Introduction

Wolf-eels (Anarrhichthys ocellatus) are a locally abundant bottomfish ranging from San Diego, California (Hubbs and Barnhart 1944) to the Aleutian Islands (Quast and Hall 1972) and westward to the Sea of Okhotsk (Schmidt 1965). We know of no targeted fishery for wolf-eel in Washington, but current state regulations allow a recreational harvest limit of two fish per day in outer coastal waters and the Strait of Juan de Fuca. Adult wolf-eels prey primarily on commercially valuable invertebrates, particularly crabs (Cancer spp.) and sea urchins (Strongylocentrotus spp.), yet the effects of these fisheries on wolf-eel have not been evaluated. The non-consumptive value of wolf-eels to the recreational dive industry in Puget Sound is perhaps many fold times the per-pound value of bottomfish in commercial markets. Favorable weather and water conditions have attracted divers and training groups from several western states for certification and recreational diving opportunities where encounters with species such as wolf-eel are frequently pursued. Few studies have been carried out to describe the life history of this species or factors affecting their survival. Marliave (1987) reported that adult wolf-eels exhibit high mate and site fidelity in captivity, appearing to remain together as long as both partners survive. We conducted monthly scuba surveys at two sites in Puget Sound to determine mate and site fidelity, and changes in seasonal abundance.

Methods

Site Description

The selection of survey sites in Puget Sound was based on previous bottomfish surveys where rocky reef habitat was recorded (Palsson and Pacunski 1997) and where locally known concentrations of wolf-eel have been observed (Figure 1).

Days Island is located approximately 2.5 kilometers South of the Tacoma Narrows sill, on the eastern shore of southern Puget Sound. Total linear distance of rocky habitat is more than 500 m along the western and northern shores. The survey area is centered along the western wall, with rocky habitat continuing both north and south at the depths surveyed. Substrate consists of sand and gravel interspersed with hardpan wall and boulders at depths ranging from six to over twenty meters mean lower low water (M.L.L.W.). Current speeds regularly exceed three knots and may contribute to scouring along the wall that results in erosional events such as mass-wasting. The gravel/sand slope below the wall averages 30/gradient and is interspersed with boulders and cobbles deposited from erosional events.

Sunrise Beach is located approximately 9 km north of the Tacoma Narrows sill, on the western shore of Colvos Passage in central Puget Sound. Total linear distance of rocky habitat is approximately one hundred meters parallel to the shore, at depths from seven to over twenty meters M.L.L.W. The survey area consists of the entire length of rocky habitat. Substrate consists of hardpan and bedrock wall with boulder and
cobble reefs deposited below. Substrate both North and South of Sunrise Beach consists mainly of sand and gravel slope for approximately two kilometers in both directions. Current direction is northward during both flood and ebb exchanges, with maximum speeds of less than two knots.

**Survey Protocol**
Monthly scuba dives were conducted from the research vessel *Caurinus* beginning December 1998. Standardized starting points for survey sites were established using the southern extent of rocky reef habitat at Sunrise Beach and a rebar stake driven into the substrate at the northern end of the survey area at Days Island. Upon entering the water, two divers searched crevices from the shallowest depths where rocky habitat was encountered to a maximum depth of 17 meters M.L.L.W. Occupied and potentially habitable wolf-eel crevices were mapped by depth and linear distance from the survey starting point. Data were recorded on Dura-Copy® plastic paper using aluminum clipboards and pencils by one diver. Den occupancy was recorded for wolf-eel and Pacific giant octopus (*Octopus dofleini*). Videotape or 35 mm photographs of individual wolf-eels were taken *in situ* by the dive partner. The total linear distance surveyed at Sunrise Beach was approximately 100 meters, the full extent of rocky reef habitat. Total linear distance surveyed at Days Island was approximately 300 meters, increasing from an initial distance of 160 meters in January 1999. The increase in surveyed area at Days Island was the result of site familiarization and ability to traverse a greater distance by avoiding areas without rocky reef habitat.

**Tagging Procedure**
Individual wolf-eels were identified using two methods; tagging and photographic recognition. To facilitate tagging, wolf-eels were anaesthetized using a solution of clove oil mixed with equal parts ethanol and ambient seawater (Munday and Wilson 1997). The anaesthetizing solution was delivered into a wolf-eel den via a 60 cc catheter syringe and surgical tubing. Initial response by wolf-eels typically involved retreating deeper into the den, followed by exiting the den as the solution diffused and sedation commenced. Upon exiting the den, the wolf-eel was restrained in a polyester mesh bag to allow tag application while minimizing stress to the fish, potential for escape, and injury to the divers. Visible Implant Elastomer® tags were applied via a 3 cc hypodermic syringe to the anterior portion of the head (Figure 2) in a unique position and color combination for each individual tagged. Tagged fish were identified in subsequent dives using an underwater flashlight fitted with an ultraviolet filtered lens.

![Figure 2. Application of Visible Implant Elastomer tag to a male wolf-eel.](image1)

![Figure 3. Naturally-occurring marks, such as ocelli (spots), were used for photographic identification.](image2)
Photographic Identification
Photographs of V.I.E. tagged wolf-eel were used to determine the validity of visual identification of untagged individuals. Photographs or video footage were taken of as many wolf-eel as possible during survey dives to assess and identify individuals with naturally-occurring marks, consisting of ocelli (spots) and scarring patterns on the anterior and lateral regions of the head (Figure 3). Images were processed using Adobe Photoshop® and Optimas® software, and recognition was based on visual comparisons of monthly photographs for as many individuals as possible. Point morphometry of ocelli were measured relative to a fixed point, usually the center of the eye, for individuals that could not be positively identified by visual comparisons alone.

Data Analysis
Seasonal abundance was compared between spawning season (October through March) and non-spawning season (April through September) for 25 dens initially located in January 1999 and persisting throughout the study period. Chi-square statistics were applied to the totals, where the null hypothesis was no change in seasonal abundance.

Mate fidelity of wolf-eels was determined in two stages. For the first stage, we summed the number of monthly observations of paired individuals made between January 1999 and March 2000. In the second stage, the number of pairs observed in each spawning year were summed and compared to the number of pairs consisting of the same individuals identified in previous years. Chi-square statistics were applied to the number of observations and pairs, respectively, where the null hypothesis was 100% mate fidelity.

Similarly, den fidelity of wolf-eels was determined using two stages of summed observations. As with mate fidelity, the first stage consisted of the number of monthly observations from January 1999 to March 2000 that individual wolf-eels were located in the same den. The second stage consisted of comparing the total number of individuals identified during the study period with the number of those individuals remaining in the same den as which they were originally located. Chi-square statistics were applied to the number of observations and individuals, respectively, where the null hypothesis was 100% den fidelity.

Results
There were no significant differences in seasonal or inter-annual abundance during the study period at both sites. Total monthly counts varied from 9 to 19 wolf-eel for 25 dens observed throughout the study period (Figure 4). Recruitment and immigration rates approximated the number of wolf-eel that disappeared from the study sites for these dens. Total numbers of individual and paired wolf-eel increased during the survey period (Figure 5) because we were able to increase the survey area at Days Island as we became more familiar with the site and locations of rocky reef habitat.
Wolf-eels were typically found in pairs and were generally paired with the same mate as the previous month, although among-site differences were found for pair bonding during the first 15 months (Figure 6). Wolf-eels at Sunrise Beach exhibited significant mate fidelity while those at Days Island did not. However, wolf-eels in our study areas maintained mate fidelity (0.025<p<0.05) when summed between sites. In contrast, the total number of pairs observed with the same mate in subsequent spawning seasons during 1999, 2000, and 2001 indicated a highly significant (0.005<p<0.01) decline in mate fidelity between subsequent spawning seasons (Figure 7).

Wolf-eels in our study sites did not maintain den fidelity during the first 15 months when data were pooled between sites (0.025<p<0.05). As with mate fidelity, a between-site difference was evident; individuals at Sunrise Beach exhibited significant den fidelity while those at Days Island did not (Figure 8).

When data were summed over subsequent spawning seasons, wolf-eels exhibited a highly significant (p<0.001) decline in den fidelity (Figure 9). No wolf-eels were observed to have migrated between survey sites during the study period.
Den use by other rocky reef species was considerable. For 33 dens surveyed 19 were occupied by both wolf-eels and Pacific giant octopus at different times. We also observed lingcod in and adjacent to occupied wolf-eel dens, and three instances of male lingcod guarding nests deposited in or near den entries. Rockfish were also observed cohabiting occupied wolf-eel and octopus dens, as well as inhabiting formerly occupied dens left vacant. Sailfin sculpins (*Nautichthys oculofasciatus*) were common in vacant and occupied wolf-eel dens but were not observed in dens occupied by Pacific giant octopus.

**Discussion**

There were no significant changes in the seasonal or inter-annual abundance of wolf-eels for 25 dens observed throughout the study period. Immigration rates have approximated emigration rates at both sites. There were only four juvenile recruits to the study sites; the remaining immigrants were over 1.5 meters long and had the body form, color pattern, and dentition characteristic of sexually mature wolf-eels (Kanazawa 1952). All juveniles were found in small crevices and were the only inhabitants observed in these dens during the study. A possible explanation for our results is that densities of adult wolf-eels at our study sites are high enough to preclude additional juvenile recruitment. To the contrary, the habitat and dietary needs of juveniles differ from those of adults, which suggests the juvenile recruitment rates we observed may be characteristic for the species in Puget Sound.

Differences in mate fidelity between sites were noted for the first 15 months, with wolf-eels at Days Island exhibiting lower rates than those at Sunrise Beach. Several factors may serve to explain this disparity. Since we are sampling only a portion of the available wolf-eel habitat and population at Days Island, there is a higher likelihood of intraspecific competition with individuals initially residing immediately outside the study area. In contrast, the rocky reef habitat at Sunrise Beach is surveyed in its entirety (To the depth which we are limited while diving) and does not have similar habitat for over two kilometers along the adjacent depth contours. While the home-range of wolf-eels is unknown, the relative isolation of wolf-eels at Sunrise Beach is likely to provide fewer opportunities for conspecific encounters than at Days Island. Sunrise Beach is also a popular recreational dive site. The behavior of wolf-eels at Sunrise Beach has been modified by recreational divers, who have habituated many individuals to hand feeding. The effects of habituating wolf-eels to feeding is likely to include a decrease the frequency and extent of foraging excursions, which in turn may allow them to remain in the same den and with the same mate for extended periods. Wolf-eels at popular recreational dive sites in British Colombia have been reported to remain in the same den for up to 25 years (Bill Weeks, personal communication).

Our results for den fidelity of wolf-eels were similar to those for mate fidelity; we noted a between-site difference for den fidelity during the first 15 months. The factors attributable to our results for mate fidelity may also explain the disparity between our observations of den fidelity. Additional factors have also contributed to our results. We initially assumed the habitat at our survey sites would remain stable in time. To the contrary, we noted the appearance of new wolf-eel and octopus dens formed by the active excavation of sand and gravel from under rocks and hardpan by their occupants at both sites. Conversely, we also noted that some dens left vacant by wolf-eel and octopus for more than three months were obscured by sand and gravel filling them in. Geomorphic processes also caused changes to habitat at Days Island. We have documented three mass-wasting events that have obliterated five dens along 40 meters of the wall, while creating new potential den sites in the wall and rocky reefs deposited below. These mass-wasting events appear to be the result of natural decomposition of hardpan exacerbated by current scouring on relatively soft underlying layers of glacial deposits. Since these events, we have noted the establishment of two Pacific giant octopus and one mating pair of wolf-eels among newly exposed wall and rocky reefs. We conducted survey dives on February 20 and March 21, 2001; one week prior to and three weeks after a 6.8 magnitude earthquake epicentered 17 kilometers southwest of Days Island. We observed little habitat alteration at our survey sites and no loss of wolf-eels or octopus at dens surveyed.

We observed a considerable decline in mate and den fidelity through subsequent spawning seasons at both survey sites. One of the original eight pairs remained together and five of 21 individuals remained in the same den throughout the duration of the study. Our results contrast with mate and site fidelity resulting from captive observations (Marliave 1987) and the generally accepted belief that wolf-eels mate for life (Love 1996). The adult life history and reproductive strategy of wolf-eels in our study sites is different than
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previously described. We suggest our findings represent an empirical life history description for this species, but cannot dismiss the effects of other influences in the natural environment.

Factors that may contribute to a decline in mate and site fidelity of wolf-eels include the harvest management of competing and prey-base species. Pacific giant octopuses have been observed displacing wolf-eels from their dens (Marliave 1987), and we have observed evidence of such occurrences at our study sites. Octopuses are harvestable by recreational fishers in Puget Sound, but wolf-eels are not. This management regime may result in an increase in the carrying capacity of wolf-eel populations and reduced inter-specific competition for food and habitat by Pacific giant octopuses. It follows that such an increase in wolf-eel populations would result in an increase in conspecific competition for mates and shelter. Reports of over 25 Pacific giant octopus harvested near the study area at Days Island in a single day have been substantiated (Dr. Roland Anderson, personal communication). Total numbers of Pacific giant octopus observed in the study site varied from zero to six during our monthly surveys.

Wolf-eels in Puget Sound prey primarily on crabs and urchins that are subject to recreational and commercial fisheries. Episodic depletion of prey species in and near the study sites may result in an increase in the frequency, distance, and duration of foraging excursions or reduce the carrying capacity of wolf-eel populations at the study sites. In either case, prey-base depletion may result in an increase in den and mate abandonment or territorial displacement among wolf-eels. The survey area at Sunrise Beach was declared a marine protected area in April 2000, closed to harvest of sub-tidal marine life except salmon by trolling. Closure of this area to harvest was followed closely by the breakdown of mate and site fidelity of wolf-eels previously observed. It is unclear whether or not regulatory changes contributed to our observations, as the conclusion of wolf-eel spawning season was coincident with this period.

Symbiotic relationships with other species observed in and proximal to wolf-eel dens have not been described. The crevices excavated and maintained by wolf-eels and Pacific giant octopus benefit several rocky reef fishes. Sailfin sculpin were common in occupied wolf-eel dens, and may exist commensally as a consumer of ectoparasites or food waste of wolf-eels. Rockfish were common in occupied and vacant dens. Lingcod were frequently observed near occupied dens and cohabiting with wolf-eels in larger dens. The instances of lingcod spawning at the entry to occupied wolf-eel dens suggest a competitive or commensal relationship exists between them and wolf-eels. In all three instances of male lingcod guarding nest, the wolf-eels occupying the dens were nest-guarding pairs.

Acknowledgements
The authors would like to thank Jim Beam, Paul Clark, and Don Velasquez for their piloting skills and for providing a safe vessel from which to conduct dive operations. Dr. Ray Buckley provided instruction in the application and detection of Visible Implant Elastomer tags. Project funding was provided in part by the federal Sport Fish Restoration Act, project # F110-R.

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