11%) were 81–120 mm L_T. The size distribution of Pacific halibut collected in August was more continuous, with 75% of the fish 41–70 mm L_T (Fig. 4).

Habitat of juvenile Pacific halibut was defined more often by sediment characteristics than any other variable (Table IV). The highest canonical correlation coefficients were usually assigned to either per cent sand or per cent mud. Exceptions were the high positive correlation of newly settled Pacific halibut (<30 mm) with temperature in May, and 71–80 mm Pacific halibut in August. Eighty-five per cent of the newly settled fish were captured in the warmest temperatures, between 5·5 and 6·5° C, while the larger fish were

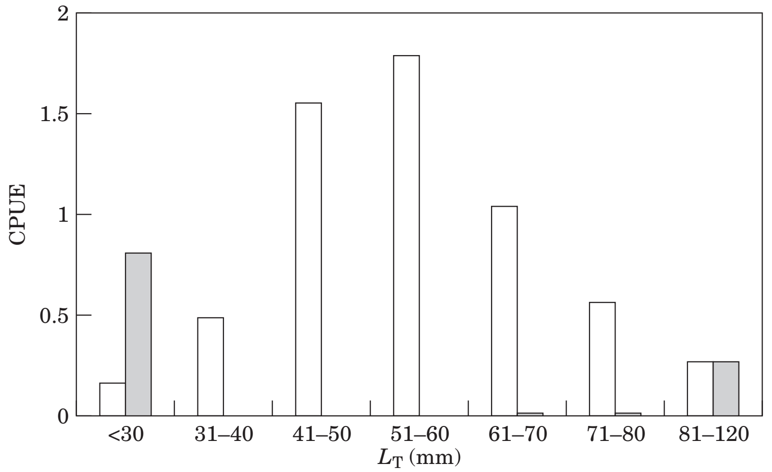

FIG. 4. Length distribution of juvenile Pacific halibut captured in August 1994–1999 (□) and May 1995–1996 (▨). Data on catch-per-unit-effort (CPUE) were combined for all years in each month. Fish <30 mm L_T collected in August were omitted from statistical analysis because they represented only 1·9% of the Pacific halibut captured during that month.

associated with both warm temperatures and substrata with high sand content. Pacific halibut 61–70 mm also showed a positive relationship with temperature but sediment characteristics had higher canonical correlation coefficients. Negative canonical correlation coefficients for per cent mud reflect the converse of positive association with the larger sediment categories. While sediment was the most important variable for fish 31–40 mm L_T, they also had a significant negative correlation with depth. Ninety-six per cent of these small Pacific halibut were captured in depths <30 m. There was a similar trend with depth for fish 61–70 mm L_T. Salinity did not correlate significantly with distribution in any size group, but there was little salinity variation in the system (Table III). The lack of significant canonical correlations for Pacific halibut 81–120 mm in May was probably a result of low numbers collected (Table IV). Descriptive data corresponding with the canonical correlation analysis show that the vast majority of Pacific halibut except for fish 81–120 mm L_T were captured on sediments dominated by a high percentage of sand (Fig. 5).

An expanded analysis of Pacific halibut captured on all of the different sediment types (Fig. 6) showed that none were ever collected on gravel or sandy gravel. Newly settled Pacific halibut, captured in May, were most abundant on sand and muddy sand, with a few found on sandy mud and mud. The majority of 81–120 mm fish collected in May were on gravelly mud. In August most fish 31–120 mm were found on sediments comprised primarily of sand.

COMPARISON OF LABORATORY AND FIELD RESULTS

One hundred and ninety-three tows were associated with data on median grain size (phi scale), permitting some direct comparisons with the laboratory experiments. CPUE of newly settled fish was greatest on sediments with grain sizes 3–4 phi (very fine sand), and fish 31–40 were most abundant on sands in the range of 2–4 phi (fine to very fine sand). This is analogous to the selections for

TABLE IV. The first canonical correlation coefficients of the environmental variables depth, bottom temperature, bottom salinity, per cent sand and per cent mud for presence or absence of Pacific halibut. Data are combined for all years, 1994–1999. —, P>0·05. The total number (n) of Pacific halibut in each size-class is listed by month. P in the weight column, presence was weighted more than absence, A and vice versa. If presence is weighted more heavily than absence, a positive coefficient is interpreted to mean that Pacific halibut abundance increased with an increase in that variable. The two highest coefficients >0·7 are shown in bold as they account for the most variation in presence or absence of Pacific halibut

Month	Size group (mm)	P (d.f.=5)	F value	n	Weight	Depth	Temp	Salinity	% Sand	% Mud
May	<30	0·0235	2·84	58	P	0·2397	**0·7072**	0·0736	0·2522	− 0·0393
	81–120	0·2830	1·29	19	—	—	—	—	—	—
August	31–40	0·0012	4·32	85	P	− **0·7588**	0·5973	0·1971	**0·7934**	− 0·6779
	41–50	<0·0001	6·72	272	P	− 0·4406	0·3595	0·2163	**0·9418**	− **0·7773**
	51–60	0·0004	4·90	312	P	− 0·5524	0·5112	0·2292	**0·7367**	− **0·9068**
	61–70	<0·0001	10·90	181	P	− 0·7355	0·8032	− 0·2459	**0·8713**	− **0·8265**
	71–80	<0·0001	8·11	98	P	− 0·5096	**0·9478**	− 0·1569	**0·7157**	− 0·6834
	81–120	0·0006	4·70	46	A	− 0·6306	0·6052	− 0·5131	**0·8203**	− 0·6876

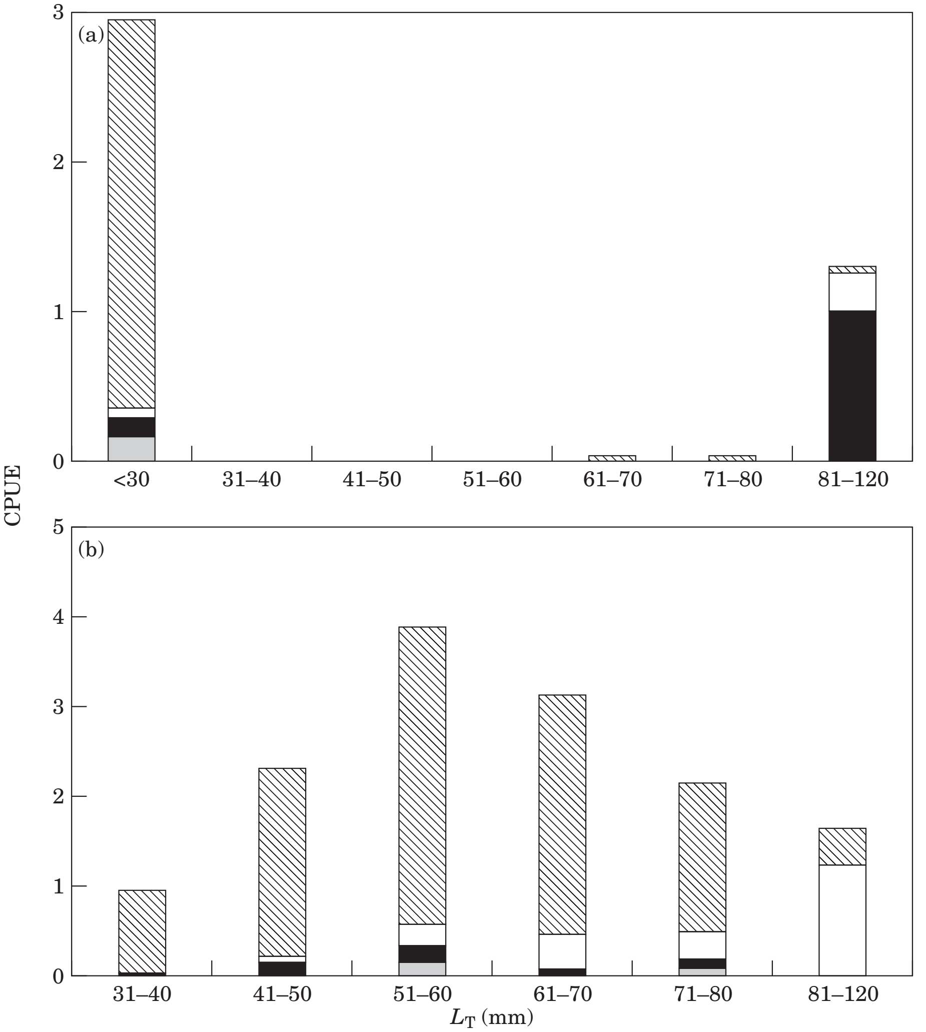

FIG. 5. Distribution of juvenile Pacific halibut in relation to per cent sand [75–100 (▧), 51–75 (□), 25–50 (■) and <25% (□) %] in the sediment in (a) May and (b) August. Bars represent average catch-per-unit-effort (CPUE) by size class for all survey years combined.

fine grains observed in the laboratory with the smallest Pacific halibut. Highest levels of burial in the smallest fish occurred on fine sediments. In the field, Pacific halibut 41–80 mm were found primarily on fine sand. This pattern partially supports the laboratory findings. While 41–70 mm fish demonstrated highest selectivity for either fine or medium sand, none in the field were captured on medium sand. In close correspondence with laboratory results, however, very few were associated with sediments in either the mud or granule categories. As observed in the laboratory, fish 81–120 mm were found over a broad range of sediments from fine sand to mud, but unlike the laboratory findings, none were found on medium sand or coarser sediments. In general, Pacific halibut were found in sediments somewhat finer than predicted from the laboratory

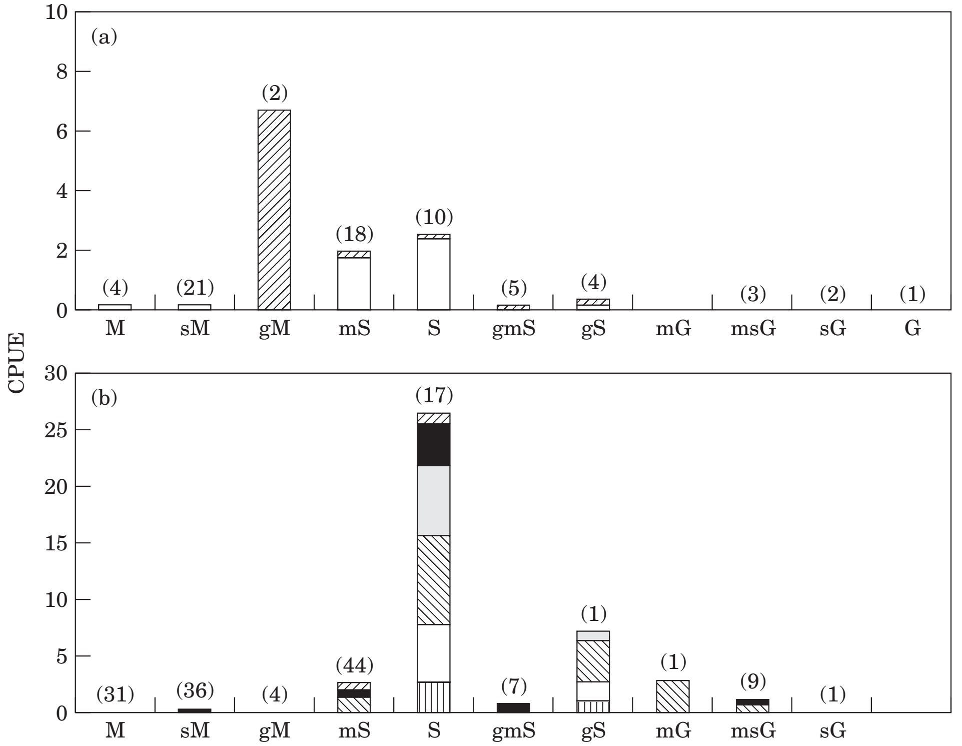

FIG. 6. Distribution of juvenile Pacific halibut by size class in (a) May [81–120 (▨) and <30 (□) mm L_T] and (b) August [81–120 (▨), 71–80 (■), 61–70 (▢), 51–60 (▧), 41–50 (□) and 31–40 (▥) mm L_T] in relation to sediment type classified on the basis of Folk's (1954) ternary system. Bars represent the average catch-per-unit-effort (CPUE) on each of the sediment types for all survey years combined. Sediment types are listed in increasing grain size from mud (M) to gravel (G). Sediment codes are analogous to those in Fig. 2, such that S is comparable with fine sand (fs), gmS with medium sand (mS), and gS with coarse sand (cS). No pebble sediments were sampled in the field. The number of stations sampled in each sediment type is given in parentheses above the bars.

experiments. In fact, distribution was conservative in terms of burial, whereby virtually all of the fish were distributed in sediments where they would be capable of burying easily.

DISCUSSION

Gibson & Robb (1992) hypothesized that large fishes should be less selective for sediment grain-size than small fishes because they can bury in a wider range of sediments. Both elements of this hypothesis were supported with yoy Pacific halibut which demonstrated a distinct size-dependent shift in habitat choice. The present burial experiments showed that sediment preference was closely related to the ability of Pacific halibut to cover themselves, where very few fish in any size class chose substrata where burial capability was <90%. Because large Pacific halibut have greatest burial capabilities in coarse sediments, they have a wider range of suitable substrata and this was reflected in a very broad range of choices made by fish >80 mm L_T. A similar association between burial and sediment choice was reported for both of the flatfishes *Limanda yokohamae* (Günther) and *Paralichthys olivaceus* Temminck & Schlegel (Tanda, 1990). Preference for fine-grained sediments was also observed in smallest winter flounder with breadth of choice increasing with fish size (Phelan *et al.*, 2001). Although they found that presence of food affected habitat choices in the laboratory, field distribution closely followed results from laboratory experiments with inorganic and azoic sediment. It is clear from all of these studies that size-specific preferences need to be considered when describing the habitats of fishes, particularly during early post-settlement life.

The results presented in this paper deviate considerably from the results of sediment preference experiments with Pacific halibut conducted by Moles & Norcross (1995). They found that muddy sand was chosen by 100% of 50 individually tested Pacific halibut in the size range 50–80 mm L_T. The results of the experiments described here showed a preference for somewhat coarser sediment and a much broader response to a similar array of substrata and if the results for 50–80 mm fish are pooled, the selections are primarily medium sand (41%) and fine sand (32%), with lower numbers of fish choosing coarse sand (14%), muddy sand (9%) and sandy mud (4%). Size-specific responses within that group (Fig. 2) can not explain deviation from the earlier study. Fish for both studies were collected near Kodiak Island in a variety of habitats, and Moles & Norcross (1995) reported that sediments in which Pacific halibut were held prior to testing had no effect on the choices made. The most likely reason for difference in the two studies is that mud mixtures in the earlier study were prepared from sediments collected in the field while the present ones were azoic and inorganic. The natural muds may have contained organic or other chemical compounds that were attractive to the Pacific halibut. It might be argued that chemical compounds are present in all natural field sites, but the intent of the new experiment was to test the effect of sediment grain size in the absence of chemical cues, while Moles & Norcross (1995) used a combination of natural marine sediments (albeit frozen and sieved) and dry sand from terrestrial sources. An alternate explanation is that Moles & Norcross (1995) defined fine sand as grain sizes ranging from 0·062–0·500 mm, which combines the present sediment categories of medium, fine and muddy sand (Table I). This difference, however, does not explain why none of their Pacific halibut chose coarse sand or sandy mud. The preliminary studies described here also show that locomotion, burial and habitat choices in juvenile Pacific halibut are all strongly influenced by feeding history. Moles & Norcross (1995) noted that their fish remained essentially motionless after making an initial sediment choice. It is possible that their well-fed fish had little motivation to move about and chose more broadly from the choices available.

Earlier field studies, along with the laboratory and field investigations presented in this paper provide substantial support for the hypothesis that fine-scale distribution of yoy Pacific halibut is associated with sediment grain size. Large-scale distribution may be determined by depth and temperature, but sediment characteristics, which vary over a relatively small scale, probably provide for zones or patches of suitable habitat. Using discriminant functions analysis Norcross *et al.* (1995) found that depth and presence of sandy sediment were the best predictors of Pacific halibut distribution in the nearshore waters of

Kodiak. Pacific halibut were present on substrata comprised of sediments ranging from 0–100% sand, but most were in habitats that were >80% sand. The mean length of fish in their surveys was 47 mm (Norcross *et al.*, 1995), so the findings correspond well with the present observation of preference for sand in small Pacific halibut. A subsequent analysis using regression tree analysis (Norcross *et al.*, 1997) indicated that location (e.g. outer parts of bays) was a critical feature of Pacific halibut habitat, followed by depth (<40 m), with temperature and high-sand sediment being secondary variables. Using non-metric multidimensional scaling Mueter & Norcross (1999) determined that depth and temperature accounted for 55% of the variability in abundance of age 0 and 1 year Pacific halibut, while sand content of the sediment accounted for 13% of the variability. Distribution for both age groups corresponded with shallow (<50 m), warm water and substrata with a relatively high sand content. Depth was the most important environmental variable in a canonical correlation analysis made for collections of Pacific halibut in Kachemak Bay when all yoy fish (26–100 mm L_T) were considered together (Abookire *et al.*, 2001). The majority of fish were in <20 m depth, however, the authors speculated that Pacific halibut may have been responding more directly to sediment type than depth because sandy sediments were found only in shallow water. A direct relationship to depth is doubtful because small Pacific halibut have been collected in large numbers in Sitkinak Strait (60–70 m) where tidal currents produce a sandy substratum in relatively deep water (Holladay & Norcross, 1995). The expanded analysis of beam-trawl survey data from Kachemak Bay with Pacific halibut divided into small size classes resulted in per cent sand being the environmental variable most closely correlated with the distribution of most classes, instead of depth or temperature. Because the statistical functions associated with the sand relationship shifted with fish size class, pooling of yoy fish in previous studies may have masked important effects of sediment.

It is likely that distribution of flatfishes is affected by a combination of variables, as pointed out by previous authors (Gibson, 1994). Surveys for yoy fishes conducted over large scale (Norcross *et al.* 1995, 1997; Nash & Geffen, 2000; Stoner *et al.* 2001) reveal that geographic location has a large effect on the presence or absence of newly settled fishes. This is undoubtedly related to the fact that pelagic larvae are dispersed and supplied to the benthic environment differentially through space. It is also clear that large-scale boundaries may be set by temperature. For example, a preliminary analysis of survey data collected by the International Pacific Halibut Commission in the south-eastern Bering Sea from 1970 to 1980 (Best, 1974, 1977; Best & Hardman, 1982) shows that the vast majority of juvenile Pacific halibut (<65 cm) were found where temperatures were >5° C. Norcross *et al.* (1997) reported that yoy Pacific halibut in the Kodiak nearshore were usually associated with temperatures >9° C.

These comparisons help to illustrate one of the problems inherent in distribution-based analysis or modeling of habitat requirements for fishes. The variables identified statistically as being most important in distribution depend substantially upon the ranges of conditions under which the fishes were surveyed, and the spatial scale of the survey. Fish for this study were collected over a wide range of depth and sediment conditions, but ranges of temperature and salinity were relatively narrow. Based upon past investigations it is reasonable to believe that larval dispersal and temperature probably set the large-scale distribution of Pacific halibut, and sediment characteristics define a fine-scale dimension of habitat for this species. Laboratory experiments, such as those reported in this study, provide the hypothesis-testing approach to mechanisms of habitat choice and distribution not possible in descriptive field studies.

Survivorship and recruitment to the larger size classes will depend upon young flatfishes finding shelter from predation and acquiring the appropriate foods. The experiments described here show that burial capability is a relatively critical habitat feature for all yoy Pacific halibut, and sediments that permit burial may allow small flatfish to avoid predation. Experimental results relative to this possible benefit are mixed. For example, some studies show positive effects of sediment on survivorship (Ellis *et al.*, 1997) while others have reported that sand did not protect juvenile flatfishes from predators (Ansell & Gibson, 1993; Manderson *et al.*, 1999). Clearly, the role of sediment in providing refuge will depend upon the foraging strategy of specific predators. Pacific halibut in the field were associated with finer sediments than in the laboratory. A plausible explanation is that the presence of bottom currents or sediment compaction make it more difficult to bury with the same efficiency in a given sediment type.

Habitat choice in flatfishes is also affected by the presence of food (Neuman & Able, 1998; Wennhage & Gibson, 1998; Phelan *et al.*, 2000), and sediment grain-size has a well known effect on the sediment dwellers that comprise the food items for flatfishes (Stoner *et al.*, 2001). Holladay & Norcross (1995) found an ontogenetically related shift in the diet of yoy Pacific halibut and an association between prey items and substratum type. The observation reported here that Pacific halibut bury in finer sediments in the field than in the laboratory may be due, in part, to certain prey items being available only in fine sand in the field. Choices for sediment grain-size may be adapted to place the fish in locations that are likely to provide appropriate foods but, as yet, it is not known which variables are assessed directly by the fish. Other experiments conducted in the laboratory indicate that juvenile Pacific halibut can make habitat choices related to the presence of structural elements of the habitat including sponges, bryozoans and sand waves (A. W. Stoner & R. H. Titgen, unpubl. data).

Regardless of the mechanisms for habitat choice and the adaptive significance, it is clear from this combination of field and laboratory results that sediment choice in Pacific halibut is strong in the smallest fish and varies with size. The sediment requirements for Pacific halibut when they achieve a total length of 70–80 mm are probably broad because of increasing burial capabilities and decreasing vulnerability to predators associated with size observed in other species (Witting & Able, 1993; Van der Veer *et al.*, 1997). Consequently, after 6–9 months in the benthos, Pacific halibut probably have a relatively wide range of suitable habitat available to them. Because of the changing relationships between flatfishes and sediment during the first year of life in the benthos, size-related shifts in capabilities and preferences must be considered in any habitat model for the species. For some species such as winter flounder (Stoner *et al.*, 2001), and especially for fast growing species like Pacific halibut, pooling yoy fish for distributional analysis may result in lost information on habitat requirements.

We thank E. Munk in Kodiak for logistical help, boat operation and assistance with collections, and B. Stevens, R. Otto and the Borough of Kodiak for providing laboratory space to hold Pacific halibut prior to shipping. T. Tripp, E. Sturm, S. Sogard and M. Spencer assisted in Kodiak field collections, and M. Ottmar, E. Sturm, M. Spencer, R. Titgen, L. Meier and K. Rhemke provided help with laboratory experiments in Newport. M. Davis acquired the appropriate permits for collecting and transporting Pacific halibut, and assisted with quarantine procedures. We thank R. Geagel, M. Geagel and G. Snedgen for assisting with field collections in Kachemak Bay, and all who assisted with fish collections, especially those who helped during several years: M. Arimitsu, E. Chilton, J. Figurski and F. Mueter. We thank B. Holladay for her identification of newly settled flatfishes and B. Norcross for her advice and support with Kachemak Bay sampling. D. Holt processed sediment samples, and C. Armistead kindly provided the study area map. A. Moles and B. Phelan provided helpful criticism of the manuscript.

References

Abookire, A. A. & Norcross, B. L. (1998). Depth and substrate as determinants of distribution of juvenile flathead sole (*Hippoglossoides elassodon*) and rock sole (*Pleuronectes bilineatus*), in Kachemak Bay, Alaska. *Journal of Sea Research* **39,** 113–123.

Abookire, A. A., Piatt, J. F. & Robards, M. D. (2000). Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. *Estuarine, Coastal and Shelf Science* **51,** 45–59.

Abookire, A. A., Piatt, J. F. & Norcross, B. L. (2001). Juvenile groundfish habitat in Kachemak Bay, Alaska, during late summer. *Alaska Fishery Research Bulletin* **8,** 45–56.

Amezcua, F. & Nash, R. D. M. (2001). Distribution of the order Pleuronectiformes in relation to the sediment type in the North Irish Sea. *Journal of Sea Research* **45,** 293–301.

Ansell, A. D. & Gibson, R. N. (1993). The effect of sand and light on predation of juvenile plaice (*Pleuronectes platessa*) by fishes and crustaceans. *Journal of Fish Biology* **43,** 837–845.

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F. & Weinstein, M. R. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51,** 633–641.

Berghahn, R. (1986). Determining abundance, distribution and mortality of 0-group plaice (*Pleuronectes platessa* L.) in the Wadden Sea. *Journal of Applied Ichthyology* **2,** 11–22.

Best, E. A. (1974). Juvenile halibut in the eastern Bering Sea: Trawl surveys, 1970–1972. *Technical Report No. 11*. Seattle, WA: International Pacific Halibut Commission.

Best, E. A. (1977). Distribution and abundance of juvenile halibut in the southeastern Bering Sea. *Scientific Report No. 62*. Seattle, WA: International Pacific Halibut Commission.

Best, E.A. & Hardman, W. H. (1982). Juvenile halibut surveys, 1973–1980. *Technical Report No. 20*. Seattle, WA: International Pacific Halibut Commission.

Ellis, T., Howell, B. R. & Hughes, R. N. (1997). The cryptic responses of hatchery-reared sole to a natural sand substratum. *Journal of Fish Biology* **51,** 389–401.

Folk, R. L. (1954). The distinction between grain size and mineral composition in sedimentary rock nomenclature. *Journal of Geology* **62,** 344–359.

Folk, R. L. (1980). *Petrology of Sedimentary Rocks*. Austin, Texas: Hemphill.

Gibson, R. N. (1994). Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32,** 191–206.

Gibson, R. N. & Robb, L. (1992). The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* **40,** 771–778.

Gibson, R. N. & Robb, L. (2000). Sediment selection in juvenile plaice and its behavioural basis. *Journal of Fish Biology* **56,** 1258–1275. doi:10.1006/jfbi.2000.1250.

Goldberg, R., Phelan, B., Pereira, J., Hagan, S., Clark, P., Bejda, A., Calabrese, A., Studholme, A. & Able, K. W. (2002). Variability in habitat use by young-of-the-year winter flounder, *Pseudopleuronectes americanus*, in three northeastern U.S. estuaries. *Estuaries* **25,** 215–226.

Gunderson, D. R. & Ellis, I. E. (1986). Development of a plumb staff beam trawl for sampling demersal fauna. *Fisheries Research* **4,** 35–41.

Holladay, B. A. & Norcross, B. L. (1995). August diet of age-0 Pacific halibut in nearshore waters of Kodiak Island, Alaska. *Environmental Biology of Fishes* **44,** 403–416.

IPHC (1998). The Pacific halibut: biology, fishery, and management. *Technical Report No. 40*. Seattle, WA: International Pacific Halibut Commission.

Jager, Z., Kleef, L. & Tydeman, P. (1993). The distribution of 0-group flatfish in relation to abiotic factors on the tidal flats in the brackish Dollard (Ems estuary, Wadden Sea). *Journal of Fish Biology* **43,** 31–43.

Johnson, R. A. & Wichern, D. W. (1992). *Applied Multivariate Statistical Analysis*. Englewood Cliffs, NJ: Prentice Hall.

Kuipers, B. (1977). On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research* **11,** 56–91.

Langton, R. W., Steneck, R. S., Gotceitas, V., Juanes, F. & Lawton, P. (1996). The interface between fisheries research and habitat management. *North American Journal of Fisheries Management* **16,** 1–7.

Manderson, J. P., Phelan, B. A., Bejda, A. J., Stehlik, L. L. & Stoner, A. W. (1999). Predation by striped searobin (*Prionotus evolans*, Triglidae) on young-of-the-year winter flounder (*Pseudopleuronectes americanus*, Walbaum): examining prey size selection and prey choice using field observations and laboratory experiments. *Journal of Experimental Marine Biology and Ecology* **242,** 211–231.

Manderson, J. P., Phelan, B. A., Meise, C., Stehlik, L. L., Bejda, A. J., Pessutti, J., Arlen, L., Draxler, A. & Stoner, A. W. (2002). Spatial dynamics of habitat suitability for the growth of newly-settled winter flounder (*Pseudopleuronectes americanus*) in an estuarine nursery. *Marine Ecology Progress Series* **228,** 227–239.

McConnaughey, R. A. & Smith, K. R. (2000). Associations between flatfish abundance and surficial sediments in the eastern Bering Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **57,** 2410–2419.

Moles, A. & Norcross, B. L. (1995). Sediment preference in juvenile Pacific flatfishes. *Netherlands Journal of Sea Research* **34,** 177–182.

Mueter, F. J. & Norcross, B. L. (1999). Linking community structure of small demersal fishes around Kodiak Island, Alaska, to environmental variables. *Marine Ecology Progress Series* **190,** 37–51.

Nash, R. D. M. & Geffen, A. J. (2000). The influence of nursery ground processes in the determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin Bay, Irish Sea. *Journal of Sea Research* **44,** 101–110.

Neuman, M. J. & Able, K. W. (1998). Experimental evidence of sediment preference by early life history stages of windowpane (*Scophthalmus aquosus*). *Journal of Sea Research* **40,** 33–41.

NMFS (1999). Our living oceans. Report on the status of U.S. living marine resources, 1999. *U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-F/SPO-41.*

Norcross, B. L., Holladay, B. A. & Muter, F. J. (1995). Nursery area characteristics of pleuronectids in coastal Alaska, USA. *Netherlands Journal of Sea Research* **34,** 161–175.

Norcross, B. L., Muter, F. J. & Holladay, B. A. (1997). Habitat models for juvenile pleuronectids around Kodiak Island, Alaska. *Fishery Bulletin, U.S.* **95,** 504–520.

Norcross, B. L., Holladay, B. A., Abookire, A. A. & Dressel, S. C. (1998). Defining habitats for juvenile groundfishes in Southcentral Alaska, with emphasis on flatfishes. *OCS Study Minerals Management Service, Final Report No. MMS 97-0046*. Fairbanks, Alaska: University of Alaska.

Norcross, B. L., Blanchard, A. & Holladay, B. A. (1999). Comparison of models for defining nearshore flatfish nursery areas in Alaskan waters. *Fisheries Oceanography* **8,** 50–67.

Phelan, B. A., Goldberg, R., Bejda, A. J., Pereira, J., Hagan, S., Clark, P., Studholme, A. L., Calabrese, A. & Able, K. W. (2000). Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries. *Journal of Experimental Marine Biology and Ecology* **247,** 1–28.

Phelan, B. A., Manderson, J. P., Stoner, A. W. & Bejda, A. J. (2001). Size-related shifts in the habitat associations of young-of-the-year winter flounder (*Pseudopleuronectes americanus*): field observations and laboratory experiments with sediments and prey. *Journal of Experimental Marine Biology and Ecology* **257,** 297–315.

Pihl, L. & Van der Veer, H. W. (1992). Importance of exposure and habitat structure for the population density of 0-group plaice, *Pleuronectes platessa* L., in coastal nursery areas. *Netherlands Journal of Sea Research* **29,** 145–152.

Rijnsdorp, A. D., Van Beek, F. A., Flatman, S., Millner, R. M., Riley, J. D., Giret, M. & DeClerck, R. (1992). Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. *Netherlands Journal of Sea Research* **29,** 173–192.

Rogers, S. I. (1992). Environmental factors affecting the distribution of sole (*Solea solea* (L.) within a nursery area. *Netherlands Journal of Sea Research* **29,** 153–161.

SAS (1996). *SAS User's Guide: Statistics, Version 6.11*. Cary, NC: SAS Institute, Inc.

Schmitt, C. C. (1985). Review of a trawl survey program for juvenile Pacific halibut. Seattle. Unpublished MS thesis, University of Washington, Seattle.

Schmitten, R. A. (1999). Essential fish habitat: Opportunities and challenges for the next millennium. In *Fish Habitat: Essential Fish Habitat and Rehabilitation* (Benaka, L., ed.), pp. 3–10. Bethesda, MD: American Fisheries Society.

Sokal, R. R. & Rohlf, F.J. (1969). *Biometry: The Principles and Practice of Statistics in Biological Research*. San Francisco, CA: W. H. Freeman & Co.

Stoner, A. W., Manderson, J. P. & Pessutti, J. P. (2001). Spatially explicit analysis of estuarine habitat for juvenile winter flounder: combining generalized additive models and geographic information systems. *Marine Ecology Progress Series* **213,** 253–271.

Swartzman, G., Huang, C. & Kaluzny, S. (1992). Spatial analysis of Bering Sea groundfish survey data using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 1366–1378.

Tanda, M. (1990). Studies on burying ability in sand and selection to the grain size for hatchery-reared marbled sole and Japanese flounder. *Nippon Suisan Gakkaishi* **56,** 1543–1548.

Van der Veer, H. W., Ellis, T., Miller, J. M., Pihl, L. & Rijnsdorp, A. D. (1997). Size-selective predation on juvenile North Sea flatfish and possible implications for recruitment. In *Early Life History and Recruitment in Fish Populations* (Chambers, R. C. & Trippel, E. A., eds), pp. 279–303. London: Chapman & Hall.

Van der Veer, H. W., Dapper, R. & Witte, J. I. J. (2001). The nursery function of the intertidal areas in the western Wadden Sea for 0-group sole *Solea solea* (L.). *Journal of Sea Research* **45,** 271–279.

Wennhage, H. & Gibson, R. N. (1998). Influence of food supply and a potential predator (Crangon crangon) on settling behaviour of plaice (*Pleuronectes platessa*). *Journal of Sea Research* **39,** 103–112.

Witting, D. A. & Able, K. W. (1993). Effects of body size on probability of predation for juvenile summer and winter flounder based on laboratory experiments. *Fishery Bulletin, U.S.* **91,** 577–581.