

AN ABSTRACT OF THE THESIS OF

Megan E. Petrie for the degree of Master of Science in Fisheries Science presented on May 23, 2005.

Title: Habitat Associations and Determinants of Refuge Use in Post-Settlement Lingcod (*Ophiodon elongatus*)

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Lingcod are an overexploited fish species in the Pacific Northwest and although there has been extensive study of the habitat requirements of adults, particularly during spawning, relatively little is known regarding the habitat requirements of post-settlement juveniles. Many juvenile fish use structural components of habitat to alleviate the risk of predation, as well as for foraging. Laboratory experiments and a field tagging study were performed in order to investigate habitat preference in juvenile lingcod, as well as factors that govern habitat use. Initial laboratory experiments demonstrated an affinity by juvenile lingcod for structure over bare sand habitats, whether the structure was rock, shell or seagrass. Body size, nutritional state, and light level were also found to be determinants of the extent to which juvenile lingcod use structural refuges. In the laboratory, older, larger individuals exhibited a higher propensity for structure use than did smaller juvenile fish. In fish of both body sizes, increasing hunger levels caused fish to emerge more readily from refuges than did those that were satiated. Diel patterns of ambient illumination were simulated in the laboratory, and refuge use decreased significantly in response to

lower nocturnal light levels, a pattern that was not observed in the smaller size class.

An acoustic tagging study conducted in Yaquina Bay, Oregon corroborated the basic habitat preferences seen in laboratory experiments. Juvenile lingcod showed a high degree of site fidelity, remaining in discrete areas of significant structural complexity, as revealed by underwater video of benthic habitat. The way in which an animal utilizes structural refuges adds or detracts from individual fitness, making this investigation into the habitat requirements of post-settlement lingcod an important step in understanding the life history and ecology of an important recreational and commercial species.

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Habitat Associations and Determinants of Refuge Use in Post-Settlement Lingcod
(*Ophiodon elongatus*)

by
Megan E. Petrie

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CONTRIBUTION OF AUTHORS

Dr. Cliff Ryer assisted with formulating the research question, lent expertise during the field and laboratory phase of this project, provided help on the analysis and interpretation of the data, and provided helpful comments on the manuscript.

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Habitat Associations and Determinants of Refuge Use in Post-Settlement Lingcod (*Ophiodon elongatus*)

General Introduction

A federal mandate by Congress in 1996, the re-named Magnuson-Stevens Act, called for identification of Essential Fish Habitat for all federally managed species, with further provisions for the conservation and enhancement of such habitat. With this piece of legislation, it was widely recognized that fish habitat requirements are not only poorly understood, but also that the presence of these intact habitats are important factors in the survival and propagation of fishery species.

Lingcod (*Ophiodon elongatus*) is a popular recreationally and commercially caught species, with distribution along the Pacific Coast of North America from Baja California to the Shumagin Islands, AK. In the U.S., lingcod stocks off the California coast and those located along the Pacific Coast up to Canada were declared overfished in 1999. Management fell under federal jurisdiction with a mandate to instate a rebuilding plan (Federal Pacific Coast Groundfish Regulations 2005). Stocks seem to be recovering at a rate that reportedly will achieve target levels by 2009 (Jagiello & Hastie 2001), but the fishery is still heavily regulated. Commercial fishing in open access and limited-entry fixed-gear lingcod fisheries are completely closed from November to April throughout the U.S. EEZ from Point Conception to Vancouver, BC. A size limit of 24 inches also applies to captures by both commercial and recreational fishers along the U.S. Pacific Coast. (Federal Pacific Coast Groundfish Regulations 2005). Rockfish Conservation Areas, time/area

closures set up to reduce fishing pressure on overfished species at depths where bycatch is likely to occur, are additional management strategies that serve to alleviate pressure on lingcod populations along the Pacific Coast (Pacific Coast Groundfish Fishery Management Plan 2004). Research continues as to how best to incorporate life history information into management plans for this fishery.

Adult lingcod are typically found at depths between 10 and 100 m, while juveniles inhabit shallower near-shore areas (Cass et al. 1990). Lingcod grow rapidly during the first few years of development, achieving average lengths of 21 cm at 8 months, and 33 cm at 20 months (Cass et al. 1990). Growth strategies diverge at age 2, and females begin to show higher growth rates than do males, with females maturing at lengths of 70-76 cm and males at lengths of 46-51 cm (Hart 1973). Both males and females migrate inshore to spawn during the months of January and February, with the male defending territory and subsequently guarding the fertilized egg mass after spawning takes place. Aside from spawning migrations, however, lingcod adults are thought to be relatively sedentary, and exhibit a high degree of site fidelity (Starr et al. 2004). Males generally inhabit shallower reef habitats while females prefer deep, sandier bottom areas, a preference that may govern movement patterns (Smith et al. 1990).

Limited research has focused on spawning behavior and adult movement and migration patterns of lingcod (Hart 1973, Low and Beamish 1978, Mathews & LaRiviere 1987, Starr et al. 2004), but even less attention has been paid to the post-settlement stage of development. Larval lingcod are present in inshore pelagic zones near the end of May, and then settle out to the benthos in early June when they reach

a total length of between 70 and 80 mm (Philips and Barraclough 1977). Between early June and the time when lingcod move to the rocky relief habitat characteristic of mature individuals, it is unclear what habitat requirements are necessary for optimal survival and growth. This lack of information prevents holistic management of this species, as successful recruitment processes may be associated with the presence of certain biotic or abiotic aspects of juvenile lingcod habitat.

Certain unpublished evidence points to a preference of juvenile lingcod for open sandy habitats (Buckley et al. 1984). In this study, SCUBA surveys were conducted in nearshore waters of the Strait of Juan de Fuca between the months of June and October. The authors noted the presence of early demersal juveniles in the different habitats encountered there. No overwhelming preference for any one type of habitat was observed, but a greater number of fish were reported in sandy areas near eelgrass beds, with slightly lower counts in areas of open sand and areas dominated by clam shell/cobble. No SCUBA surveys were conducted in September, and no fish were observed in October. From this evidence, it seems that a habitat shift occurs during these months, and fish are moving to areas not observed by the survey methods. However, the terminus of this shift is unknown. In this study, laboratory methods and field tagging procedures are employed to critically examine what types of habitat juvenile lingcod utilize during early developmental phases. Also considered are potential drivers of this habitat selection behavior, namely hunger, body size and light level.

Structural affinity of juvenile lingcod: an undercover view of habitat use

Introduction

The habitat of an organism encompasses a diverse array of variables, many of which play an important role in shaping the life history and directing the behavior of fishes. Temperature, depth, water chemistry, varying light intensities, tidal cycles and current, sediment type, and surrounding biotic and abiotic structures represent important habitat characteristics to which fish respond. Structurally complex habitats (i.e., seagrass meadows, shell material, macroalgal beds, rocky reefs) have been shown to support higher densities of fish and contain greater species richness than do areas with less structure (Lewis and Stoner 1983, Orth et al. 1984, Jenkins and Wheatley 1998). Individual species have also been shown to actively choose structurally complex habitats over those with similar characteristics but no cover (Stoner and Titgen 2003, Schofield 2003). Reasons for this demonstrated affinity for structurally complex habitat include increased food availability and refuge from predation, both of which are considered paramount motivators in non-reproductive fish (Milinski 1993). Carr (1994) found that kelp bass recruitment was positively correlated with kelp biomass in a temperate reef system, indicating that survival of juveniles was dependent on the amount of available biogenic structure. More specifically, structurally complex habitats serve to increase survival by reducing predation risk, effectively alleviating the risk of exposure by providing cover, impeding predatory maneuvers and facilitating escape (Ryer et al. 2004, Tupper and Boutilier 1997, Bartholomew et al. 2000). Knowledge of habitat affinities and

patterns of refuge use help identify essential fish habitat and further our understanding in regard to spatial distribution of a given species. In this study, habitat preference by juvenile lingcod was tested in both the laboratory and field, with the goal of advancing knowledge of what constitutes Essential Fish Habitat for the early demersal stage of this important commercial and recreational species.

Adult lingcod reside primarily within rocky, high relief habitat in nearshore areas off the Pacific Coast between Baja California and the Shumagin Islands, AK, in depths from 10 to 100 m (Cass et al. 1990). Documentation of spawning behavior exists for older fish, citing evidence of inshore migration and male nest-guarding behaviors during winter months (Low & Beamish 1978, Cass et al. 1990). Studies on migration and movement show that adults demonstrate a high degree of site fidelity throughout the rest of the year, with little movement of individuals between inshore and offshore reefs (Barss and Demory 1989, Smith et al. 1990, Jagielo 1990).

Relative to what we know about adult lingcod life history characteristics, very little is known about juvenile life stages. It is known that larval lingcod hatch in early to late May at a total length of 6-10 mm. The larvae reside in nearshore pelagic environments until early June, at which time the 70-80 mm larvae settle to the bottom (Cass et al. 1990). Little is known about post-settlement habitat associations, diet or behavioral patterns. Anecdotal evidence maintains that post-settlement juveniles are often found in close proximity to eelgrass and kelp beds. Surveys indicate that juvenile lingcod disperse from inshore areas to deeper, flat bottom areas by September (Cass et al. 1990). However, experimental work has never been done to clearly establish patterns of habitat use.

In 1999, lingcod were declared overfished, and management fell under federal jurisdiction in the United States, with a call for implementation of a rebuilding plan (Federal Pacific Coast Groundfish Regulations 2005). Populations seem to be increasing, but stocks are still below target levels (Jagiello & Hastie 2001). A gap in the natural history knowledge of such an important Pacific Coast species could limit effective management, as disturbance or alteration of habitats required for early developmental stages could have implications for recruitment of adult populations. Through both laboratory habitat preference experiments and acoustic tagging/field tracking, this study tested the hypothesis that juvenile lingcod preferentially utilize structurally complex benthic habitats. A secondary hypothesis, that juvenile lingcod display diel differences in habitat use, was additionally tested by comparing animal locations during the day and at night.

Methods

Fish collection

Young-of-the-year lingcod used for laboratory habitat preference experiments were collected between May and June of 2003 in Yaquina Bay using a 5m otter trawl equipped with a 3-mm-mesh cod-end. Fish were sorted and transported back to the lab in coolers. All fish were held in circular 1 m diameter tanks at the Hatfield Marine Science Center, Newport, OR and provided with $9 \pm 1^\circ \text{C}$ filtered flow-through seawater. Fish were fed a variety of live foods collected from the bay, including juvenile striped surf perch (*Embiotoca lateralis*), black rockfish (*Sebastes*

melanops) and copper rockfish (*Sebastes caurinus*), with younger fish fed Mysid species.

Laboratory habitat preference study

In three separate experiments, lingcod were given the choice of occupying a bare sand habitat or a more structurally complex habitat. Trials were conducted in four 2.3 m diameter tanks, and the entire bottom of each tank was covered with sand of 1.0 mm grain size. A wedge of the tank, constituting 1/7 of the bottom area also contained one of three structured habitats: seagrass, rock or shell. For the seagrass trials, *Zostera marina* (~ 1 m tall) collected from Yaquina Bay was placed in the tank at a density of 10 shoots/m². These densities correspond to those encountered on the edge of seagrass beds in Yaquina Bay (personal observation). For the shell and rock trials, either about 20 Pacific oyster shells (*Crassostrea gigas*) (~1-15 cm each) or 6-10 rocks (~ 25 cm x 15 cm) covered the entire wedge area. Eleven subjects in groups of three or four were transferred from holding tanks, and an individual fish was placed in the experimental tank and allowed to acclimate for two days. Fish were fed at 1200 h on the day preceding the trial. On the day of a trial, between 800 h and 1600 h, fish position was observed every 15 minutes from a blind to prevent observer disturbance. The observer noted where the fish were positioned, in structure or over bare sand, at each designated time. If any part of the fish was within the structured area, the observation was categorized as within structure. Distinction was not made as to whether the fish was swimming or stationary, though position outside of structure was most often characterized by active behavior. Eleven fish were

subjected to each of the three habitat structure treatments in a random order (different for each trial). Structure was removed immediately preceding the last observation, and replaced by the next type in the series. Trial days were separated by a period of 48 hours. Fish were removed from the experimental tanks after the three treatments were completed and lengths recorded. The resulting data from each structure type were first analysed for differences between fish using a heterogeneity G-test (Sokal & Rohlf 1969). Pooled data (i.e., fish) were then analyzed for each structure type using an extrinsic hypothesis G-test (Sokal & Rohlf 1969), testing the null hypothesis that the frequency distribution of observations in structured vs. sand habitats conformed to a 1:7 ratio. Deviations from a 1:7 ratio were considered significant at $P < 0.5$. Next, frequencies for individual subjects were analyzed in the same manner to determine the number of fish conforming to a 1:7 ratio of habitat use. Finally, a Friedman test was used to test for differences in the number of observations outside of structure for each habitat type.

Preliminary Tag Retention Study

Two sizes of acoustic transmitters were tested to observe impact upon recovery time in juvenile lingcod during December, 2003. Fish used in this preliminary experiment were between 192 and 195 mm, and weighed between 45.8 and 54.2 grams. Two transmitters of two different kinds (Sonotronics dummy tags, SMT-01 and IBT-96-1), having lengths of 17 and 25 mm, diameters of 7 and 8 mm, and weights of 0.75 and 1.5 grams, respectively, were tested in this study. One tag was inserted into each of four lingcod. Each fish was first anesthetized by immersion

in an aqueous solution of 25 grams/liter of buffered MS-222 then transferred to a tray suspended above a receptacle containing filtered seawater. This seawater was used to irrigate the gills during the procedure using a syringe. A small incision was made in the body cavity with a scalpel on the ventral surface of the fish, directly anterior to the anal pore. The tag was inserted and the opening closed using Elmers Krazy® Glue. Fish were then returned to tanks for recovery.

Tagged fish recovered rapidly, engaging in swimming activity within a few minutes of returning to holding tanks. Fish returned to normal swimming activity within 2-3 hours. All fish fed after a period of 48 hours, and there was no delayed mortality after 1 month, after which the fish were released back into Yaquina Bay.

Field Tagging/Tracking Study

Sonotronics IBT-96-1 miniature acoustic tags, each with unique frequencies, were inserted into 10 lingcod in order to track both movement and habitat choices. Signal detection was achieved using a Sonotronics DH-4 hydrophone and USR-91 receiver. The equipment was tested in the field by attaching a test tag to a mooring and float at three depths (1.0, 2.0 and 8.8 meters). Range and precision of location of the tag were tested using waypoints and measured distances generated by a Garmin MapSource GPS unit. By starting at a location immediately adjacent to the tag, the precision was tested by floating away from it until a reduction in signal volume was noted. A waypoint was marked at that location, and the distance from the tag to this point was measured. The range was found in the same fashion, noting the point at which the tag frequency could no longer be heard.

Precision was found to be within 10 m of the tag location, so a 10 m radius of uncertainty was assumed for each fish location. Range was measured in deeper 8-9 m open sand locations with no seagrass, as well as in shallower 1-2 m locations in which seagrass was present and at the edge of seagrass habitat. The range in deep water devoid of seagrass was approximately 150 m, but the transmission in seagrass was severely dampened and the range here was approximately 25 m. This range can be altered both by background noise and water turbidity (Sonotronics, personal communication).

The ten lingcod tagged for this study were collected as described above, and were held in the laboratory for 2-3 months until they grew to the minimum size required for tagging (at least 40 g). Fish are not typically available in trawlable areas by the time they have reached this size at the end of the summer. Tagged fish were 176 and 185 mm total length, and weighed between 40.1 and 54.7 grams. Fish were tagged using the same procedure described above, and allowed to recover until feeding resumed, which was 48 h in all cases. Ten fish were released at three different times, each at the location where most juveniles were captured for the tagging study. The depth of the release site varied depending on the tide. Release took place at varying tidal stages, and varying times during the day and night. In subsequent analysis of release conditions, there was no apparent pattern between the number of fish relocated after each release event and the water depth or time of release. Tracking took place at both high tides daily, but when no patterns of diel movement were detected after comparing 10 night tracking events to 20 day tracking events, location efforts were limited to daylight hours.

Fish locations were determined after release by systematically surveying the bay study site. The hydrophone was lowered from the boat at least every 250 m, motoring parallel to the shoreline at a distance of approximately 250 m. In this way, the entire area of the bay was searched from 4 km upstream of the release point to the Pacific Ocean. The fish location would be determined by listening to the received signal in all four quadrants and moving in the direction of highest volume. When the signal was loudest and equal in all four directional quadrants it was assumed that the hydrophone, and thus the boat, was directly above the fish and the location was recorded. When locations were within 10 m of one another and of the same frequency they were considered to denote the same site.

Random sites were chosen by superimposing a grid above a polygon within the study site that comprised habitat having depths similar to those at which fish were found (below 7 m mllw). Random numbers were used to select locations on the grid. Nine random sites were selected to correspond to the nine sites at which fish were found.

Habitat was filmed and recorded for eight out of nine fish locations and for nine random locations using an underwater camera sled (Spencer et al., in press). Briefly, this apparatus consisted of an Aqua-Vue® underwater camera harnessed to an aluminum benthic sled (dimensions: L=114.3 cm, W=67.3 cm, H=41.9 cm) providing an oblique view of the seafloor. Audio-visual cable was strung from the camera along the tow-line behind the boat, and was connected to a Sony digital video camera recorder (model no. DCR-PC110). Routes upon which to record habitat were selected by taking into account the precision of the detection equipment. Since there

was a 10 m radius of uncertainty around each detection point, the borders of the sites were drawn 10 meters away from the outermost detection point using Garmin MapSource software. In this way, a polygon was constructed around the cluster of detection points for each site. Parallel transects were drawn every four meters within the boundaries of each site. The area of the random site polygons, not having a cluster of points to dictate the polygon area, was the average of the areas for the fish site polygons, and their borders encompassed identically constructed transects. The camera sled was towed along the transect lines, as referenced by the on-deck GPS map.

The percent of the area covered by structure other than the naturally occurring sediment was quantified for each site from video analysis by averaging the percent cover on the screen every ten meters. Since the distance traveled and the travel time was known, the time it took to travel ten meters was calculated and the video sampled at these intervals. Cover was defined as any type of biotic or abiotic structure, both low and high relief, including shell, rock, vegetation and invertebrates. Percent cover values were arcsine transformed to normalize the distribution. Fish were found in nine locations throughout the bay. First, eight filmed sites in which fish were found (1 fish site was inaccessible to camera sled because it was under a dock) were compared to the nine random sites using a Welch's modified t-test. However, some of these sites were not independent because they represented multiple locations for the same fish. Therefore, additional analysis was carried out on the average percent cover of sites for each individual fish to avoid pseudoreplication (Hurlbert 1984). Thus, data for four fish were ultimately pooled then to get a sample size of four. The

average percent cover values for these four fish were then compared to percent cover at the nine random sites using a Welch's modified t-test.

The water current was also tested at each fish site and each random site using a General Oceanics Inc. mechanical flowmeter Model 2030R. Measurements at each site were completed within one hour midway between the tide change to minimize variation on each sampling occasion. Comparison between fish sites and random sites for data taken once during a flooding tide, and once during an ebbing tide was made using two separate t-tests.

Results

Habitat Preference Experiments

When given the choice, juvenile lingcod consistently chose to position themselves in the structurally complex habitat. In an extrinsic hypothesis G-test conducted on the pooled data for each structure type, the null hypothesis that fish were using habitat in accordance with a 1:7 ratio was rejected (shell, $G = 935.8$, $p < 0.001$; eelgrass, $G = 1098.7$, $p < 0.001$; rock, $G = 825.7$, $p < 0.001$). In fact, fish were choosing either shell, eelgrass, or rock habitat over bare sand, with no difference in the magnitude of preference between structure types (Friedman test, $\chi^2 = 0.45$, $df = 2$, $P = 0.643$). To examine individual variation, a G-test for heterogeneity was used for exploratory purposes. In all experiments comparing bare sand habitat to habitat containing rock, shell, or eelgrass, ratios of habitat use differed significantly between one or more subjects (shell, $G = 147.1$, $p < 0.001$; eelgrass, $G = 53.7$, $p < 0.001$; rock, $G = 83.6$, $p < 0.001$), indicating variation in structural preference between individuals. However, though the proportions spent in each habitat differed, in an

extrinsic hypothesis G-test for single subjects ($G > 32.3$, $p < 0.001$ for 32 out of 33 subjects) patterns of habitat use were found to conform to a ratio consistent with no habitat preference only one out of 33 times. So 32 out of 33 subjects showed a significant preference for structure, but the degree to which this preference was displayed was variable.

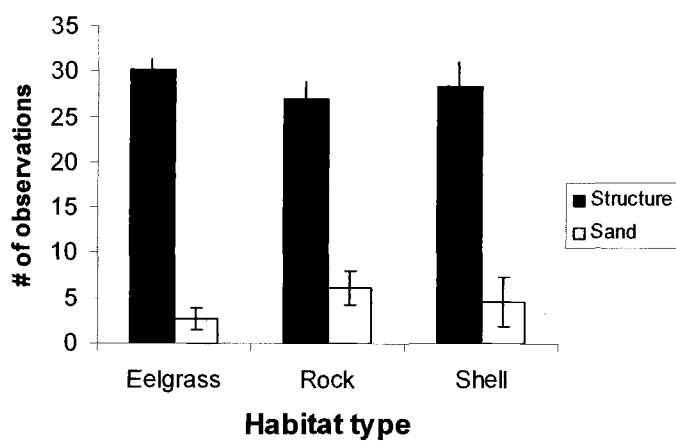


Figure 1: Mean number of observations (\pm SE) in each habitat for three laboratory experiments testing eelgrass, rock, and shell habitats against bare sand. Positions of twelve fish were observed every 15 minutes from 800 h to 1700 h for each type of structure.

Tagging Study

Of the 10 tagged fish that were released into Yaquina Bay, six were relocated and subsequently found at least twice (Table 1, Fig. 2). One fish (#71) was assumed to have been eaten, leaving five fish, which were tracked to one or more discrete sites, all of which were downriver from the release site. Two fish (#72 and #76) were each tracked to one site, while the remaining three fish (#70, #73, and #76) moved to at least one other site during the duration of the study, suggesting that they were not eaten by a predator and excreted, but moving of their own volition. The remaining four fish (#74, #75, #78, and #79) were never located after release.

Table 1: Fate of each tag released in order of frequency

Tag Frequency	Fate of individual
70	Initially located under Newport bridge and found continuously in the same location, then moved approximately 100 m further out to sea after 14 days and stayed there until battery expired
71	Found moving rapidly around release site at time of release, then again the next morning near the mouth of the bay. Movement was uncharacteristic of the other released individuals – it is suspected that this individual was eaten by a seal or sea lion.
72	Continually located under a dock for 7 days, after which the signal could no longer be located.
73	Located at one mid-bay site for a period of 3 days, then moved approximately 100 meters downriver for a period of five days, then moved approximately 700 m farther downriver for three days, then lost signal.
74	Never found after release
75	Never found after release
76	Located for duration of tag life (30 days) in one location.
77	Located initially for one day in a mid-bay location, then located approximately 450 m downstream and remained there for the duration of tag life.
78	Never found after release
79	Never found after release

Time of day did not affect the location site, as fish were found to inhabit the same area whether they were detected during the day or at night. Unfortunately, times at which the fish were located do not allow for any conclusions to be drawn as to when the fish were moving in between chosen sites.

All located fish showed a high degree of affinity for structured habitat. Fish sites were all characterized by nearly 100% cover, with shell, rock, kelp and invertebrates providing a high degree of structural complexity. While some of the random sites contained similar amounts of structure, these were often in the vicinity of sites chosen by fish. Six out of the nine random sites had little to no structural complexity, indicating a high probability that much of the seafloor in the estuary is comprised of bare sand habitat. Personal experience trawling corroborates this conclusion, as tows in most areas of the bay brought up little physical structure. One can infer what is on the bottom from what is brought up in the catch or from incidences of getting the net entangled on various large pieces of physical structure. Though only eight fish sites were filmed, the ninth site, identified as being inhabited by fish #72, was also a structured habitat. It was located under a dock and thus could not be filmed, but pilings visible from the surface certainly provide at least some degree of structure. The bay bottom, at sites where fish were found, had significantly higher mean percent emergent structure than that of randomly sampled areas when all fish sites were analyzed (Welch's modified t-test, $df = 10.70$, $P = 0.005$). Furthermore, when data from individual fish were averaged, sites chosen by fish still contained significantly higher percent cover than that of random sites (Welch's modified t-test, $df = 10.71$, $P = 0.009$).

From video analysis of random sites, it was observed that much of the habitat over which the tagged lingcod traversed in order to get from the release site to their final destinations was relatively devoid of structure. In some cases, travel time was less than 24 hours, so fish were quick to choose structured habitat over less complex areas.

Current did not differ between fish sites and random sites (t-test, ebbing tide, $t = -0.112$, $df = 16$, $P = 0.912$; flood tide, $t = -0.085$, $df = 16$, $P = 0.933$), and thus was not an integral characteristic of site desirability.

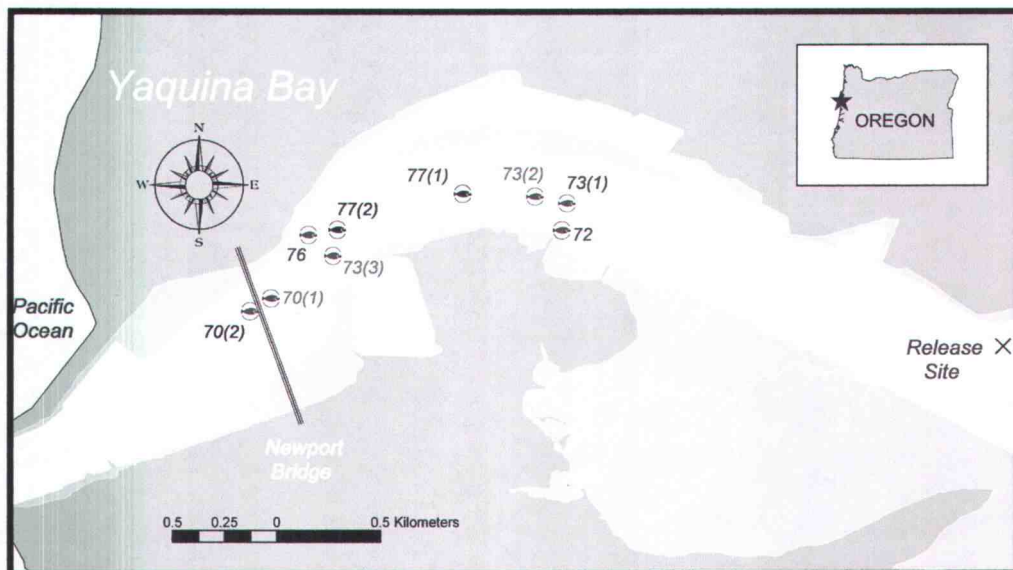


Figure 2: Tagged fish locations. All fish movement was directed downstream of the release site. Number labels represent the tag frequency for the indicated fish, with the number in parenthesis indicating the order from first (1), to second (2), to third (3) movement when applicable. Number labels without parenthetical numbers indicate fish that remained stationary.

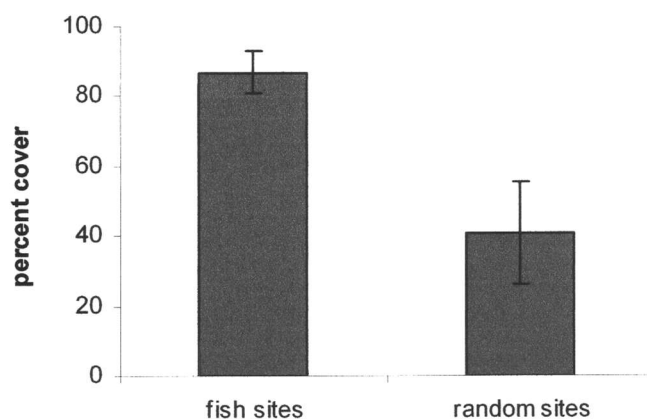


Figure 3: Mean percent cover (\pm SE) for sites in which fish were found compared to randomly chosen sites of comparable depth. Fish site values are averages of percent cover for all sites visited by each individual fish.

Discussion

Many juvenile fish in both marine and freshwater environments have been found to associate with structural components of habitat (Jones 1984, Stoneman & Jones 2000, Koenig & Coleman 1998). Juvenile Nassau grouper utilize the interstices of macroalgal clumps within shallow nursery areas, with increasing fish densities corresponding to increasing percent cover of macroalgae for the first two months post-settlement (Eggleston 1995). In a study conducted by Dean et al. (2000), cod (*Gadus macrocephalus*), greenling species (*Hexagrammidae*), sculpin species (*Cottidae*) and crescent gunnels (*Pholis laeta*) were found to have very specific distributions that could be predicted on the basis of physical habitat type. Knowledge of such habitat associations refines our understanding of how a species is spatially distributed within its broader range. Though there is not a specific type of structure with which lingcod were found to associate, the fact that these fish prefer structurally complex environments to bare sand lends understanding of how juvenile lingcod are utilizing habitat within a protected nearshore environment.

Skepticism often arises as to the applicability of laboratory findings to field situations. Adding a tagging component to the study allowed for a more holistic approach, and complementary results lend credibility to appease dubious critics. Here, laboratory results were confirmed by the field portion of this study, where fish were tagged and tracked in Yaquina Bay. Nine different sites were chosen by five fish throughout the study, and each site was structurally complex. Furthermore, the habitat chosen by the fifth fish also contained significant physical structure, though percent cover could not be quantitatively assessed. This fish was found under a large

dock, so the camera sled could not be employed, but the fact that the habitat contained large pilings ensures at least a certain degree of structural complexity and availability of refuge habitat. Visually, it was obvious that all of the sites chosen by fish were highly complex, with more opportunities for refuge than many areas in the bay. Compared to randomly selected sites throughout the bay, lingcod actively chose sites that contained a significantly higher percent cover of physical structure.

Furthermore, it should be pointed out that statistical significance was demonstrated using the average percent cover of only four fish to avoid pseudoreplication (see Hurlbert 1984), but utilizing data from all eight filmed sites in which fish were found yields important information about the movement of the subjects, which notably emphasized the preference for structured habitat.

Juvenile lingcod also seemed to prefer deeper habitats, always choosing sites that were at least 7 mllw, a depth at the more extreme end of the spectrum in Yaquina Bay. Whether habitat choice was a function of structure availability and depth or solely of habitat complexity is confounded in this study. A better understanding of how these fish are choosing habitat would be possible from a more extensive habitat survey of Yaquina Bay, but such undertakings have not been pursued as of this date. In light of laboratory results, and due to the fact that these fish were all released in a shallow, relatively bare area then migrated (often within 24 hours) to areas of higher relief, there is a strong indication that structural components are important indicators of optimal habitat. This finding may be very important for the growth and survival of juvenile lingcod.

Current speed did not differ between fish sites and random sites, suggesting that flow is not a factor that guides lingcod habitat preference on a large scale. However, currents within an estuary are variable and can change significantly over small time and spatial scales (Day et al. 1989), and measurement of current was obviously not possible at the precise location of the fish. Therefore, these data do not rule out the possibility that certain flow parameters contribute to the characterization of preferred lingcod habitat. On the contrary, it is possible that stronger currents are associated with deeper areas of the estuary, thus contributing to the suitability of the habitats observed in this study.

Tagged fish were initially tracked at each high tide, so fish were located at night in some instances. No pattern of greater nocturnal mobility was observed. Rather, fish were found in the same locations both during the day and at night. This contradicts one of the a priori predictions of this study, that juvenile lingcod would take advantage of night hours to move between and sample patches of complex habitat, but would remain stationary during daytime. It is important to note, however, that smaller scale movements in and out of structured habitats could be occurring within the location radius of the tag. In laboratory experiments, it was observed that lingcod of this size made forays outside of refuge habitat, and chose less complex habitat during times of less illumination, i.e., night (this thesis). Possibly, these fish were taking advantage of decreased conspicuousness to engage in safer foraging. Unfortunately, low sample size and the relatively imprecise nature of acoustic tagging precludes this type of fine-scale spatial observation in the field.

Once the tagged lingcod were tracked to their respective locations, there was little movement throughout the duration of the study. Three fish showed a high degree of site fidelity, with one fish staying in its initial location for the entire 30 days, and the other two moving distances of less than 200 m only once. This pattern is consistent with that of older individuals, who are considered to be relatively sedentary, with the exception of inshore spawning migrations (Hart 1973, Mathews & LaRiviere 1987, Starr et al. 2004). Two of the fish, though, stayed within the bay for short periods of time, with one fish only staying seven days, and the other for eleven days. Inability to locate these two fish could have been a result of either predation or of their volitional movement out of the bay. Unfortunately, the short duration of tag activity did not lend itself to revealing longer term movement patterns in the bay.

In summary, post-settlement lingcod showed a strong affinity for structured habitat both in the lab and in the field, indicating that these types of habitats may be important for this life history stage. Results from additional laboratory experiments have yielded information about the effects of hunger and diel patterns on the use of habitat by different sizes of lingcod, indicating an ontological shift in habitat preference (this thesis). Further evidence for this shift is reported by Buckley et al. (1984), who found that post-settlement juveniles spent the majority of their time in open sand and adjacent to eelgrass beds in early summer months, while fish could no longer be found in these areas during October. Whether these habitat associations hold true in other Pacific Coast estuaries and nearshore locations has not been explored. However, the innate tendencies of juvenile lingcod indicate a propensity for occupying emergent benthic structure, the availability of which may dictate their

distribution within estuaries and nearshore coastal areas. The findings of this study therefore aid in identification of both basic life history requirements and essential fish habitat for an important recreational and commercial species.

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Determinants of refuge use by post-settlement lingcod

Introduction

Many fish use structurally complex habitat features to mediate conspicuousness and therefore reduce predation risk (Savino & Stein 1982, Tupper and Boutilier 1997). However, since hiding in a refuge is often chosen at the expense of foraging, regular use of structure often presents a conflict in time management (Sih 1992). Decisions made in regard to feeding, reproduction and predator avoidance behavior are all associated with costs and benefits integrated over a lifetime to affect the overall survival and fitness of an individual (McNamara & Houston 1985). For non-reproductive individuals, fitness increases as a function of increased probability of survival to the next size class and is dependent upon the individual's ability to maximize growth while simultaneously employing behaviors that prevent mortality (Werner & Gilliam 1984, Mangel & Clark, 1986). Structural components of habitat play a pivotal role in how this challenge is met. An animal outside of a refuge is more vulnerable to predation. Yet, in many species, individuals must risk abandoning structure in order to feed (Lima & Dill 1990). Selection favors individuals that most efficiently weigh this trade-off, thus optimizing growth against mortality risk within the constraints imposed by the environment and phylogeny. Ultimately, reproductive success is dependent on the efficiency with which these constraints are managed throughout an individual's lifetime.

Throughout the lifespan of an organism, internal and external determinants of behavior are not only fluctuating, but are also of differential importance as the fish's body size changes in relation to the environment. As a fish grows, it experiences

differing predation pressures, energetic requirements and trophic considerations, causing a shift in the trade-off relationship between feeding and avoiding mortality in a given habitat (Werner & Gilliam 1984). Consequently, habitat preferences change throughout a lifetime because selection favors fish that are able to minimize the ratio of mortality rate to growth rate (Werner and Gilliam 1984). This balancing depends on the food resources and predation risk associated with specific habitats. For example, post-settlement grouper occupy macroalgal habitats that provide a lower growth rate than more open areas, yet yield a lower mortality risk. However, larger juvenile grouper are able to shift to post-algal habitats that offer increased food availability as they have outgrown their predators and thus, have a lower mortality rate in this more open habitat. In this way, groupers are selecting habitats that minimize the ratio of mortality rate to growth rate (Dahlgren & Eggleston 2000). Size-mediated ontogenetic shifts in habitat have also been documented for bluegill sunfish (Werner and Hall 1988), and for a number of additional species (Eggleston 1995, Ruzycki and Wurtsbaugh 1999, Phelan et al. 2001). It is nearly universal for fish species to experience a habitat shift as they mature, and it becomes important, from an ecological perspective, to understand the mechanisms that drive these changes.

Though fitness is measured by reproductive output, the choices made by an animal throughout a lifespan are a means to this end. Each activity (or lack of) influences growth rate and survival. Both internal and external factors, referred to more specifically as physiological state and environmental cues, affect the motivation of a fish to utilize refuge (Hart 1993). Nutritional state has been shown to play a role

in refuge use, as hungry fish are more apt to risk predation than are satiated fish (Gotceitas & Godin 1991, Pettersson & Brönmark 1993, Krause et al. 1998). There is a cost associated with refuge use due to decreased availability of food in these sheltered areas in relation to open habitats (De Roos et al. 2002). Thus, conflict arises when an animal's energetic demands must be met. At a certain point, the cost of decreased nutritional state outweighs the cost of predation risk, making it profitable for a fish to abandon structure in search of food.

Environmental cues are also integral in shaping fish behavior, and assessment of these variables is crucial to the survival of an individual. More specifically, light level has been shown to alter patterns of refuge use in many fish species (Helfman 1981). Changes in the way fish perceive prey and how they are perceived by predators come with differing light conditions. These different light conditions theoretically shift the parameters of both predation risk and foraging return (Pitcher & Turner 1986). Low light levels (i.e., at night) could potentially allow a fish to venture from a refuge in search of food while remaining less conspicuous to predators, although a trade-off may exist in the effectiveness of foraging in low light conditions. Light level has been shown to influence the reaction distance of prey fish and location distance of predatory fish (Howick & O'Brien 1983). Seine sampling by Gray et al. (1997) revealed differential habitat use by some fish species according to whether sampling occurred during the day or at night. Most species emerged from structured seagrass habitats in favor of bare sand at night. Holierhoek and Power (1995) demonstrated a decrease in use of cover at night by Arctic char, and suggested that open habitats simultaneously provide increased foraging opportunity due to

conspicuousness of prey but are associated with higher predation risk. Further evidence of the positive correlation between light level and refuge use is important in understanding the dynamics of habitat use and the strategies used by animals to achieve optimal fitness.

In this study, the influence of body size, hunger, and ambient illumination on the use of refuge by juvenile lingcod is examined. Anecdotal evidence indicated an affinity for structure during the post-settlement stage of development, and has been recently corroborated in a formal laboratory and field study investigating juvenile lingcod habitat associations (this thesis). In this study it was concluded that post-settlement fish consistently chose areas of higher structural complexity than areas containing little physical structure. In this study, the influence of body size, hunger, and ambient illumination on the use of refuge by juvenile lingcod is examined. By characterizing habitat requirements and refuge use patterns for this commercially important fishery species, we gain insight into what areas constitute essential fish habitat for juvenile lingcod. Ultimately, this knowledge will provide the necessary information for the construction of a fully informed management plan.

Methods

Fish collection

Young-of-the-year lingcod were collected between May and June of both 2002 and 2003 in Yaquina Bay using a 5m otter trawl equipped with a 3-mm-mesh cod-end. Fish were sorted and transported back to the lab in coolers. All fish were held in circular 1 m diameter tanks at the Hatfield Marine Science Center, Newport,

OR and provided with $9 \pm 1^\circ$ filtered flow-through seawater. Fish were fed a variety of live foods collected from the bay, including juvenile striped surf perch (*Embiotoca lateralis*), black rockfish (*Sebastes melanops*) and copper rockfish (*Sebastes caurinus*), with younger fish fed mysid spp.

Effect of Hunger on Refuge Use Experiments

An experiment testing the effect of hunger on refuge use was carried out using nine young-of-the-year lingcod that ranged in size from 161-210 mm (mean = 182.3, SE = 4.9). Flow-through seawater of between 28 and 33 ‰ circulated the tank, and temperature was kept constant at $9 \pm 1^\circ$ C. Light level was held constant at $2.5 \times 10^{-1} \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during the day and $1.0 \times 10^{-7} \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at night. The experimental setup consisted of 2 - 2.3 m arenas, each with an area of 1/10 of the tank bottom covered by structured habitat (a pile of 6-8 ~25 cm x 15 cm rocks arranged in a wedge shape), while the rest of the tank contained bare sand. Fish were transferred from holding and allowed to acclimate in experimental tanks for three days. Fish were fed one surf perch that constituted approximately 12% of their body weight at 800 h on day 1, and on day 5 of the experiment. With each day, hunger increased as a function of time since last feeding. Behavior was recorded from overhead video cameras for the last 15 minutes of every hour from 845 h to 1700 h for five days. Video was analyzed for percent time spent outside of structure during fifteen minute intervals every hour (845-900 h, 945-1000 h, 1045-1100 h, 1145-1200 h, 1245-1300 h, 1345-1400 h, 1445-1500 h, 1545-1600 h, 1645-1700 h). Percents from each time period were averaged to yield one value per fish per day. A Friedman test for

repeated measures was used to test for difference in refuge use between days. Multiple comparison tests were conducted using methods described by Conover (1980).

To check for any patterns of diurnal refuge use, a Friedman test was conducted. No differences were found between discrete time periods, suggesting equal use of habitat throughout the day ($t^2 = 1.19$, $df = 50$, $P = 0.328$).

Effect of Body Size and Hunger on Refuge Use Experiments

To explore how body size affects the response of juvenile lingcod to hunger, a series of similar experiments was conducted on two size classes of juvenile lingcod. Individual fish of lengths between 78 and 103 mm (mean = 88.9, SE = 2.5) for the small size class and 134-162 mm (mean = 148.9, SE = 3.6) for the larger size class were placed in one of five 2.3 m diameter circular tanks with identical structural refuges (described above). Large fish were tested immediately after small fish trials, so none of the small fish were reused for the large size class experiments. Ambient day light levels ranged from 3.07×10^{-1} to $4.53 \times 10^{-1} \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ throughout the laboratory. Again, flow-through seawater of between 28 and 33 ‰ was kept at a constant temperature of $9 \pm 1^\circ \text{C}$. Fish were transferred from holding tanks and allowed to acclimate for a period of at least 48 h. Fish were fed at 1200 h on the day before day 1 of the experiment, and were given approximately 8% of their body weight (instead of the 12% that was provided in the above experimental procedure). Fish were not fed again throughout the experiment (unlike previous experiment). Behavior was quantified as detailed above, and data was handled in the same manner.

Two missing data values which arose due to recording malfunction were dealt with using an iterative method (Snedecor and Cochran, 1980).

A Friedman test for differences between time periods within each day was employed for both sizes of fish and found to show no difference (large fish $t^2 = 1.88$, $df = 28$, $P = 0.142$; small fish $t^2 = 0.85$, $df = 40$, $P = 0.499$). Thus, fish were spending equal amounts of time outside of the refuge throughout each day. Spearman rank correlation coefficients comparing body size of individuals within a given experiment to time spent outside of the refuge revealed no significant relationships (small fish, $\rho = -0.005$, $P = 0.990$; large fish, $\rho = -0.180$, $P = 0.663$), indicating that, within the size range of the experimental fish, fish size had no influence on habitat use.

To test for differences in the mean percentage of time spent outside of the refuge in small versus large fish, percentages of time spent outside of the refuge were compared from day 1. The percentage data did not conform to the assumptions for normality, so a Wilcoxon Rank-Sum test was used to test for inequality of means. The differences in refuge use between days 1 and 2 for each size were also compared using a Welch modified t-test. Finally, refuge use means for days 2 through 5 were compared for individual fish of the two sizes classes using a Wilcoxon Rank-Sum test to test for differences after the initial change in behavior.

Effect of Light Level on Refuge Use Experiments

Small fish of lengths between 99 and 121 mm (mean = 105.0, SE = 3.2) and large fish of lengths between 199 and 220 mm (mean = 203.0, SE = 3.4) were tested

for the combined effect of body size and light on refuge use. Small fish trials took place in July and August, 2004, while large fish trials were conducted in September and October, 2004. Small fish in holding tanks grew quickly, and between two and four large fish were likely to have been previously tested in the small size class.

All trials took place in 2.3 meter diameter arenas equipped with 60 W LED infra-red illumination under the tank bottom (for detailed description see Ryer & Olla 1998). This allowed behavior to be recorded at low visible light levels (i.e. fish are insensitive to IR illumination, Douglas & Hawryshyn 1990). Ambient low visible light conditions were created through an overhead network of LED lights, which were configured to produce a range of light levels. Individual fish were acclimated for three days in the experimental tanks after transfer from holding. Fish were fed between 6 and 8% of their body weight at 1600 h every day, to control for hunger effects. If an experimental fish failed to feed immediately upon introduction of prey, the prey was removed and the experiment delayed one day until the fish fed readily again.

Four light levels, 1×10^{-4} , 1×10^{-5} , 1×10^{-6} and $1 \times 10^{-7} \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, were presented randomly during each of the four nights of the trial. Light levels during the day were approximately $2.5 \times 10^{-1} \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The arenas were video taped from overhead for the last 15 minutes of every hour, 24 hours a day, for four days. The percent of time spent outside of structure was quantified for five 15-minute intervals during the day and five 15-minute segments during the night. Each analyzed segment was spaced 2 hours apart, with the day intervals starting at 745 h and the night intervals beginning at 2045 h (day intervals = 745-8 h, 945-10 h, 1145-12 h, 1345-14

h, 1545-16 h, night intervals = 2045-21 h, 2245-23 h, 045-1 h, 245-3 h, 445-5 h).

Data were averaged for each day and night period for each fish. Day values, after being checked for acclimation effects, were randomly chosen for each fish as opposed to using the average. This was done in order to retain the same variance structure as the night light level values of time spent outside of the refuge. The combined data set, incorporating both small and large fish, did not meet variance and normality assumptions for analysis of variance (Sokal and Rohlf 1969), even after various transformations. As a result, data from small and large fish were analyzed separately using a Friedman nonparametric ANOVA (Conover, 1971). Spearman rank correlation analysis was performed on day and night data within each experiment. There were no significant correlations between body size and time spent outside of refuge for either size class (small fish, $\rho = 0.120$, $P = 0.750$; large fish, $\rho = -0.443$, $P = 0.268$).

Results

Effect of Hunger on Refuge Use

Hunger influenced how much time lingcod spent away from the refuge habitat (Fig. 4). Percentage of time spent out of the refuge habitat differed significantly between days (Friedman test, $t^2 = 6.92$, $df = 32$, $P < 0.001$), with fish spending more time in the refuge on days when they were fed than during the three intervening days when fish were unfed (Friedman multiple comparison, $P < 0.05$).

Effect of Hunger and Body Size on Refuge Use

In the second experiment, fish body size controlled how fish responded to hunger (Fig. 5). Increased hunger level caused both small and large fish to emerge from structured habitat for a greater percentage of time, although a linear relationship was not observed. In a Friedman test for repeated measures, a significant difference was found between days (Small fish, $\chi^2 = 2.88$, $df = 40$, $P = 0.035$; Large fish, $\chi^2 = 6.58$, $df = 28$, $P < 0.001$). For small fish, day 1 differed significantly from all subsequent days. For large fish, day 1 differed from all days except day 5 (Friedman multiple comparison, $P < 0.05$). Small fish showed no difference between the four last days of the experiment when the fish were becoming increasingly hungry (unlike the first experiment, fish were not fed on the 5th day). In contrast, large fish refuge use increased significantly between days 4 and 5, indicating a response to longer periods of sustained hunger.

Overall, small fish tended to spend more time outside the refuge than did large fish (Fig. 5). Evidence comparing day 1 levels of refuge use was not conclusive, but was strongly suggestive of a lesser degree of refuge use by small fish (Wilcoxon rank-sum test, $Z = -1.93$, $P = 0.054$). Similarly, smaller fish appeared more responsive to hunger, as indicated by a strong trend towards a greater increase in time spent outside of refuge from day 1 to day 2 in small as compared to large fish (Welch's modified t-test, $t = -2.07$, $df = 13.19$, $P = 0.058$). When refuge use for days 2 through 5 were compared between small and large fish, it was again apparent that small fish spent significantly more time outside of structure than did large fish (Exact Wilcoxon Rank-Sum test, $W = 49$, $n = 8$, $m = 11$, $P = 0.009$).

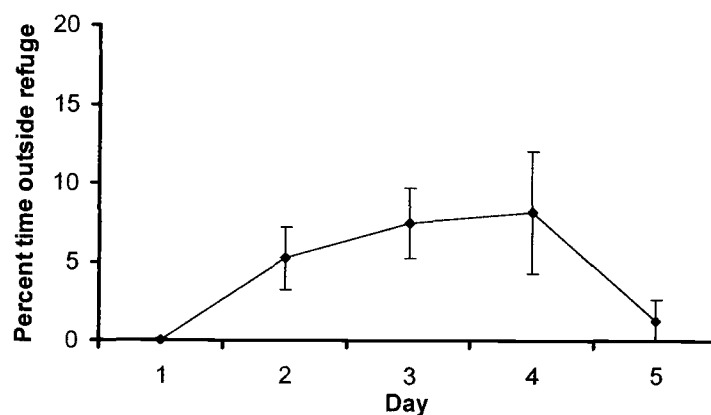


Figure 4: Mean percent time spent outside of structured habitat (\pm SE) for large fish (161-197 mm) at different hunger levels for trials conducted in 2003. Fish were fed 12% of their body weight the morning of day 1, and again on the morning of

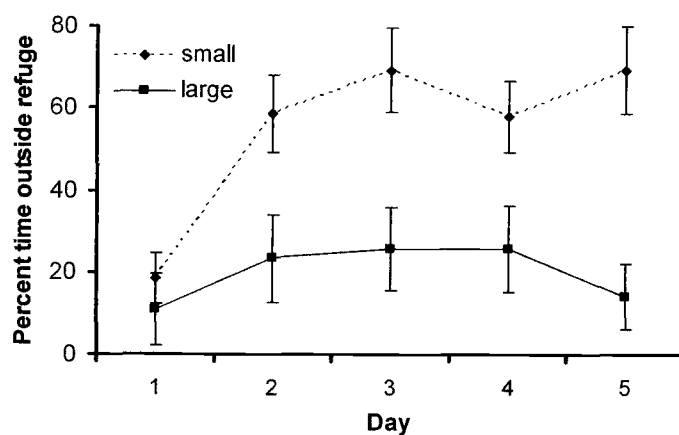


Figure 5: Mean percent time spent outside of structured habitat (\pm SE) for eleven small (78-103 mm) and eight large (134-162 mm) fish at different hunger levels.

Effect of Light Level on Refuge Use

Again, fish body size affected how lingcod responded to ambient light level (Fig. 6). Refuge use by small fish did not differ between daytime and nighttime light levels, (Friedman test, $t^2 = 0.67$, $df = 49$, $P = 0.696$). In contrast, larger lingcod refuge use differed significantly between day and nighttime light levels (Friedman test, $t^2 = 7.63$, $df = 49$, $P < 0.001$), with fish spending a greater percentage of time outside of structure at night (Friedman multiple comparisons, $P < 0.05$). Neither size class showed differences in refuge use with varying night light levels.

In addition to investigating differences in refuge use between light levels, patterns of refuge use within the day were also examined (Fig. 7). In a Friedman test comparing data from each time period averaged over all treatment days, it was found that within the day and within the night small lingcod showed no difference in refuge use ($t^2 = 1.02$, $df = 63$, $P = 0.434$). For large fish though, significant differences in refuge use were observed in relation to time period (Friedman test, $t^2 = 7.72$, $df = 63$, $P < 0.001$), with refuge use during the day being significantly higher than at night (Friedman multiple comparisons, $P < 0.05$).

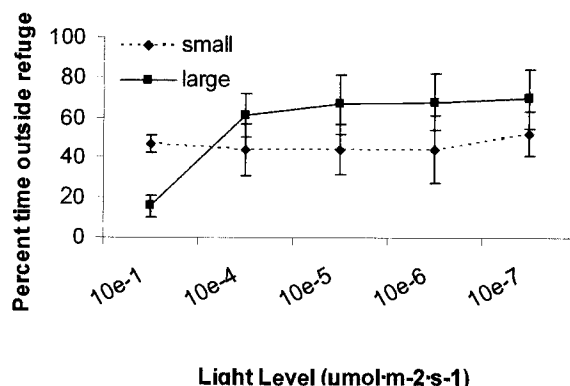


Figure 6: Mean percent time spent outside of the refuge (\pm SE) for both small (97-115 mm) and large (190-220 mm) fish at different light levels. Day values are averages of percents for all four days.

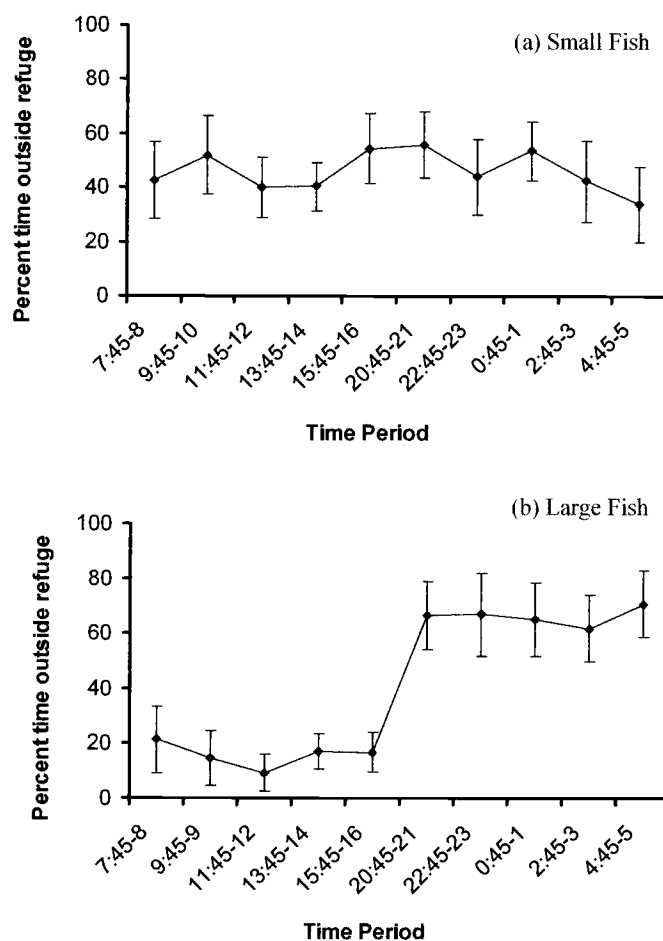


Figure 7: Mean percent time spent outside of habitat (\pm SE) for (a) small fish (97-115 mm) and (b) large fish (190-220 mm) during discrete time periods. The response at each time period is an average of individual fish responses over each light level.

Discussion

Fish size, and hence age, had a strong influence on use of refuge habitats by juvenile lingcod. It has been shown for a variety of species that juvenile fish use structured habitats over less complex habitats, despite the fact that more open areas may present better foraging opportunities (Mittelbach 1981, Dahlgren and Eggleston 2000). In these cases, the increased threat of predation for smaller individuals alters the overall fitness value of higher growth rates, as heightened risk of being preyed upon outweighs the benefit of growing fast. Apparently, juvenile lingcod show an opposite pattern of habitat use. During daylight hours, when fish are vulnerable to visual predators, small individuals tend to spend less time in structured habitats than older/larger conspecifics, which show a strong structure affinity. This influence of size/age was manifest in experiments examining both the influence of hunger and ambient illumination on refuge use. Small juvenile lingcod may have a higher fitness incentive for fast growth in order to outgrow predators, and are attempting to reach a so-called refuge in size (Paine 1976, Ellis and Gibson 1995, Orth and Montfrans, 2002). This hypothesis states that as animals grow larger, there are fewer predators that can handle them, and the animal may additionally gain an increased ability to escape. In this case, with every foraging opportunity the risk of predation gradually decreases, and the ratio of the mortality rate to growth rate (μ/g) is driven down by the nominator. If there is greater food availability in open habitats as opposed to structurally complex habitats, small fish could achieve faster growth rates by spending less time in structured areas. An alternative explanation for the greater association with structured habitat by larger individuals is that there may simply be a

higher predation risk for larger lingcod in nearshore areas and estuaries where development occurs. Large mammalian predators, in whose stomachs juvenile lingcod have often been found (Cass et al. 1990), may not waste searching and handling time on smaller individuals, if larger fish stand a higher chance of being recognized and consumed. This predatory threat may motivate larger fish to utilize structure more readily than smaller, less vulnerable fish. An example of this was documented by Werner et al. (1983), who demonstrated that bluegill sunfish are relatively inconspicuous to fish predators at early stages of development, and reside in more open areas where prey is abundant. As they grow, and thus become more of a target for larger piscivores, the sunfish take refuge in structured habitat at the expense of diminished food resources.

The difference in refuge use between small and larger juvenile lingcod, and the potential role of differential growth/predator avoidance strategies, is revealed by the hunger experiments. Hunger is undoubtedly a variable that drives foraging behavior, and was shown in this study to differentially affect the extent to which small and large lingcod used refuges. Although both small and large juveniles were observed to spend more time outside of the refuge when hungry, this effect was particularly pronounced in the smaller fish. It is possible that smaller fish, having a higher mass specific metabolic rate, may need to forage more frequently. Krause et al. (2000) found that larger sticklebacks incurred relatively less weight loss per unit time than did younger conspecifics, and thus could metabolically afford to be more cautious, therefore spending longer times in hiding. An alternate explanation presented by Werner and Gilliam (1984) describes situations in which piscivore

morphology constrains prey handling ability at early stages when the primary food source is invertebrates. Specifically, the piscivorous morphology may limit the ability of small fish to compete for planktonic prey. For species that do not metamorphose, the cost of withstanding sub-optimal foraging conditions for a period of time fails to outweigh the large energy expenditure of metamorphosing (Werner & Gilliam 1984). If this were the case, small fish would need to spend more time foraging to make up for their lack of efficiency. Small fish may also still be in the process of learning how best to locate and handle prey. Furthermore, the information primacy hypothesis outlined by Inglis et al. (2001) suggests that the performance of sub-optimal behaviors may relate to an animal's need to continually obtain information in order to assess environmental variability. Within this theoretical framework, if fish are spending more than optimal time outside of a refuge, it could be that they need to spend more time assessing conditions than do older, more experienced fish.

After a certain time spent foraging there is no longer a net benefit, and predation risk imposes a greater cost than failing to find food. On day 5, seven out of eight experimental large fish showed an increase in refuge use, which resulted in a significant difference in habitat use between days 4 and 5. In light of these results, it would seem that after an extended period of foraging without return, large fish no longer risk emerging from a refuge. This theory partially coincides with the optimality model predicting that a fish will be located in a habitat where the ratio of mortality rate to growth rate (μ/g) is minimized (Werner and Gilliam 1984, Gilliam and Fraser 1987, Dahlgren and Eggleston, 2000). If a fish has sampled a habitat and

found food intake to be negligible, it would be beneficial to make fewer forays outside of structure, thus, conserving energy. It should also be noted that food was not available during the experiment, but was introduced prior to each trial. Though this design does not reflect natural conditions, experiments were set up to measure the fish's innate responses to variations in hunger level, and responses were assumed to be independent of food availability.

Diel changes in light level have been shown to affect the behavior of many aquatic species, as associated changes in perception and in being detected occur (Howick and O'Brien 1983, Rountree and Able 1993). Helfman (1981) found that many species varied their behavior in response to changes in light level. Some species such as banded killifish and pumpkinseed sunfish were observed to decrease activity during the night, while the opposite was true in brown bullhead and black crappie, with these responses changing with stage of development in other species (e.g., golden shiner). Habitat associations were also noted to change with the onset of nightly decreases in illumination. In this study, varying light levels at night (i.e., moonlight, starlight, no light) were shown to have no effect on the habitat use of either small or large fish. Furthermore, small lingcod showed no difference in refuge use during the day compared to that at night. Constant use of habitat throughout the 24 hour cycle suggests that predation rate for this size class is either not affecting foraging behavior, or is constant throughout. While metabolic requirements may preclude predator avoidance behavior, it is curious that no adjustment is made during the nocturnal period. Large fish, on the other hand, make large-scale adjustments in behavior, spending significantly less time in refuges at night. These fish are most

likely responding either to reduced predation pressure or increased foraging opportunities. Unfortunately, a continuum of light levels was not tested in this study, so the timing of the switch from high refuge use is unknown. However, there seems to be a slight inverse relationship between time spent outside of habitat and light level at night. Though not statistically significant, this trend suggests that fish are taking advantage of decreased conspicuousness. Sea lions are a dominant predator in Yaquina Bay and are present in large numbers, along with other large mammalian predators along the Pacific Coast. When lingcod become large enough to serve as prey for a larger mammal, they may be forced to take refuge during the day when activity is more risky. Alternatively, a switch to nocturnal foraging could be occurring with development. Helfman et al. (1982) observed that French grunts change from diurnal to nocturnal foraging at an early life history stage, a pattern suggested to be linked to improved visual acuity.

This study, taken as a whole, suggests that a shift occurs not only in juvenile lingcod habitat use, but in associated behavior as well. At an approximate length of between 120-130 mm, post-settlement lingcod abandon open habitats in favor of more structurally complex areas. With this shift come differences in responses to hunger and ambient light level. Small fish respond more quickly to hunger than do larger conspecifics. Additionally, large fish respond markedly to diel changes in light level, a behavioral pattern absent in small lingcod. As more natural history information is gained for this important fisheries species, it becomes increasingly feasible to manage the population as a whole, as opposed to just those fish currently being exploited by the fishery.

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Conclusions

Through laboratory experiments and a field tagging study, it was shown that juvenile lingcod prefer structurally complex habitat over that containing little or no emergent structure. From this identification of lingcod habitat associations, understanding of spatial distribution and habitat requirements for this life history stage is advanced. Further findings suggest an ontological shift in habitat preference, with fish associating more strongly with structure at larger body sizes. Two important factors also play a role in this shift, as hunger and light level interact with body size to affect the extent to which these juvenile fish utilize structured habitat. Hungry fish of both sizes have a tendency to emerge more readily from refuges, with small fish exhibiting a stronger response than do large juveniles. Light level, however, has no effect on small fish, whether refuge use was quantified at varying night light levels or during daytime illumination. Large fish similarly showed no difference in refuge use at any of the varying night light levels, yet showed considerable differences in diurnal versus nocturnal behavior.

Practical implications include habitat conservation and survey design. This study reveals the importance of physical structure for juvenile lingcod, so the disturbance of nearshore structurally complex habitat due to fishing activities (i.e., bottom trawling, dredging) could have implications for recruitment of juveniles into the fishery. Ensuring the presence of intact habitats is therefore an important component of a recovery plan for this species. Also, survey design can benefit from the results of this experiment, as shifting habitats could influence fish counts depending on temporal variation in sampling. Since larger lingcod move sequentially

to deeper, more structured habitats, it is logical to perform sampling methods in the early months of post-settlement development, when juveniles are utilizing more open areas and are thus more easily encountered by SCUBA or trawling methods.

The results of these experiments and their interactions not only expand the knowledge of a little-known stage of lingcod development, but also emphasize the importance of ontological development and body size on fish behavior. With these findings and with results of future habitat studies on juvenile lingcod we can begin to identify specific habitats critical for optimum growth and survival for this important fish species.

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