

# Testing the shallow water refuge hypothesis in flatfish nurseries

C. H. Ryer\*, B. J. Laurel, A. W. Stoner

Fisheries Behavioral Ecology Program, Alaska Fisheries Science Center, NOAA Fisheries, Hatfield Marine Science Center, 2030 Marine Science Drive, Newport, Oregon 97365, USA

**ABSTRACT:** The 'shallow water refuge hypothesis' (SWRH) holds that predation upon juvenile fish and crustaceans is reduced in shallow water because larger predatory fish increase in abundance with depth. We tested predictions of this hypothesis in 2 Kodiak Island flatfish nurseries, Pillar Creek Cove and Holiday Beach, using baited camera, tethering and video sled techniques. Baited camera deployments during 2007 indicated that predators increased with depth in both nurseries. In the same year, tethering indicated increased mortality of juvenile flatfish with increased depth. In contrast, video sled data from 2003 and 2004 indicated that predator abundance increased with depth at Holiday Beach, but not at Pillar Creek Cove. At Holiday Beach, juvenile abundance decreased rapidly with depth, while at Pillar Creek Cove abundance increased slightly with depth. Thus, predator–predation distribution over 3 yr at Holiday Beach was consistent with the SWRH, while at Pillar Creek Cove it was more variable. Although the SWRH is normally considered in the context of waters <2 m in depth, our results suggest that it may have efficacy for deeper water, with the relative depth distribution of predators and suitable juvenile habitat being more relevant than absolute depth.

**KEY WORDS:** Nurseries · Predation · Tethering · Baited camera · Video sled · Fish behavior

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Implicit in nearly all nursery definitions is the notion that juveniles experience higher survival in nurseries than in other habitats. Reduced predation is cited as a key habitat parameter contributing to this greater survival (e.g. Beck et al. 2001). In the case of seagrass habitats, a common nursery habitat throughout much of the world, structural complexity provides protection from predators, by interfering with predator movement (Bartholomew et al. 2000) and providing refugia (Ryer 1988, Laurel et al. 2003). Higher temperature and food abundance, which typify many shallow water nurseries, can also accelerate growth (Yamashita et al. 2001), hastening the point at which juveniles reach a size-refuge from predation (Blundon & Kennedy 1982, Sogard 1997) and can successfully migrate to adult habitat (Holtby et al. 1990). Yet, even in the absence of highly structured habitats, shallow water may, in-and-

of-itself, provide some protection from predation, and high numbers of juveniles in shallow waters has often been interpreted as an indicator of low predation (Orth & van Montfrans 1987). 'Heincke's Law' (sensu Cushing 1975), based upon plaice *Pleuronectes platessa* distribution, holds that fish size increases with depth, and has been shown to be generally applicable for demersal fishes (Macpherson & Duarte 1991). Since piscivory generally increases with fish size, it follows that the abundance of larger piscivorous fish will also increase with depth. However, the resultant hypothesis that predation is reduced in shallow water because predators are less frequent there, the 'shallow water refuge hypothesis' (SWRH, sensu Baker & Sheaves 2007), while widely held, has infrequently been rigorously tested. Tethering, whereby fish or crustaceans are secured in place by monofilament line, has become a common methodology for accessing depth-related predation risk, although, as pointed out by several

\*Email: cliff.ryer@noaa.gov

authors, care must be taken to avoid procedural artifacts (Halpin 2000, Kneib & Scheele 2000). Tethering studies conducted in several systems, i.e. temperate estuary (Ruiz et al. 1993, Clark et al. 2003, Manderson et al. 2004), temperate tidal freshwater creek (McIvor & Odum 1988) and tropical tidal creek (Rypel et al. 2007), support the existence of a shallow water refuge effect. However, at least 1 tropical estuarine study found no depth/depth effect, indicating that the shallow water refuge paradigm not be universal (Baker & Sheaves 2007). Importantly, all of these studies examined depths <5 m. We are aware of only 1 study bearing upon the efficacy of the SWRH at significantly greater depth: in a Newfoundland bay, juvenile cod *Gadus morhua* mortality increased with depth from 0.7 to 20 m (Linehan et al. 2001). Consequently, although it might be logical to consider 'shallow water' as a relative term, there presently exists scant data to support an extension of the SWRH to water deeper than 5 m.

Many species of commercially important flatfish in the northeastern Pacific utilize coastal areas as juveniles (Minami & Tanaka 1992), typically nearshore bays and estuaries (Abookire & Norcross 1998, Stoner et al. 2007). During summer months, when temperatures are highest, Kodiak embayments are dominated by age 0 yr northern rock sole *Lepidopsetta polyxystra* (>90%) as well as lesser numbers of Pacific halibut *Hippoglossus stenolepis* (Hurst et al. 2007). While widely distributed on sedimentary bottom, juveniles are most abundant on gently sloping bottoms just outside of, or in the mouths of, open and semi-enclosed embayments, with the highest densities of juveniles at depths <30 m (Hurst et al. 2007, Stoner et al. 2007). Ambient summer bottom temperature at these depths is higher than in deeper offshore areas, thereby promoting more rapid growth of juvenile flatfish (Hurst & Abookire 2006). Laboratory and field studies suggest that larger flatfish are the dominant predator upon juveniles in these nurseries (Ryer et al. 2007). Since there is no structure-forming vegetation at the depths utilized by juvenile flatfish, these embayments are appropriate deeper model systems for testing the SWRH.

In this study, we examine the efficacy of the SWRH for understanding the depth distribution of juvenile flatfish in 2 Kodiak nurseries. Specifically, we (1) utilized baited camera deployments (Stoner et al. 2008) to test the hypothesis that the abundance of juvenile flatfish predators increases with depth, (2) conducted tethering experiments to test the hypothesis that predation risk increases with depth, and (3) conducted video sled surveys (Spencer et al. 2005, Stoner et al. 2007) to determine whether the distribution of juvenile flatfish is inversely related to the abundance of predators over the depth range of these nurseries.

## MATERIALS AND METHODS

**Study sites.** Field work was conducted at 2 sites in the coastal waters of Kodiak Island, Alaska (Fig. 1): Holiday Beach (57° 41' N, 152° 27' W) and Pillar Creek Cove (57° 49' N, 152° 25' W). The sites are believed to be summer nursery areas for age 0 yr rock sole and Pacific halibut (Hurst & Abookire 2006, Ryer et al. 2007, Stoner et al. 2007). Both sites have gently sloping sandy bottoms just offshore from relatively sheltered beaches. The Holiday Beach site comprises ~123 ha, with 1.4 km separating the 5 and 30 m mean low low water (MLLW) depth contours. Pillar Creek Cove comprises ~30 ha, with 0.6 km between the 5 and 30 m depths. Summer salinities and water temperatures range from 30 to 32‰ and 6 to 11°C, respectively.

**Baited camera.** Baited camera data were acquired during July 2007 to quantify the relative abundance of potential predators over a range of depths at both sites. The baited camera system utilized in this study is described in detail by Stoner et al. (2008) and is a modification of the camera sled system described by Spencer et al. (2005). Briefly, the 71 cm wide by 114 cm long sled was modified for vertical deployment, with a 2 cm diameter aluminum arm that held a nylon bait bag (8 × 15 cm; 2.5 cm stretch mesh) 68 cm in front of the low-light monochrome video camera with a wide-angle (92°) lens (Aqua-Vu ZT 120, Nature Vision). For each deployment, the bait bag was loaded with ~300 g of freshly thawed whole Pacific sardine *Sardinops sagax* and the bag was gently squeezed to initiate the

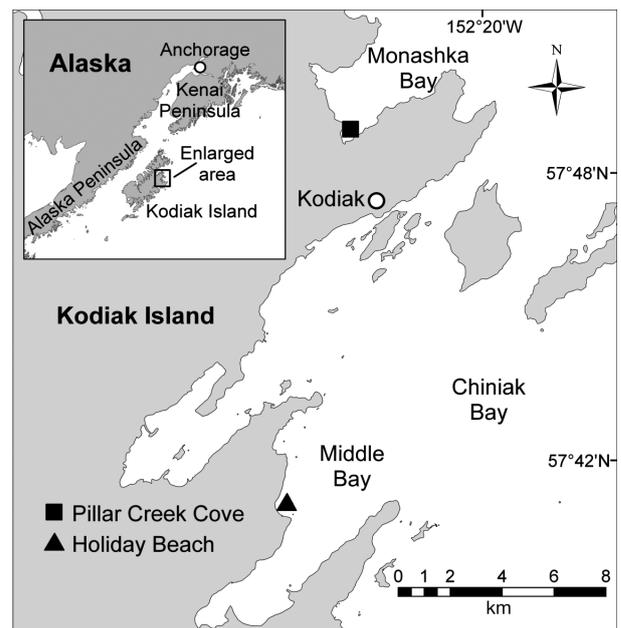


Fig. 1. Study sites Pillar Creek Cove and Holiday Beach in relation to Kodiak Island, and greater Alaska (inset)

release of scent. The sled was then lowered to the bottom and the support vessel anchored at least 10 m away. After 15 min, the sled was retrieved, re-baited and redeployed at another location. Deployments were conducted over the course of 2 d. At each site, 4 deployments were completed at each of 4 depths (4.6, 9.2, 13.7 and 18.3 m MLLW), except for Holiday Beach, where only 2 replicates of the greatest depth were accomplished due to technical problems with recording. Deployment was completed at each of the 4 depths before the series was again repeated, thereby stratifying depth sampling across time to avoid bias associated with time of day or tidal change.

During video playback, the arrivals and departures of fish, as well as fish species and approximate fish size were noted. Utilizing this same apparatus for studying gadid abundance around Kodiak, Stoner et al. (2008) concluded that cumulative arrivals of fish during a set time period was most closely correlated with independent abundance estimates from beach seines, despite the potential for multiple counts of individual fish. Preliminary review of tapes indicated that age 2+ yr flatfish were numerically dominant at these sites. Accordingly, we chose the number of age 2+ yr flatfish arrivals over 15 min as our metric of potential predator abundance. Data were natural log-transformed to achieve homogeneity of variance and analyzed by 2-way analysis of variance (ANOVA), with depth and site as independent variables, followed by *a posteriori* Tukey's multiple comparisons (Sokal & Rohlf 1969).

**Tethering.** Juvenile Pacific halibut were tethered during July 2007 to assess relative predation rates at depths of 4.6, 9.2, 13.7 and 18.3 m MLLW, at both Holiday Beach and Pillar Creek Cove. These juvenile Pacific halibut ranged in total length from 40 to 60 mm and were hooked (no. 12 live bait hook, 1 cm long, Mustad & Sons) midway between the spine and the anal fin, from the light side, so that the hook barb protruded from the body on the eyed side without penetrating the abdominal cavity or major blood vessels. Laboratory trials verified that fish hooked in this way were still able to move about and bury themselves in sandy sediment, but did not become unhooked. Hooks were tied to a 60 cm long monofilament leader (1.8 kg breaking strength), which was in turn attached to a 0.34 kg weight by a snap swivel. A heavier (18 kg breaking strength) monofilament line connected the weight to a float at the water surface. Fifteen tethered flatfish were lowered to the bottom at 1 min intervals, 5 at each depth. After 30 min, these tether sets were recovered, again at 1 min intervals, so each set experienced the same 30 min soak time. This procedure was repeated 7 times at each nursery site, resulting in 105 tether sets at each. This level of replication was dictated by logistical constraints, as opposed to any *a pri-*

*ori* statistical analysis. Upon recovery, each set was scored for presence/absence of the juvenile halibut. Additionally, if a larger fish had been hooked it was identified and measured for total length. Absence of the juvenile halibut was assumed to represent a mortality. Mortality data were analyzed using a Generalized Linear Model for data with binary logit data link (GLZM: SPSS).

**Towed camera sled data.** Video surveys were conducted during July 2003 and 2004 at both Holiday Beach and Pillar Creek Cove using a towed camera sled (Spencer et al. 2005). Briefly, the sled was towed at an average vessel speed of 60 cm s<sup>-1</sup> along multiple transects in each study site, covering depths from 3 to 27 m. It was equipped with a tickler chain, which causes flatfish to flush from the bottom. The abundance of age 0 yr flatfish was quantified via playback of video acquired with a camera set at an angle of 35° below horizontal. With the typical water clarity around Kodiak, this allowed us to view ~3.2 m ahead of the sled. Cumulative counts of age 0 yr flatfish observed between the 2 runners of the sled (67 cm) were recorded for 15 sec intervals. Data from trawls towed during the same weeks revealed that juveniles were >95% northern rock sole, with lesser numbers of Pacific halibut and English sole (Stoner et al. 2007, Hurst et al. 2007, C. Ryer unpubl. data). From concurrently recorded GPS positions, the distance traversed during each interval was calculated, allowing us to derive fish densities, which were standardized to age 0 yr fish 100 m<sup>-2</sup>. Intervals were excluded when visibility was <30 cm, the view was obscured by heavy algae, or the tickler chain was not in close contact with the bottom. For larger flatfish, all fish in the camera view were enumerated from video with >2 m visibility, and were similarly standardized to counts of age 2 yr fish 100 m<sup>-1</sup>. For small flatfish, these protocols resulted in 430 transect segments (intervals) from 2003 and 439 from 2004 at Holiday Beach. At Pillar Creek Cove, this resulted in 225 segments from 2003 and 223 from 2004. For large flatfish, there were 442 segments from 2003 and 448 from 2004 at Holiday Beach, compared to 246 segments from 2003 and 212 from 2004 at Pillar Creek Cove. For purposes of analysis, we make the explicit assumption that the counts of fish from each segment represent independent samples. Data for age 2+ yr flatfish followed a poisson distribution and were initially analyzed using Generalized Linear Models with a poisson data link (GLZM) to examine the effects of site and year. In a second analysis, we pooled data across years, and recoded the data to '0's and '1's (absence/presence) to conduct logistic regressions for each site, exploring the influence of depth upon large flatfish probability of occurrence. For the Pillar Creek Cove regression, we were suspicious that a high occur-

rence probability at the shallowest depth might exert inordinate influence on the regression due to its high potential leverage. However, no data points had a Cook's distance measure  $>1$ , indicating that none were 'influential' (Cook 1977). Small flatfish density data more closely conformed to a normal distribution. We conducted ANOVA to examine potential site and year effects. Subsequently, density data were pooled by year and linear regressions conducted to examine the influence of depth upon small flatfish density for each field site. All regression analyses were conducted to explore main trends in data, rather than to fit explicative models.

## RESULTS

### Baited camera

During 30 baited camera deployments, 356 fish were observed at depths ranging from ~4 to 18 m. Flatfish estimated to be age 2+ yr constituted 92% of this total. These flatfish appeared to be predominantly rock sole *Lepidopsetta* spp., yellowfin sole *Limanda aspera* and the occasional Pacific halibut. Other fish included Pacific cod *Gadus macrocephalus*, Pacific spiny dogfish *Squalus acanthias*, greenlings *Hexagrammos* spp. and sculpins *Cottidae*. Sightings of age 2+ yr flatfish (Fig. 2) increased significantly with depth ( $F_{[3,22]} = 3.26$ ,  $p = 0.041$ ), such that more fish were sighted at 18 m than 4 m (Tukey's,  $p < 0.05$ ). Although these large flatfish tended to be more abundant at Pillar Creek Cove, this trend was not significant ( $F_{[1,22]} = 1.61$ ,  $p = 0.218$ ) and the overall depth pattern was comparable at both Holiday beach and Pillar Creek Cove (site  $\times$  depth interaction:  $F_{[3,22]} = 0.62$ ,  $p = 0.608$ ).

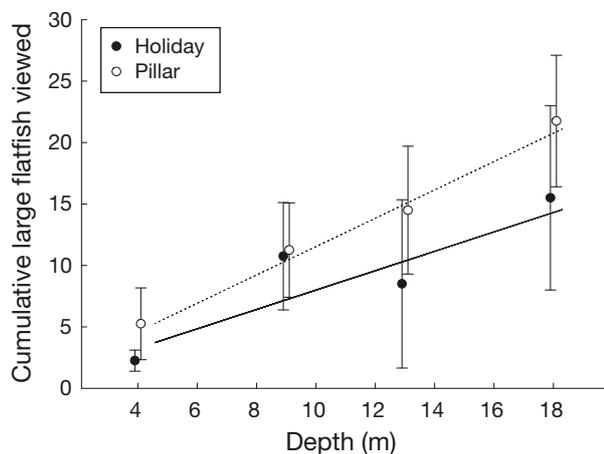


Fig. 2. Cumulative arrivals (mean  $\pm$  SE) at baited camera over 15 min of age 2+ yr flatfish by depth for Holiday Beach and Pillar Creek Cove, Kodiak Island, Alaska, during 2007

### Tethering

Of 207 juvenile flatfish tethered, mortality, defined as fish absent upon retrieval, averaged 42% during the 30 min set period. Of these, 27 sets were recovered with hooked predators. All were either rock sole or yellowfin sole ranging in size from 18 to 38 cm total length. Thirty-seven sets were recovered with the hook bare (no juvenile halibut) and 22 with the leader broken, i.e. the hook was missing. Mortality was 23 to 40% at 5 and 9 m depth, increasing to 60 to 70% at 14 m depth (Fig. 3, GLZM,  $\chi_{[2]} = 20.172$ ,  $p < 0.001$ ), with no difference between nurseries (GLZM,  $\chi_{[1]} = 0.00$ ,  $p = 0.961$ ). There was a tendency for mortality at 5 m at Pillar Creek Cove to be higher than that at Holiday Beach, but this interactive depth  $\times$  nursery trend was not significant (GLZM,  $\chi_{[2]} = 3.59$ ,  $p < 0.166$ ).

### Camera sled

Age 2+ yr flatfish abundance was greater at Pillar Creek Cove than at Holiday Beach, but also more variable, differing between the 2 yr (Fig. 4), as indicated by a significant interaction between site and year (GLZM,  $\chi_{[2]} = 63.70$ ,  $p < 0.001$ ). After accounting for differences in sled tract segment length, the occurrence of age 2+ yr flatfish increased with depth at Holiday Beach, as indicated by logistic regression analysis of presence/absence data (slope = 0.070,  $Z = 4.56$ ,  $p < 0.001$ ) (Fig. 5). In contrast, there was no significant effect of depth on age 2+ yr flatfish abundance at Pillar Creek Cove (slope = 0.020,  $Z = 1.52$ ,  $p = 0.127$ ).

As was the case with larger fish, the influence of site upon age 0 yr flatfish abundance differed between years (site  $\times$  year,  $F_{[2,1313]} = 20.19$ ,  $p < 0.001$ ); however, in this instance abundances were comparable over both years at Pillar Creek Cove and during 2004 at Holiday Beach, but were lower at Holiday Beach dur-

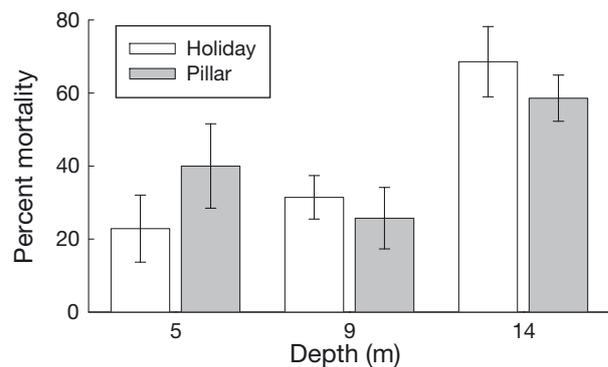


Fig. 3. *Hippoglossus stenolepis*. Mortality (mean percent  $\pm$  SE) of juveniles tethered for 30 min, at 5, 9 and 14 m depth, at both study sites

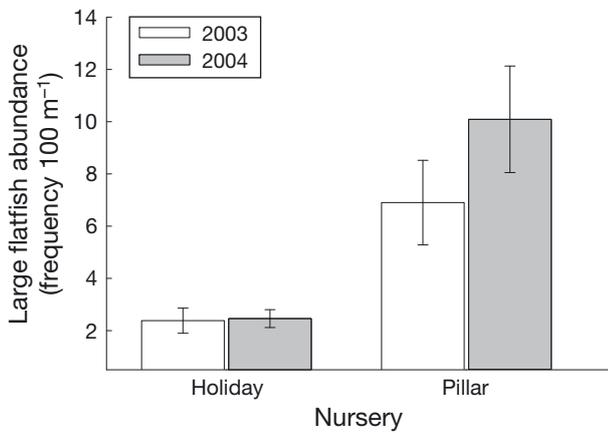


Fig. 4. Number (mean ± SE) of age 2+ yr flatfish 100 m<sup>-1</sup> derived from camera sled video at both study sites during 2003 and 2004. Data have been pooled across depth

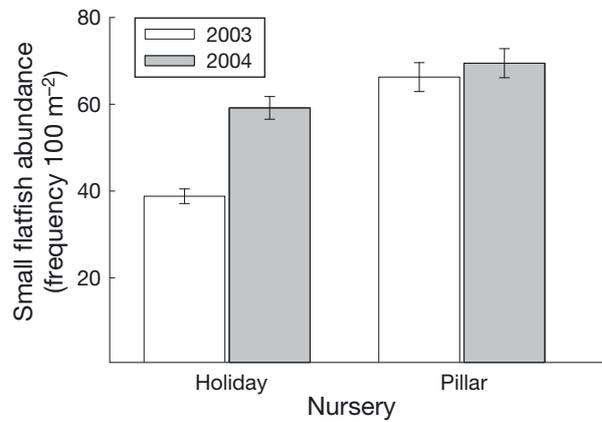


Fig. 6. Number (mean ± SE) of age 0 yr flatfish 100 m<sup>-2</sup> derived from camera sled video at both study sites during 2003 and 2004. Data have been pooled across depth

ing 2003 (Tukey's,  $p < 0.05$ ) (Fig. 6). Most importantly, the depth distribution of age 0 yr flatfish at Holiday Beach was the inverse of that seen among larger fish; small fish were most abundant in the shallows, and became less abundant with increasing depth (slope =  $-4.33$ ,  $t = -18.93$ ,  $p < 0.001$ ) (Fig. 7). In contrast, small fish abundance increased slightly with depth at Pillar Creek Cove (slope =  $0.88$ ,  $t = 2.98$ ,  $p < 0.030$ ).

### DISCUSSION

Predation risk influences the behavior, distribution, growth and survival of juvenile fish (e.g. Laurel et al. 2003, Ryer et al. 2007, Ryer & Hurst 2008), and ultimately the effectiveness of nursery habitats in contributing recruits to adult populations (Dahlgren et al. 2006). The results of our 2007 baited camera deployments indicate that the abundance of larger flatfish, the presumed dominant predators in this system,

increased from 4 to 18 m. These results are consistent with Heincke's Law (sensu Cushing 1975), which holds that the mean size of fish generally increases with depth. It follows that the abundance of larger, potentially piscivorous fish increases with depth, and predation upon juveniles should follow a similar pattern; i.e. the SWRH. This is precisely what we observed in our 2007 tethering experiment, where mortality of tethered juveniles doubled from ~30% at 5 and 9 m, to 60% at 14 m depth, with larger flatfish being the most common predator recovered from tethers.

The merits and shortfalls of tethering have been considered at length by various authors (e.g. Halpin 2000, Kneib & Scheele 2000). Briefly, behavior is compromised, exaggerating mortality and enlarging the suite of functional predators (Adams et al. 2004). Puncturing the body, e.g. by a hook, releases body fluids, potentially attracting olfactory-oriented predators. Accordingly, tethering produces relative predation rates, e.g. to compare habitats (e.g. Linehan et al. 2001, Laurel

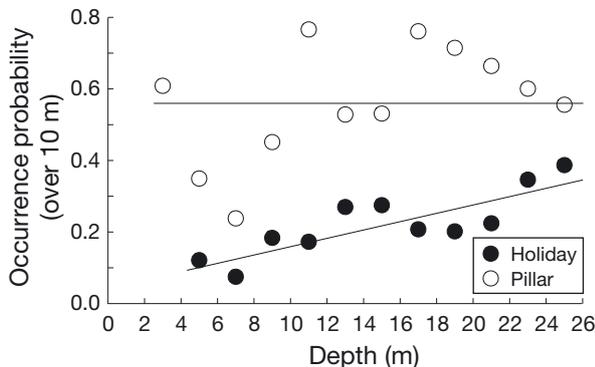


Fig. 5. Probability of occurrence for age 2+ yr flatfish, i.e. encountering 1 or more fish over a 10 m transect segment, by depth for each study site. The regression was not significant for the Pillar Creek Cove site, hence the plotted line has a 0 slope. Data have been pooled across years

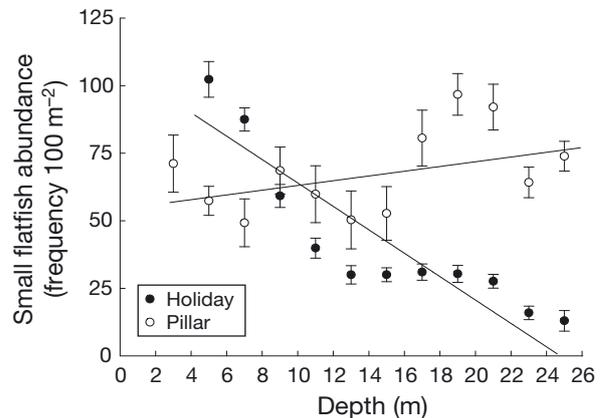


Fig. 7. Number (mean ± SE) of age 0 yr flatfish 100 m<sup>-2</sup> derived from camera sled video at both study sites, by depth. Data have been pooled across years

et al. 2003). However, if artifacts apply differentially across habitats (Peterson & Black 1994), comparisons may be flawed (Haywood et al. 2003, Adams et al. 2004). Clearly, the predation rates we observed, 20 to 70% over 30 min, greatly exceed those expected for free-ranging juveniles, indicating a tethering artifact. Juvenile flatfish utilize a detection minimization strategy, incorporating the tactics of reduced movement, burial and camouflage, followed, as a last resort, by flight (Ryer et al. 2004). Our laboratory observations indicate that juveniles readily bury, even when tethered (hooked), and observations of juvenile winter flounder indicate tethered fish actually bury more than control fish (Manderson et al. 2004). Although mean sediment grain size decreased slightly with depth at both sites (Stoner et al. 2007), sediments nonetheless allowed for effective juvenile burial at all depths (Stoner & Ottmar 2003). Also, predators recovered from tether sets at all depths were larger flatfish. Accordingly, we conclude that the tethering artifact was likely constant across depths, justifying the use of this technique to compare 'relative' predation rates across the range of depths we examined. These observed relative rates are also in concordance with baited camera data from the same year, and indicate that juvenile flatfish in Kodiak nursery embayments achieve some degree of refuge from predation in shallow water.

However, this begs the question: What is shallow? The SWRH grew out of the observation that juvenile nurseries for many commercially important fishes and crustaceans occur in water <2 m in depth, often in structurally complex habitats, e.g. marshes (Boesch & Turner 1984, Cattrijsse et al. 1997), seagrasses (Orth & van Montfrans 1987, Heck & Orth 1980, Laurel et al. 2007) or mangroves (Robertson & Duke 1987, Tobias 2001). Yet, because these occur only in shallow water, these studies do not provide direct evidence of a depth/predation effect. Even studies in non-vegetated systems have tended to focus upon species concentrated in water <2 m deep (Ruiz et al. 1993, Clark et al. 2003, Rypel et al. 2007). For example, recently settled plaice *Pleuronectes platessa* concentrate in water <1 m deep, with the abundance of *Crangon crangon*, a principle predator, increasing over a depth range of 0 to 4 m (Gibson et al. 2002). Similarly, in New Jersey estuaries, winter flounder *Pseudopleuronectes americanus* settle over a depth range of 1 to >5 m, but are either consumed at depth, or actively migrate to shallows, such that they become concentrated at 1 to 2 m depth (Manderson et al. 2004). Using tethering techniques, the authors demonstrated that predation upon age 0 yr winter flounder rapidly increased with depth from <1 to 5 m. As in our study, larger flatfish (*Paralichthys dentatus*) were the dominant predators implicated in tether mortalities. These studies suggest that, from the

perspective of the SWRH, 'shallow' means <2 m depth. Yet our study indicates that the SWRH may be applicable to deeper nursery systems as well. Age 0 yr rock sole are widely distributed in the Gulf of Alaska and Bering Sea, occurring on the continental shelf out to depths of >70 m, yet concentrate in the mouths of coastal bays at depths of 5 to 30 m on sandy sediment (Stoner et al. 2007). We documented increases in predator abundance and relative predation rates with depth across the inner portion of this nursery area (4 to 18 m). Similarly, Linehan et al. (2001) found that predation upon tethered age 0 yr cod *Gadus morhua* also increased with depth over a range of <1 to 20 m. We contend that our results, and those of Linehan et al. (2001), indicate that shallow water refuge is a more general paradigm, the applicability of which is not limited to a specific depth range, but is dependent upon the depth distribution of predators along with other relevant factors defining juvenile habitat.

Importantly, the applicability of the SWRH may vary both temporally and spatially. Flatfish abundance estimates at Holiday Beach were consistent with SWRH predictions: as the density of larger fish increased with depth, predation risk increased and the abundance of juveniles decreased. Results at Pillar Creek Cove were mixed: while baited camera and tethering during 2007 indicated increased predation risk with increasing depth, camera sled surveys during 2003 and 2004 indicated no significant influence of depth on large flatfish abundance. During a more recent 2009 field study (C. Ryer unpubl. data), baited camera, camera sled and tethering all indicated predator abundance and juvenile mortality not only increased with depth, but were substantially higher at Pillar Creek Cove compared to Holiday Beach. To us, this suggests not methodological bias, i.e. baited camera or tethering versus camera sled, but variability in predator distribution and therefore shallow water refuge, between nurseries and between years.

We can only speculate as to why, in some years, larger flatfish are more abundant and uniformly distributed across depth at Pillar Creek Cove compared to Holiday Beach. One possible explanation involves the proximity of deep water. At Holiday Beach, water <30 m deep extends 3 km offshore. Pillar Creek Cove is at the head of Monashka Bay, and as such, 20 m deep water in the cove is <1 km from channel waters that are >80 m in depth. Thus, larger fish may, on occasion, more readily spill over into the shallows.

This study did not identify the possible mechanism by which predators shape juvenile flatfish distribution. Predators in Kodiak embayments include large yellowfin and rock sole, Pacific halibut, and possibly Pacific cod and sculpins. It is possible predators actively remove juveniles, shaping their distribution

(Gibson 1994, Stoner 2003), although numerous studies suggest that juvenile fishes distribute themselves to avoid predation risk and increase fitness (Lima & Dill 1990). Juvenile rock sole, halibut and English sole all alter behavior in the presence of predators (Lemke & Ryer 2006, Boersma et al. 2008). Further, Ryer et al. (2007) demonstrated that juvenile rock sole will move to avoid co-occupancy of habitat with a variety of larger flatfish, both in the field and in laboratory experiments. Hence assume that the juvenile distributions observed in this work were at least partially a consequence of juveniles avoiding predators, as opposed to solely an effect of juvenile removal by predators.

The physical and biological parameters controlling juvenile habitat quality are varied and likely necessitate fish accepting trade-offs (Stoner 2003). At the most basic level, temperature and salinity must be within the species' range of physiological tolerance. In Kodiak embayments, temperature and salinity change little over the range of depths where fish are found (Stoner et al. 2007), suggesting these variables play little direct role in habitat selection within the nurseries. Structural features of the habitat, in this case sediment, must be compatible with the detection minimization anti-predator strategy of flatfish, e.g. allowing for burial. The silt/clay content of the sandy sediments within these embayments increases with depth (Stoner et al. 2007), but remains within the range generally preferred by juvenile rock sole, halibut and English sole, allowing effective burial in laboratory experiments (Stoner & Ottmar 2003, A. Camp et al. unpubl.). Of the structural habitat features which increase habitat complexity and enhance flatfish habitat, the ampharetid polychaete *Sabellides sibirica* may be the most important in these systems (Stoner et al. 2007). In addition to providing food, these polychaetes create habitat which may provide juvenile fish with refuge from predation (C. Ryer pers. obs.). However, *S. sibirica* abundance varies annually and this polychaete was largely absent during the 3 yr of this study (2003, 2004 & 2007). Food is another principle factor controlling habitat quality. The infaunal/epifaunal organisms upon which juvenile rock sole feed (Hurst et al. 2007) increase in abundance and diversity with depth in both embayments studied here (C. Ryer unpubl. data). Thus, deeper water should offer better foraging. In spite of this, juvenile flatfish abundance at Holiday Beach was negatively correlated with depth, suggesting that fish may have been trading off foraging for reduced risk of predation.

In summary, our field data on the distribution of juvenile flatfish and their predators in Kodiak nurseries is consistent with the premise of the shallow water refuge hypothesis: that predators control the depth distribution of juvenile flatfish, either through differential settlement, removal, or behaviorally medi-

ated redistribution. However, our results also indicate that the depth distribution of predators can vary from one locale to another and from year to year, with the result that small flatfish do not always concentrate in shallow water. While originally developed for very shallow water (<2 m), our results, along with those of Linehan et al. (2001), suggest that the SWRH may be applicable to coastal waters with significantly greater depths. We contend that the efficacy of a general shallow water refuge paradigm is less constrained by absolute depth, than by the relative depth distribution of predators as well as the overall habitat requirements of prey species.

*Acknowledgements.* We thank M. Spencer, P. Iseri, B. Knoth, S. Haines and M. Ottmar for assistance in the field and laboratory. This project was supported in part by grant no. R0301 to C.R., A. Abookire, I. Fleming and A.S., and grant no. R0710 to C.R., B.L., B. Knoth, T. Hurst and A.S. from the North Pacific Research Board (NPRB publication no. 269). Support was also provided by the Habitat and Ecosystem Processes Program of the Alaska Fisheries Science Center, NOAA Fisheries, and a National Science Foundation REU internship administered by the Hatfield Marine Science Center of Oregon State University.

#### LITERATURE CITED

- Abookire AA, Norcross BL (1998) Depth and substrate as determinants of distribution of juvenile flathead sole (*Hippoglossoides elassodon*) and rock sole (*Pleuronectes bilineatus*), in Kachemak Bay, Alaska. *J Sea Res* 39:113–123
- Adams AJ, Miller RJ, Ebersole JP (2004) Tethers make juvenile surgeonfish (Acanthuridae) vulnerable to attacks by benthic invertebrates. *Bull Mar Sci* 74:207–211
- Baker R, Sheaves M (2007) Shallow-water refuge paradigm: conflicting evidence from tethering experiments in a tropical estuary. *Mar Ecol Prog Ser* 349:13–22
- Bartholomew A, Diaz RJ, Cicchetti G (2000) New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. *Mar Ecol Prog Ser* 206:45–58
- Beck MW, Heck K, Able K, Childers D and others (2001) The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Blundon JA, Kennedy VS (1982) Refuges for infaunal bivalves from blue crab, *Callinectes sapidus*, predation in Chesapeake Bay. *J Exp Mar Biol Ecol* 65:67–81
- Boersma KS, Ryer CH, Hurst TP, Heppell SS (2008) Influences of divergent behavioral strategies upon risk allocation in juvenile flatfishes. *Behav Ecol Sociobiol* 62:1959–1968
- Boesch DF, Turner RE (1984) Dependence of fisheries species on salt marshes: the role of food and refuges. *Estuaries* 7:460–468
- Cattijisse A, Dankwa H, Mees J (1997) Nursery function of an estuarine tidal marsh for the brown shrimp *Crangon crangon*. *J Sea Res* 38:109–121
- Clark KL, Ruiz GM, Hines AH (2003) Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. *J Exp Mar Biol Ecol* 287:37–55

- Cook RD (1977) Detection of influential observations in linear regression. *Technometrics* 19:15–18
- Cushing DH (1975) Marine ecology and fisheries. Cambridge University Press, Cambridge
- Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, and others (2006) Marine nurseries and effective juvenile habitats: concepts and applications. *Mar Ecol Prog Ser* 312: 291–295
- Gibson RN (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Neth J Sea Res* 32: 191–206
- Gibson RN, Robb L, Wennhage H, Burrows MT (2002) Ontogenetic changes in the depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Mar Ecol Prog Ser* 229: 233–244
- Halpin PM (2000) Habitat use by an intertidal salt marsh fish: trade-offs between predation and growth. *Mar Ecol Prog Ser* 198:203–214
- Haywood MDE, Manso FJ, Loneragan NR, Toscas PJ (2003) Investigation of artifacts from chronographic tethering experiments—interactions between tethers and predators. *J Exp Mar Biol Ecol* 290:271–292
- Heck KL Jr, Orth RJ (1980) Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—decapod Crustacea. *Estuaries* 3:289–295
- Holtby LB, Andersen BC, Kadowaki RK (1990) Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon, *Oncorhynchus kisutch*. *Can J Fish Aquat Sci* 47:2181–2194
- Hurst TP, Abookire AA (2006) Temporal and spatial variation in potential and realized growth rates of age-0 year rock sole. *J Fish Biol* 68:905–919
- Hurst TP, Ryer CH, Ramsey JA, Haines SA (2007) Divergent foraging strategies of three co-occurring north Pacific flatfishes. *Mar Biol* 151:1087–1098
- Kneib RT, Scheele CEH (2000) Does tethering of mobile prey measure relative predation potential? An empirical test using mummichogs and grass shrimp. *Mar Ecol Prog Ser* 198:181–190
- Laurel BJ, Gregory RS, Brown JA (2003) Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. *Mar Ecol Prog Ser* 251:245–254
- Laurel BJ, Stoner AW, Ryer CH, Hurst TP, Abookire AA (2007) Comparative habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras and laboratory techniques. *J Exp Mar Biol Ecol* 351:42–55
- Lemke JL, Ryer CH (2006) Risk sensitivity in three juvenile (Age-0) flatfish species: Does estuarine dependence promote risk-prone behavior? *J Exp Mar Biol Ecol* 333: 172–180
- Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Linehan JE, Gregory RS, Schneider DC (2001) Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. *J Exp Mar Biol Ecol* 263:25–44
- Macpherson E, Duarte CM (1991) Bathymetric trends in demersal fish size: is there a general relationship. *Mar Ecol Prog Ser* 71:103–112
- Manderson JP, Pessutti J, Hilbert JG, Juanes F (2004) Shallow water predation risk for a juvenile flatfish (winter flounder; *Pseudopleuronectes americanus*, Walbaum) in a northwest Atlantic estuary. *J Exp Mar Biol Ecol* 304: 137–157
- McIvor CC, Odum WE (1988) Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69:1341–1351
- Minami T, Tanaka M (1992) Life history cycles in flatfish from the northwestern Pacific, with particular reference to their early life histories. *Neth J Sea Res* 29:35–48
- Orth RJ, van Montfrans J (1987) Utilization of a seagrass meadow and tidal marsh creek by blue crab *Callinectes sapidus*. 1. Seasonal and annual variations in abundance with emphasis of post-settlement juveniles. *Mar Ecol Prog Ser* 41:283–294
- Peterson CH, Black R (1994) An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar Ecol Prog Ser* 111:289–297
- Robertson AI, Duke NC (1987) Mangroves as nursery sites: Comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar Biol* 96:193–205
- Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Mar Ecol Prog Ser* 99:1–16
- Ryer CH (1988) Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Mar Ecol Prog Ser* 48: 37–45
- Ryer CH, Hurst TP (2008) Indirect predator effects on age-0 northern rock sole *Lepidostetta polyxystra*: growth suppression and temporal reallocation of feeding. *Mar Ecol Prog Ser* 357:207–212
- Ryer CH, Stoner AW, Titgen RH (2004) Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar Ecol Prog Ser* 268:231–243
- Ryer CH, Stoner AW, Spencer ML, Abookire AA (2007) Presence of larger flatfish modifies habitat preference by Age-0 northern rock sole *Lepidopsetta polyxystra*. *Mar Ecol Prog Ser* 342:227–238
- Rypel AL, Layman GA, Arrington DA (2007) Water depth modifies relative predation risk for a motile fish taxon in Bahamian creeks. *Estuar Coast* 30:518–525
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60: 1129–1157
- Sokal RR, Rohlf FJ (1969) Biometry. WH Freeman, San Francisco, CA
- Spencer ML, Stoner AW, Ryer CH, Munk JE (2005) A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: comparison with beam trawls and divers. *Estuar Coast Shelf Sci* 64:497–503
- Stoner AW (2003) What constitutes essential nursery habitat for a marine species? A case study of habitat form and function for queen conch. *Mar Ecol Prog Ser* 257:275–289
- Stoner AW, Ottmar ML (2003) Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes. *J Exp Mar Biol Ecol* 282:85–101
- Stoner AW, Spencer ML, Ryer CH (2007) Flatfish-habitat associations in Alaska nursery grounds: use of continuous video records for multi-scale spatial analysis. *J Sea Res* 57:137–150
- Stoner AW, Laurel BJ, Hurst TP (2008) Using a baited camera to assess relative abundance of juvenile Pacific cod: field and laboratory trials. *J Exp Mar Biol Ecol* 354:202–211
- Tobias WJ (2001) Mangrove habitat as nursery grounds for recreationally important fish species—Great Pond, St. Croix, U.S. Virgin Islands. *Proc Gulf Caribb Fish Inst* 52:468–487
- Yamashita Y, Tanaka M, Miller JM (2001) Ecophysiology of juvenile flatfish in nursery grounds. *J Sea Res* 45:205–218