



# Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes

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## Abstract

Laboratory experiments with juvenile Pacific halibut (*Hippoglossus stenolepis* Schmidt) (31–150 mm TL) and northern rock sole (*Lepidopsetta polyxystra* Orr and Matarese) (15–150 mm TL) were conducted to examine relationships between sediment preference, burial performance, and general morphological characteristics. Both species demonstrated significant size-dependent changes in sediment choices during the first year of life. Highest sediment selectivity occurred in the smallest individuals of both species. There was a strong positive relationship between sediment choice and ability to bury quickly and completely, although the choices made by rock sole were less specific than those of comparably sized halibut and were less closely concordant with burial capability. In both species, fish >80 mm TL were relatively nonselective, except that they avoided sediments with the largest grain size (i.e., granules and pebbles). Pacific halibut have narrower, more powerful bodies than rock sole and were stronger burrowers than rock sole. Rock sole were more cryptic than halibut in general locomotion and color-matching capability, and appear to depend to a lesser extent on burial for survival than do halibut. Association with sediment is the first line of defense for juvenile flatfishes, and the relationships shift rapidly with fish size during the first year of benthic life. Therefore, habitat descriptions and models for young post-settlement flatfishes need to be made for narrow size classes.

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## 1. Introduction

Sediment grain size is considered to be one of the most important environmental variables determining the distribution of flatfishes (Gibson, 1994, 1997), and descriptive field studies reporting sediment associations are available for a large number of flatfish species (e.g., Rogers, 1991; Jager et al., 1993; Wennhage and Pihl, 1994; Norcross et al., 1999; Abookire and Norcross, 1998; McConnaughey and Smith, 2000; Phelan et al., 2000). Most frequently analyses are performed for fishes categorized by year class or larger size intervals. While this may be appropriate for species that show little size-related variation in sediment preference such as juvenile yellowfin sole (*Pleuronectes asper* (Pallas)) (Moles and Norcross, 1995) and plaice (*Pleuronectes platessa* L.) (Gibson and Robb, 2000), other species including starry flounder (*Platichthys stellatus* (Pallas)) (Moles and Norcross, 1995) and winter flounder (*Pseudopleuronectes americanus* Walbaum) (Phelan et al., 2000) demonstrate significant shifts during the first year of benthic life. Stoner et al. (2001) used spatially explicit modeling to show that habitats for winter flounder in a New Jersey estuary shift in time and space because of changes in environmental variables coupled with rapid size-dependent changes in habitat associations occurring in fish between 10 and 100 mm length. Some shifts in habitat preference are associated with size-related burial capabilities (Tanda, 1990; Gibson and Robb, 1992).

The adaptive significance of specific sediment preferences is probably related to shelter from predation provided by burial (particularly for small individuals), abundance of preferred food organisms in certain sediment types, and potential conservation of energy by reduced metabolism in certain substrata (Gibson and Robb, 2000). This investigation was conducted to test for size-related shifts in sediment preferences of juvenile flatfishes, with the hypothesis that choices are made on the basis of burial capabilities, morphological constraints, and feeding type. Two pleuronectid species were compared, Pacific halibut (*Hippoglossus stenolepis* Schmidt), which is a powerful, highly motile pursuit-type predator with a large mouth, and northern rock sole (*Lepidopsetta polyxystra* Orr and Matarese), a small-mouthed browser of small invertebrates that tends to be relatively slow moving and cryptic. As part of the analysis, we examined how burial capabilities in our subject species compared with that of plaice (Gibson and Robb, 1992). Little is known

Table 1  
Sediments used in substratum preference and burial experiments with juvenile Pacific halibut and rock sole

Classification (screen)	Mean grain size (mm)	Approximate phi value	Composition
Pebble	~ 10	- 3.0	river gravel
Granule	2–4	- 1.0	river gravel
Coarse sand	1	0	(#16 silica sand)
Medium sand	0.5	1.0	(#30 silica sand)
Fine sand	0.2	2.25	(#70 silica sand)
Muddy sand	~ 0.1	3.25	70% fine sand + 30% DE
Sandy mud	~ 0.04	4.5	70% DE + 30% fine sand

Composition is percent by weight. DE is diatomaceous earth.

about the early life history of Pacific halibut and rock sole; however, both settle to the benthos in early summer, and age-0 and age-1 juveniles of both are found primarily in shallow water habitats (< 50 m) of the Gulf of Alaska and Bering Sea (Norcross et al., 1997; IPHC, 1998). Both have high value in the commercial fisheries of Alaska.

## 2. Materials and methods

### 2.1. Experimental animals

Pacific halibut and northern rock sole<sup>1</sup> for our laboratory experiments were collected in Chiniak Bay on the eastern shore of Kodiak Island, Alaska (57°40'N, 152°30'W) in early August 2000, and in June and August 2001. Collections were made with a beam trawl (2-m wide, 3-mm mesh) towed at  $\sim 1 \text{ m s}^{-1}$ . 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 (HMSC) in Newport, OR. Shipping generally took <30 h and temperatures remained near 9 °C in insulated containers. Very few fish died in transport, and most fed within 24 h of arrival in Newport.

The subject species were maintained in flow-through seawater systems at HMSC. Halibut were held in multiple tanks 1.3 m in diameter, with 0.5 cm of sand on the bottom (combination of fine, medium, and coarse, Table 1), and supplied with seawater at 9 °C ( $\pm 1.5$  °C). Rock sole were held in 0.75 m square tanks (35 cm deep), with similar environmental conditions. The fish were fed to satiation three times per week on diets of chopped frozen shrimp and dry pellet foods. Growth rates in the halibut were typically 0.25–0.5 mm day<sup>-1</sup>. Growth in rock sole was slower (<0.25 mm day<sup>-1</sup>), but similar to rates observed by Moles and Scott (2002). General observations on movement and feeding mode were recorded for species comparisons.

Fish for both burial and sediment preference experiments were tested in 10-mm size classes from 31 to 80 mm TL, and in classes 81–100 and 101–150 mm. Rock sole 15–20 and 21–30 mm were also tested because they settle at a smaller size (15 mm) than halibut and were available (Orr and Matarese, 2000). Very few halibut smaller than 30 mm were collected despite attempts made in June 2001. The size classes tested span the range of size for age-0 halibut in the field and both age-0 and age-1 rock sole. All fish were tested individually (see below).

### 2.2. Sediment preference experiments

Halibut and rock sole were tested for sediment preferences in circular tanks scaled to fish size (fish  $\leq 40$  mm TL in arenas 25 cm in diameter, fish 40–60 mm in arenas 42 cm in

<sup>1</sup> Rock sole in Alaska are represented by two very similar species, *L. polyxystra* (northern rock sole) and *L. bilineata* (southern rock sole), which were distinguished only recently (Orr and Matarese, 2000). Both species occur in Kodiak, Alaska, where the experimental animals were collected, but age-0 rock sole are almost impossible to separate while alive. While it is possible that our experiments included some *L. bilineata*, a sample of fish sacrificed for species confirmation revealed that all were *L. polyxystra* (A. Matarese, personal communication).

diameter, fish 61–100 mm in 72 cm diameter tanks, and fish 101–150 mm in 110 cm tanks). Seven sediment types were tested in the choice experiments (Table 1). These were prepared from natural river gravels, silica sands, and diatomaceous earth. They were completely inorganic, thus reducing potential effects of food or olfactory cues. Each experimental tank had all seven sediment types arranged in a pattern of equal wedges 25–40 mm deep (increasing with fish size) with the fine- and coarse-grained sediment types interspersed. The same pattern was used in each of four tanks, but the tanks were rotated to different orientations to reduce any effects of the room or lighting. Flow-through seawater was provided ( $9 \pm 1$  °C) to a depth of 25 cm above the sediment, except for the smallest fish (<40 mm TL) that were tested in static water systems in a cold room. Lighting was 12-h light and 12-h dark (as in the holding areas), with a light level of  $2$  to  $3 \times 10^{-1} \mu\text{mol m}^{-2} \text{s}^{-1}$ , equivalent to dim daylight. Illumination with dim red light ( $4$  to  $6 \times 10^{-2} \mu\text{mol m}^{-2} \text{s}^{-1}$ ) allowed overhead video recordings during the night.

Gibson and Robb (2000) recommended that a knowledge of activity pattern in fish is desirable when using point measurements in habitat preference studies. Preliminary video recordings of young halibut and rock sole revealed that their locomotory activities and diurnal rhythms were somewhat different, and both species were strongly affected by feeding history. Juvenile halibut were active primarily at night; however, when fed to satiation they normally buried in the sediment and remained essentially motionless for 12–24 h. Although juvenile rock sole were active both day and night, they cleared their stomachs more slowly than halibut and remained relatively inactive for 36 h or more after feeding to satiation. After handling or transfers, both species buried into the sediment and remained motionless for several hours. Exploration of the holding tank resumed during hours of darkness, and choices appeared to be made during that time. By the time light increased in the morning, the fish were buried or quiescent again. With few exceptions, they did not shift position between 0800 and 1200 h.

On the basis of preliminary observations, the following protocol was established for sediment preference experiments. Halibut were fed in the afternoon prior to testing, and transferred to the experimental apparatus between 1300 and 1500 h on the next day. Rock sole were handled in the same way, except that they were starved for 2 days rather than 1. These starvation periods insured that the fish would be active and search the available substrata, yet they would not swim constantly in search of food. One fish was released on a sector known to be avoided by young fish (i.e., either pebbles or granules). Observations were made on the location and burial status (% covered) of the fish 1 min and 1 h after release on the first day, and at 0800 and 1000 h 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 h). The video tapes provided information on the general locomotion of the fish and their locations relative to the different sediments. The tapes were not used to quantify the amount of time spent on each sediment type because recordings were not continuous, and because the fish were often buried and not visible. A run was considered valid when the video recording revealed that the individual had been active for 3–4 h prior to 0800 h, 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 h. Runs not meeting these specifications (13%) were eliminated from the analysis. Like Gibson and Robb (2000), habitat preference was scored

during the quiescent phase. At least 15 valid replicates were acquired for each size category for each species.

The frequency distribution of sediment choices was tested with a log-likelihood test ( $G$ -test) against the null hypothesis that choices were equally distributed among the seven sediment types presented. The effects of fish size on sediment choice were tested for each species using a log-likelihood ratio test applied to contingency tables.

### 2.3. Burial experiments

Short-term tests of burial behavior were conducted for Pacific halibut and rock sole in size classes identical to those used in sediment choice experiments. Fish <40 mm TL 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 of the container. 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  $3$  to  $6 \times 10^{-1} \mu\text{mol m}^{-2} \text{s}^{-1}$ . The seven sediment types used in the sediment preference experiments (Table 1) were tested independently.

Halibut and rock sole were deprived of food for 24 and 48 h prior to testing, respectively, for reasons similar to those previously described. The fish were measured for total length and transferred from holding tanks to the experimental aquaria, one fish per aquarium. Recordings on fish behavior and coloration were made during the first 60 s after transfer, and subsequently at 5, 15, 30, 60, and 120 min. Ordinarily, the startled fish attempted to bury immediately upon transfer. 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 ordinarily increased with time up to 60 min. Burial was scored as percent of body covered with sediment. Trials were started between 0900 and 1300 h. Four different individuals in each size class were tested on each sediment type, except that fish <70 mm TL were not tested on the largest grain size (pebbles) because our experiments showed that no fish <100 mm was able to cover with this substratum type. Naïve fish were used in all of the burial trials. In the final analysis two indices were considered—maximum percent coverage during the 2-h trial and time to maximum burial.

To compare burial capability of different species our results for halibut and rock sole were compared with a size-based burial model developed by Gibson and Robb (1992) for plaice (*P. platessa*) where:

$$\text{logit } C = 3.25 + 0.069L - 6.771S$$

$C$  is the proportion of body covered,  $L$  is total length (mm), and  $S$  is the mean grain size of the sediment (mm). Paired  $t$ -tests were used to test for differences between observed and expected burial abilities.

Several measurements of body form were made for halibut and rock sole anesthetized with MS222. Total length (TL), standard length (SL), wet weight, maximum body depth (maximum distance from dorsal to ventral sides excluding fins), and minimum peduncle

depth (dorsal to ventral) were determined for both species over a range of size 20–140 mm TL. Standard regression techniques were used to explore relationships to fish length.

### 3. Results

#### 3.1. Sediment preferences

Small halibut and rock sole demonstrated significant preferences for sediments of particular grain sizes (Fig. 1). No rock sole was found on either pebbles or granules, and only one halibut individual (>80 mm TL) chose granules. The smallest halibut (31–40 and 41–50 mm TL) were found on all of the sediments classified as medium sand or finer. Halibut 51–70 mm TL preferred medium sand and were rarely observed on the finest and coarsest sediments. *G*-tests revealed that halibut in all of the classes <80 mm TL were distributed unevenly ( $p < 0.05$ ) among the sediment types. Halibut >80 mm TL demonstrated no significant preference for sediment type ( $p > 0.10$ ), although they tended to avoid the largest grain sizes. This size-dependent sediment preference was confirmed by contingency table analysis ( $G = 43.95$ ,  $p < 0.01$ ).

The smallest rock sole (<30 mm TL) demonstrated strong preference for muddy sand ( $p < 0.01$ ), while preference shifted toward larger grain sizes (particularly medium sand) in fish 31–50 mm TL (Fig. 1). Frequency of choices among the sediments broadened and became more evenly distributed with increasing fish size until rock sole >50 mm TL demonstrated an almost equal distribution over all sediments ranging from sandy mud to coarse sand. As observed in halibut, no statistically significant preference was found in fish >80 mm TL, despite the obvious avoidance of pebbles and granules. Contingency table analysis showed that fish size had a significant effect on sediment choice ( $G = 50.86$ ,  $p < 0.05$ ). Considered together, small halibut preferred finer sediment than comparably sized rock sole (31–50 mm TL), but rock sole >50 mm always demonstrated a broader range of substratum choice.

#### 3.2. Burial capabilities and relationships to sediment choice

Burial capabilities in Pacific halibut and rock sole were strongly size-dependent as expected (Fig. 2). Virtually all of the fish were capable of substantial burial (~90%) in the finest sediments (sandy mud and muddy sand) and capabilities in coarser sands increased with size. Burial of ~90% in medium sand was possible for fish >40–50 mm TL in both species, but capabilities diverged in larger fish. For example, halibut 51–60 mm TL buried 70% in coarse sand, while similar sized rock sole only buried 28%. Halibut >60 mm TL buried 24% in granules, but only rock sole >100 mm TL buried more than 11%. In sediment types where burial capabilities were high (sandy mud, muddy sand, and fine sand), rock sole responses were slightly lower and more variable than halibut, particularly in the larger fish size classes. Large rock sole frequently shifted in position and often cleared their gills when lying on the finest grains. Burial was often very shallow or just a dusting of sediment.

Burial capabilities of Pacific halibut were relatively close to the size-dependent pattern observed in plaice by Gibson and Robb (1992) (Fig. 3), and a paired *t*-test for observed

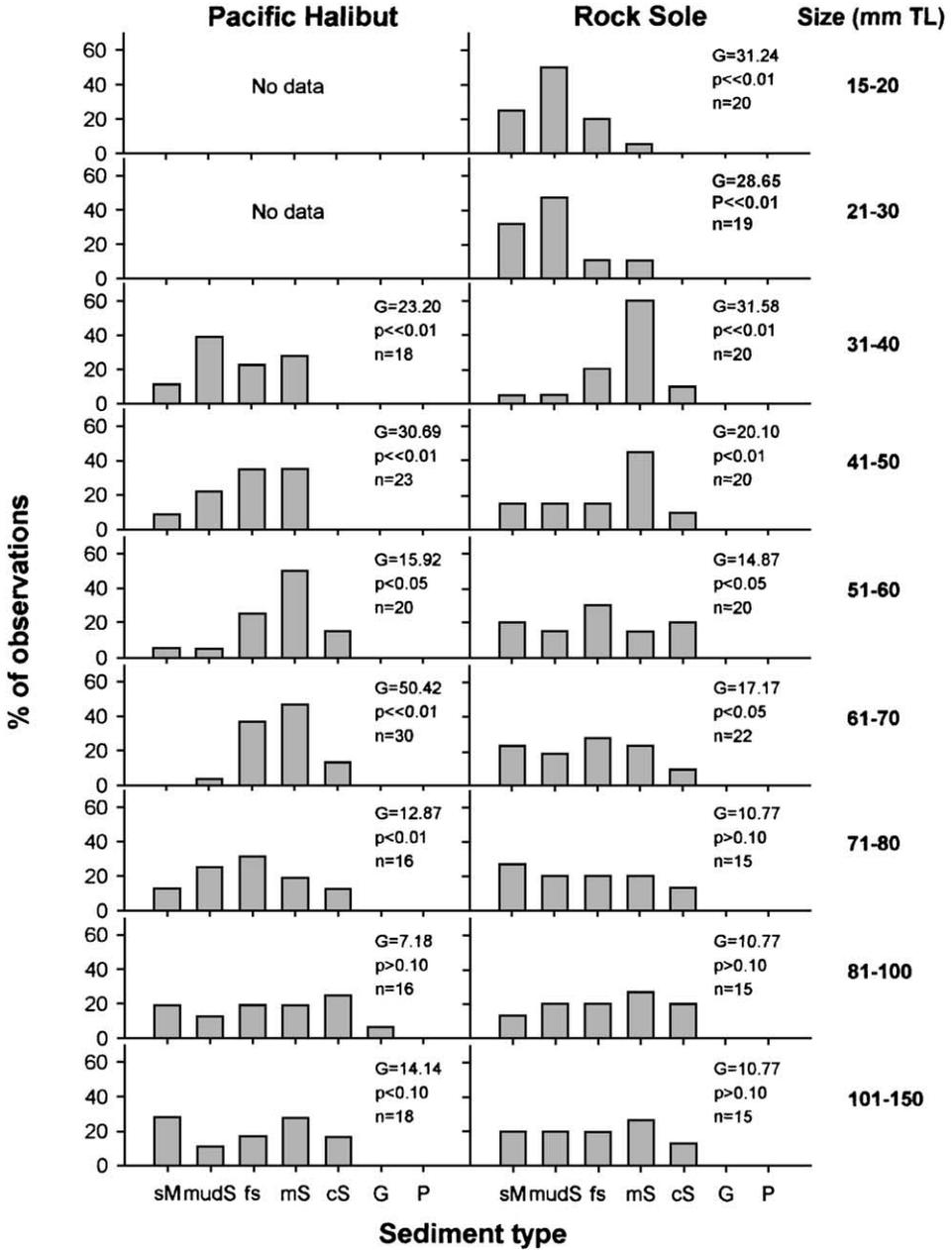


Fig. 1. Choices for sediment type demonstrated by juvenile Pacific halibut and northern rock sole. Values shown are percent of total numbers (*n*) found on each sediment type when fish were tested as individuals. Results of the log-likelihood test (*G*-test) for even distribution among the seven sediments 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 1).

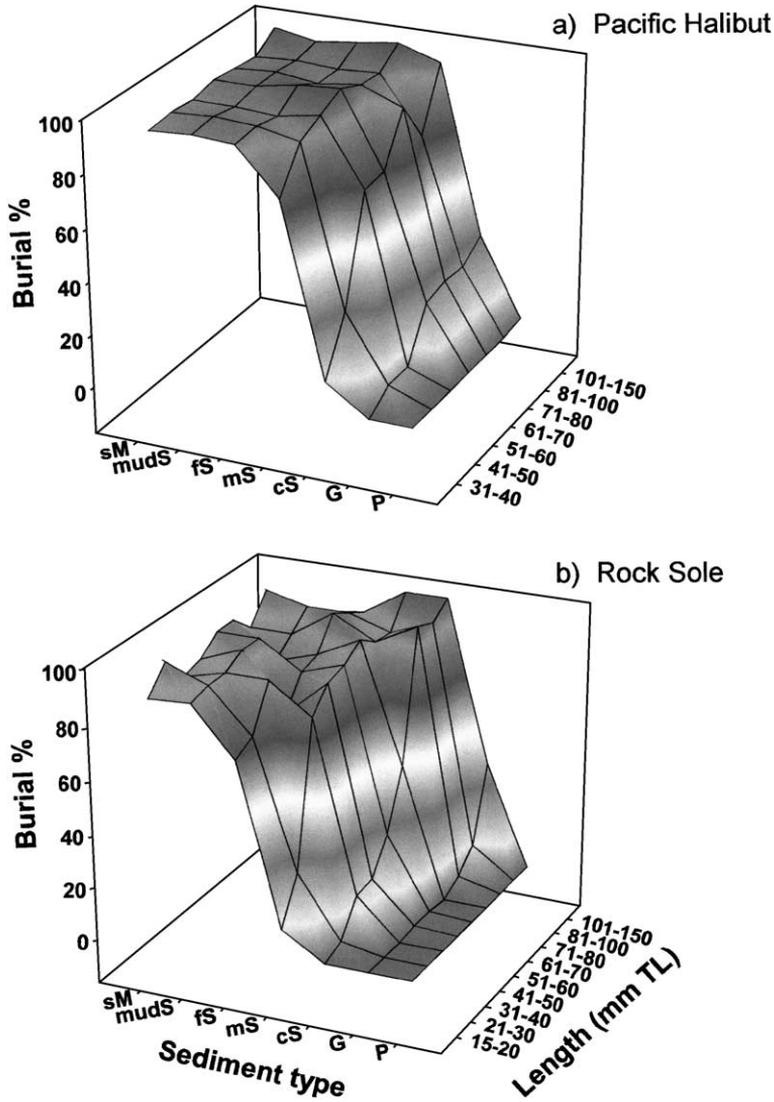


Fig. 2. Maximum burial (percent of body covered) by juvenile (a) Pacific halibut and (b) northern rock sole in seven different sediment types shown as a function of fish size. Sediment codes are the same as those in Fig. 1.

versus expected burial revealed that the patterns were not significantly different ( $t=0.289$ ,  $p=0.773$ ). Nevertheless, there was substantial burial when none was expected in certain cases, as indicated by numerous positive values along the y-axis of Fig. 3. All halibut >40 mm TL could bury at least partially in granules, while the algorithm for plaice predicted that no halibut to 200 mm TL would have that capability. Burial in coarse sand was also underestimated substantially. Burial rates in fine grains were close to expectations or slightly overestimated when values of 100% were expected. We found that halibut rarely

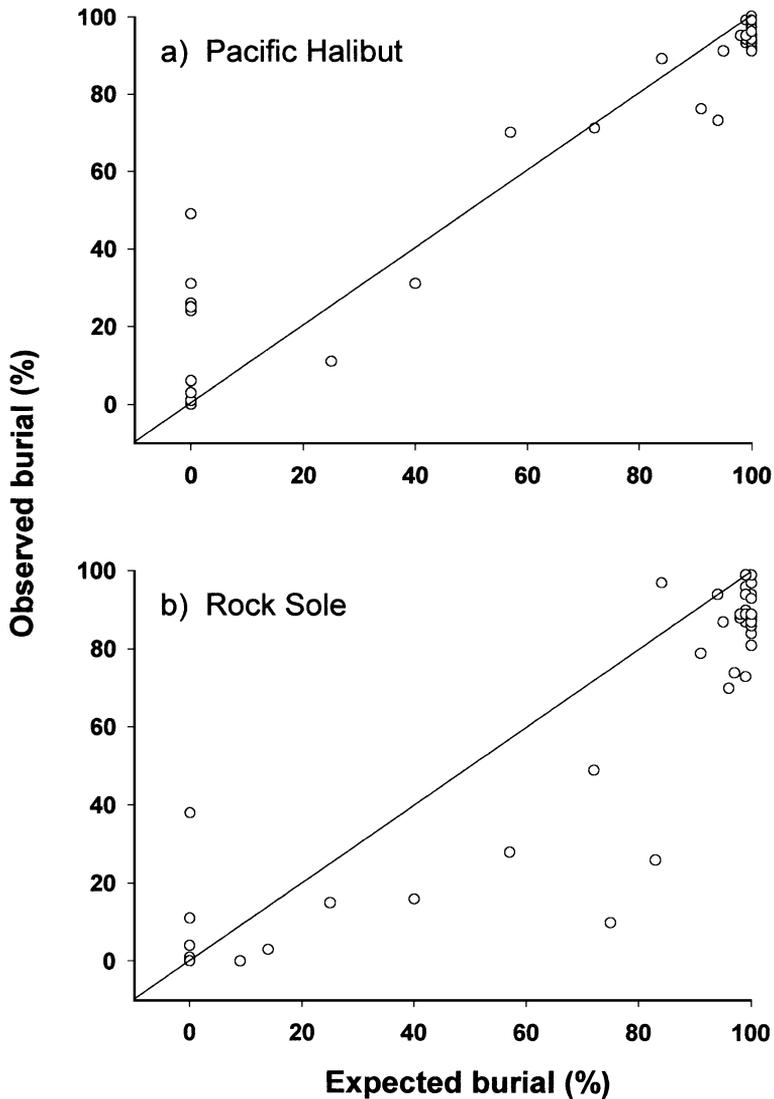


Fig. 3. Relationships between burial capability (percent of body covered) observed in laboratory trials with seven different sediment types and values expected on the basis of the equation developed by Gibson and Robb (1992) for plaice (*P. platessa*). Results are shown for (a) Pacific halibut and (b) northern rock sole. The solid lines through the points represent a fit where observed and expected are equal.

buried more than 95% under any circumstances, normally leaving the eyes and mouth exposed.

Burial in rock sole was significantly overestimated by the equation for plaice ( $t=4.711$ ,  $p<0.001$ ) (Fig. 3). The only circumstances where observed burial was higher than expected occurred in four cases where large fish were capable of partial burial in granules. Over-

estimates occurred primarily because of low burial rates in fine grains, and complete burials (100%) were rare.

Species differences in burial behavior are also evident in plots showing time to maximum burial as a function of fish size and sediment type (Fig. 4). Pacific halibut achieved maximum coverage in fine sediment in <20 min in most cases. Burial time generally increased with sediment grain size, and the smallest fish were incapable of burying in granules. Burial by rock sole was usually much slower (Fig. 4b) than halibut, with time to

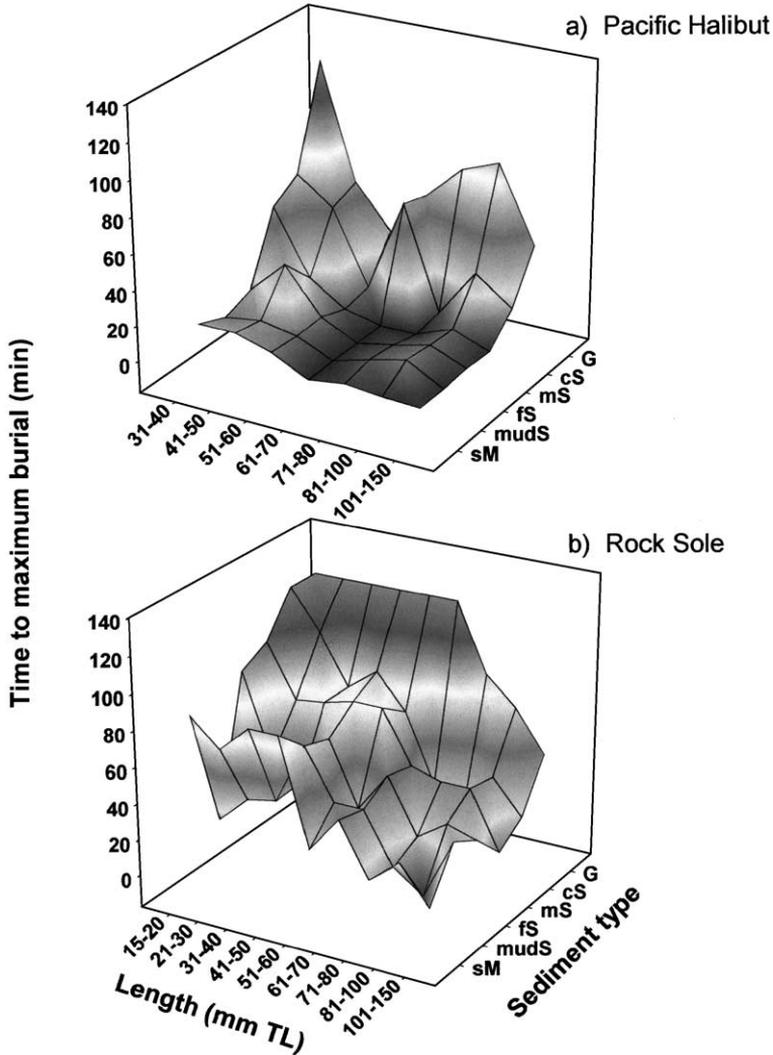


Fig. 4. Time to maximum burial by juvenile (a) Pacific halibut and (b) northern rock sole in six different sediment types shown as a function of fish size. Sediment codes are the same as those in Fig. 1. Data for burial in pebbles were not included because only halibut >100 mm TL could bury in this substratum ( $\leq 3\%$  coverage).

maximum coverage ordinarily >30 min except for the largest fish in the finest sediments. In fine sand, a sediment suitable for both species in the range 31–150 mm TL, halibut buried to maximum depth in just 9 min while rock sole took 36 min to bury.

Relationships between sediment choices and burial capabilities were shown by plots of mean maximum burial (percent coverage) versus the mean percent of fish in a particular size class choosing each sediment type for all of the sediment/fish size-class combinations

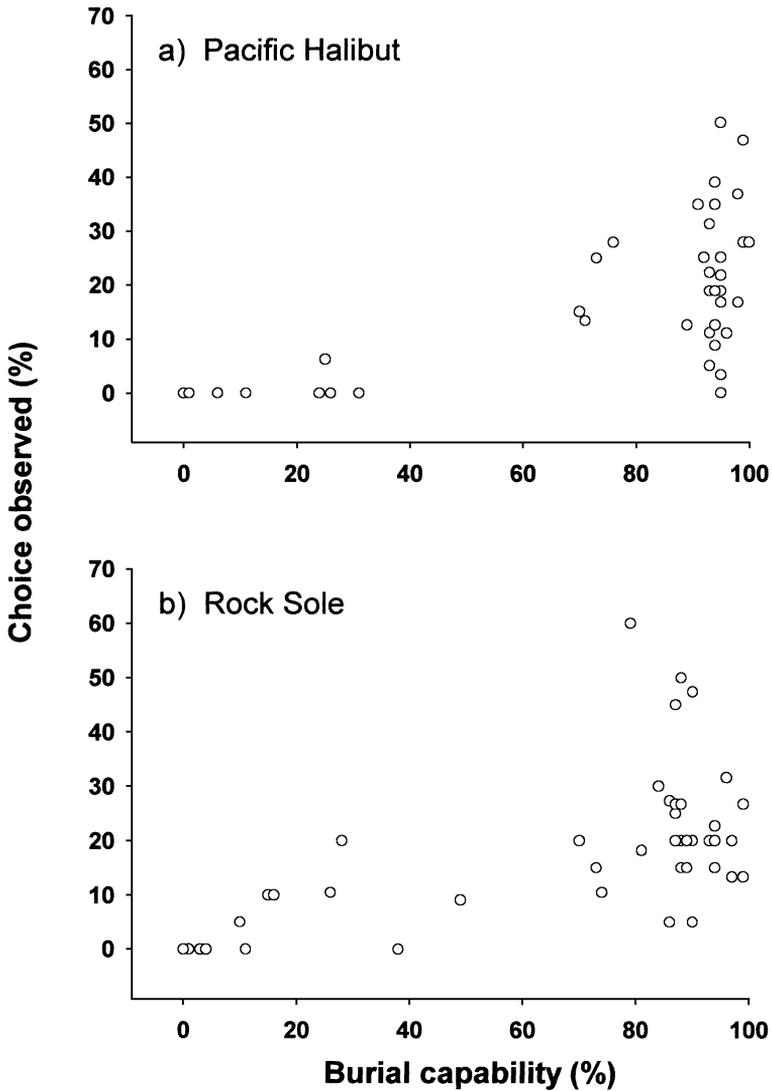


Fig. 5. Relationships between burial capability (maximum percent of body covered) in particular sediments and the percent of fish choosing that sediment. All sediment and fish-size combinations were considered for juvenile (a) Pacific halibut and (b) northern rock sole.

(Fig. 5). Halibut rarely chose sediments where burial capability was <70% (Fig. 5a). The smallest halibut always chose fine sediments where they buried quickly and easily. Conversely, among the sediments where burial capabilities were high, the choices for

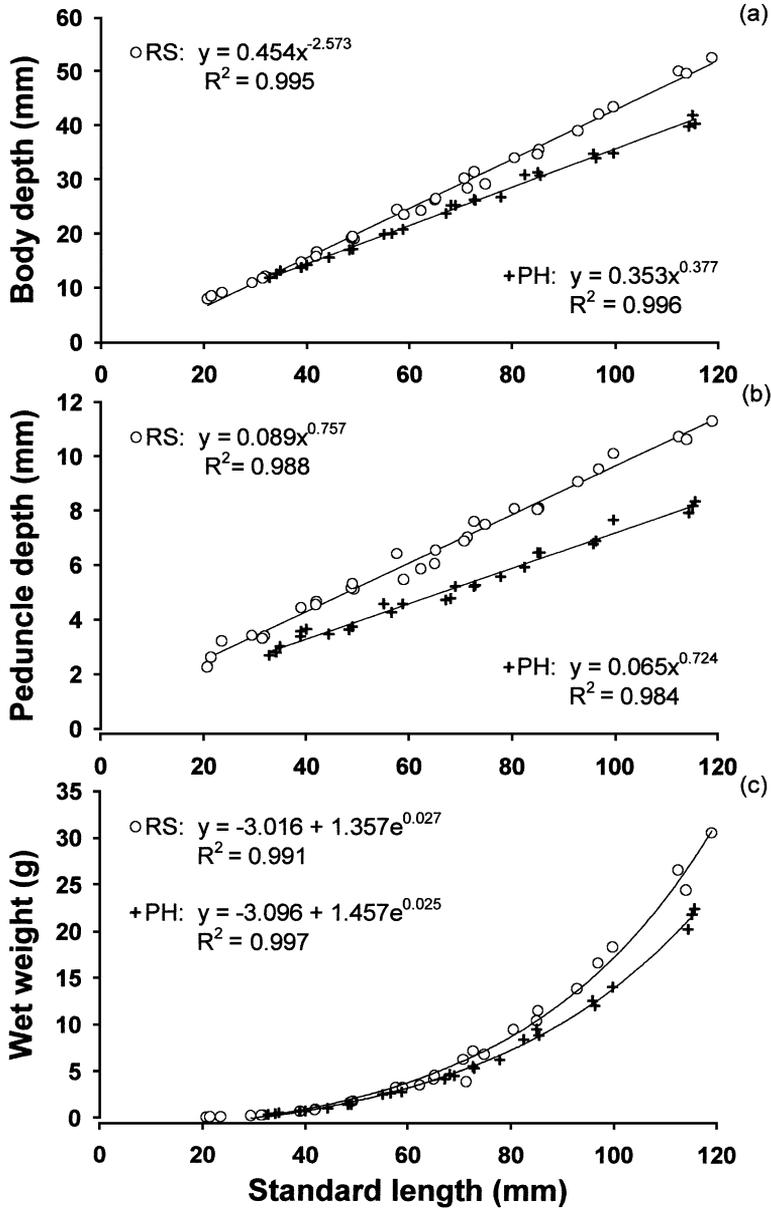


Fig. 6. Morphological comparisons between juvenile Pacific halibut (PH) (crosses) and northern rock sole (RS) (circles): (a) body depth (maximum dorsal to ventral distance excluding fins), (b) peduncle depth (minimum dorsal to ventral distance), and (c) wet weight, all shown as a function of standard length.

those sediments were highly variable. For example, medium-sized halibut had high burial capabilities in a wide variety of sediment types, but some of those sediments (e.g., sandy mud and muddy sand) were rarely chosen. Rock sole also demonstrated a positive relationship between burial capability and sediment choice (Fig. 5b); however, choice of sediment was less constrained by burial than in halibut. Sediments where burial was < 70% were chosen with less frequency than sediments where burial was high, but a few small rock sole chose coarse-grained sediments where burial was only 10%, and in numerous cases, 10–20% of the fish chose substrata where average burial was 50% or less. Halibut very rarely chose sediments where burial capabilities were low (Fig. 5).

### 3.3. Morphological and behavioral comparisons

There are several notable differences in the overall appearance of Pacific halibut and rock sole. Typical of highly motile flatfishes, the Pacific halibut has a thick, elongate body, a crescent-shaped caudal fin, and a narrow caudal peduncle. The mouth is large with the maxillary extending to the middle of the eye. These features contrast with the deeper body (dorsal to ventral), broad peduncle, and thin form (pigmented to unpigmented sides) of the rock sole. The mouth is small, with the maxillary extending just to the anterior edge of the eye and it is nearly vertical when closed. Difference in body depth between the two species diverges rapidly with fish size > 50 mm SL (Fig. 6a), and peduncle depth was different over the entire range of fish measured (Fig. 6b). Weight–length plots for the species (Fig. 6c) are almost identical up to 70 mm SL, beyond which the greater body depth of rock sole results in a higher ratio of weight to length.

The less powerful, deep body of the rock sole made it a weaker burrower than the halibut; however, upon disturbance, rock sole were more inclined to move short distances along the bottom (2–3 body lengths), then remain stationary or rebury. Halibut ordinarily fled by strong swimming when disturbed rather than reburying. While both species have high capacity to match substratum color, general observations show that rock sole have superior capability with broader ranges of pattern and color, particularly on light-colored sediment. Feeding by halibut, even small age-0 juveniles, was characterized by aggressive pursuits of live prey or moving items such as food pellets, and they often lifted off the bottom to feed. They were disinclined to attack immobile food items lying on the bottom. Rock sole were less aggressive in their movements, moving slowly over the bottom to nibble stationary food items.

## 4. Discussion

This study demonstrated that sediment preferences in Pacific halibut and rock sole shift rapidly with fish size during the first year of life and that generalizations about habitat requirements should be made with care. The smallest post-settlement size classes of both species showed strong preferences for fine-grained sediments, and larger fish had relatively specific preferences for medium sands. A similar ontogenetic shift in sediment preference has been observed for winter flounder (*P. americanus*) in both the laboratory and field setting (Phelan et al., 2000). Starry flounder (*P. stellatus*) (10–250 mm TL) also

demonstrated a shift in sediment preference from mud to sand in laboratory experiments (Moles and Norcross, 1995). In our experiments, observed sediment preferences broadened with increasing fish size, concurrent with increasing burial capability. This is similar to relationships between burial and sediment preference reported by Tanda (1990) for both marbled sole (*Limanda yokohamae* (Guenther)) and Japanese flounder (*Paralichthys olivaceus* (Temminck and Schlegel)). We also note that some size classes, most notably fish 61–100 mm, chose sediments with the largest mean grain size in which burial capability was high. We speculate that the shift to larger sediments as burial capabilities permit may be related to environmental conditions associated with different sediments. For example, oxygen levels are generally higher over sandy substrata than over mud which is often rich in organic content, and we noted that the finest sediments appeared to irritate the gills of both halibut and rock sole. Also, water is often less turbid over sand than over mud; this may be particularly important to visual predators such as Pacific halibut.

It is possible that not all flatfishes have a size-dependent response to sediment grain size; however, the relevant laboratory results are equivocal. For example, Moles and Norcross (1995) found no significant shift in preference in either yellowfin sole or rock sole comparing size classes 50–80 and 150–250 mm. They concluded that these two species are relatively nonselective. Similarly our studies with northern rock sole and Pacific halibut show low selectivity in fishes larger than ~ 80 mm, but a high degree of selectivity in smaller fish suggests that generalizations about age-0 fishes should be made cautiously. Gibson and Robb (2000) found that plaice 13–114 mm in length always chose fine sand and concluded that size did not affect preference. However, no grain size smaller than 0.25 mm (fine sand) was presented even though earlier studies (Gibson and Robb, 1992) showed that the smallest fish tested cannot easily bury in sand-sized sediments. We speculate that most flatfishes will show preference for muddy or fine-grained sediment during settlement and in early post-settlement life because of their weak burial capabilities.

Burial has been modeled for plaice (*P. platessa*) on the basis of fish length and sediment grain size (Gibson and Robb, 1992). When we applied this model to Pacific halibut and rock sole, it became obvious that halibut and plaice have relatively similar burial capacity, and that rock sole have lower capabilities. Clearly, variation in observed burial is determined not only by fish length but also by body strength and form, and perhaps by simple differences in behavior. Pacific halibut have thick, powerful bodies with the smallest ratio of body height to length, while rock sole have thin bodies with highest ratio of body height to length.

The argument that sediment choice by flatfishes will be directly linked to burial capability (Tanda, 1990; Gibson and Robb, 2000) is based on the premise that burial is the primary line of defense against predators. Sediment can increase survivorship in juvenile flatfish (Ellis et al., 1997), but this is not always the case, as demonstrated with plaice (Ansell and Gibson, 1993) and winter flounder (*P. americanus*) (Manderson et al., 2000). Some predators, such as shrimp (Witting and Able, 1995) and sea robins (Manderson et al., 1999), are particularly adept at detecting and flushing flatfish prey buried in the sediment. Nonetheless, burial may be the best strategy for very small flatfish which have few other defense mechanisms, and the smallest individuals of both northern rock sole and Pacific halibut chose fine-grained sediments where burial was accomplished easily. Halibut very rarely chose sediments where burial capability was less than 90%

regardless of fish size, while rock sole often chose sediments where burial was not easy and they appear to be less selective than halibut (Moles and Norcross, 1995; this study). Furthermore, we have noted that rock sole frequently lie exposed on the surface of the sediment (personal observation).

Defense tactics other than burial are available to flatfishes, particularly for larger juveniles. These may include escape by swimming and various cryptic adaptations. For example, juvenile Pacific halibut respond to disturbance by rapidly swimming away while rock sole are more cryptic. Rock sole make only slight movements when disturbed and have superior color- and pattern-matching capabilities (Stoner and Titgen, *in review*; personal observation). This cryptic behavior helps rock sole to elude visual predators on homogeneous sand substratum (Ryer et al., *in review*).

Habitat choices in flatfishes may also increase their fitness by placing them in good feeding environments. Two mechanisms are possible. First, because of associations between benthic invertebrates and sediment characteristics, sediment choices by fishes may place them in locations with high densities of food organisms of the preferred type. Second, prey density may affect habitat choice directly. The potential importance of food in flatfish distribution has been mentioned frequently (e.g., Norcross et al., 1997; Wennhage and Gibson, 1998; Gibson and Robb, 2000) and examined experimentally in the laboratory (Burke et al., 1991; Neuman and Able, 1998; Phelan et al., 2000), but testing the relative importance of prey availability and sediment characteristics in the field is difficult. Phelan et al. (2000) have shown that prey availability can override sediment preferences by age-0 winter flounder in the laboratory, but multivariate models revealed that temperature, salinity, and sediment organic content were the primary environmental variables associated with winter flounder distribution in a New Jersey estuarine system, while prey density contributed little to the models (Stoner et al., 2001).

Field studies reporting distributions of small juvenile Pacific halibut and rock sole have been conducted during summer months around Kodiak Island (Holladay and Norcross, 1995; Norcross et al., 1995, 1997, 1999) and in Kachemak Bay, Alaska (Abookire and Norcross, 1998). Shallow depth (< 40 m) and high temperature (>9 °C) explained most of the observed distribution pattern in Kodiak halibut, but most were collected on sediments comprised primarily of sand (>80%) (Norcross et al., 1997, 1999). Relatively similar results were obtained in Kachemak Bay (Abookire et al., 2001). However, the two studies pooled halibut 22–84 and 26–100 mm TL, respectively. When the distribution of age-0 halibut in Kachemak Bay was re-analyzed using small size classes (e.g., 10 mm intervals), sediment grain size was the most important environmental variable describing the distribution pattern for all of the size classes smaller than 80 mm TL (Stoner and Abookire, 2002). Abundance of age-0 rock sole (12–69 mm) in Kachemak Bay was negatively correlated with depth (Abookire et al., 2001), but similar to our laboratory findings, age-1 rock sole were associated with a wide diversity of sediments (Abookire and Norcross, 1998). We speculate that finer division of age-0 rock sole by size would result in significant associations with sediment type.

All of the aforementioned distributional models for Alaska flatfishes have large amounts of unexplained variability. There is little doubt that some of the variation and uncertainty in distribution is caused by pooling fish over size ranges where differences in habitat preference occur. Our laboratory results with Pacific halibut and northern rock sole show

clearly that relationships with sediment grain size shift rapidly with fish size during the first several months of post-settlement life, and other size-related changes in habitat preferences are likely. For example, choices of depth, temperature, light level, and foods all probably shift with fish size. Consequently, spatial and temporal variation in suitable habitat needs to be considered on the basis of appropriate fish size classes which may or may not be aligned with year classes. We recommend, therefore, that habitat characterization and modeling for juvenile fishes be made cautiously, with careful analysis of potential size effects before arbitrary pooling.

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