Abstract—Most shallow-dwelling tropical marine fishes exhibit different activity patterns during the day and night but show similar transition behavior among habitat sites despite the dissimilar assemblages of the species. However, changes in species abundance, distribution, and activity patterns have only rarely been examined in temperate deepwater habitats during the day and night, where day-to-night differences in light intensity are extremely slight. Direct-observation surveys were conducted over several depths and habitat types on Heceta Bank, the largest rocky bank off the Oregon coast. Day and night fish community composition, relative density, and activity levels were compared by using videotape footage from a remotely operated vehicle (ROV) operated along paired transects. Habitat-specific abundance and activity were determined for 31 taxa or groups. General patterns observed were similar to shallow temperate day and night studies, with an overall increase in the abundance and activity of fishes during the day than at night, particularly in shallower cobble, boulder, and rock ridge habitats. Smaller schooling rockfishes (*Sebastes* spp.) were more abundant and active in day than in night transects, and sharpchin (*S. zacentrus*) and harlequin (*S. variegatus*) rockfish were significantly more abundant in night transects. Most taxa, however, did not exhibit distinct diurnal or nocturnal activity patterns. Rosethorn rockfish (*S. helvomaculatus*) and hagfishes (*Eptatretus* spp.) showed the clearest diurnal and nocturnal activity patterns, respectively. Because day and night distributions and activity patterns in demersal fishes are likely to influence both catchability and observability in bottom trawl and direct-count *in situ* surveys, the patterns observed in the current study should be considered for survey design and interpretation.

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Day and night abundance, distribution, and activity patterns of demersal fishes on Heceta Bank, Oregon

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For surveys of groundfish, swept-area trawls are generally conducted and direct-counts from video cameras are recorded during daylight hours (Gunderson, 1993; Adams et al., 1995; Yoklavich et al., 2000; Wakefield et al., 2005). If activity patterns vary among species during the day versus the night, conclusions about relative abundance, community composition, and habitat affiliations could be incomplete or biased. It is not known whether diel activity and abundance patterns in fishes commonly found in shallow temperate and tropical areas are similar for fishes inhabiting deeper temperate areas along the west coast of North America, where diel changes in light levels are subtle. We used a repeat-transect (the transect was followed once during the day and again at night) visual sampling survey to examine differences in fish abundance, distribution, and behavior on Heceta Bank, a temperate reef and ridge ecosystem off the central coast of Oregon.

Diel distributions and activity patterns in fishes have been well studied in tropical areas, and these studies have shown that most fishes exhibit distinct diel behavioral patterns (Collette and Talbot, 1972; Hobson, 1972; Helfman, 1978). Generally, two-thirds of fishes are diurnal, one-third are nocturnal, and a marked change in the vertical distribution of fishes occurs between day and night (Helfman, 1978). Most fishes rigidly follow a diurnal or nocturnal activity pattern, exhibiting very low activity in shelter-providing areas and high activity during feeding. Rotation between ecological niches at daytime and at night, such as the broad replacement of diurnal planktivores with predators during the night, proceeds in predictable patterns (Hobson, 1972). Some of the largest schools encountered by day in tropical waters are nonfeeding, resting schools of nocturnal fishes, and many diurnal fishes actively school in the water column by day and then rest individually at night (Hobson and Chess, 1973; Parrish, 1992).

Although not as well studied, diel shifts in fish communities and behavioral patterns in shallow temperate habitats are less distinct than those observed in warmer water regions (Hobson et al., 1981). Deepwater habitats with low light penetration would therefore be expected to show only subtle changes in species composition, densities, or activities during night hours. Nevertheless, diel distributions and activity patterns of some species of fish have been observed in temperate areas at substantial depths. On Stonewall Bank, Oregon, *in situ* direct observations in shelf waters (41–70 m) revealed that species composition changed little from day to night, but the abundance of some fishes decreased dramatically (Hixon and Tissot[1]). Specifically, juvenile rockfishes (*Sebastes* spp.) and rosethorn rockfishes (*S. helvomaculatus*) showed much greater abundance during the day, and spotted ratfish (*Hydrolagus colliei*) and widow rockfish (*S. entomelas*) were significantly more abundant at night. Within Pribilof Canyon (181 to 240 m) in the Bering Sea, Pacific ocean perch (*S. alutus*) actively fed on euphausiids just above sea-whip "forests" during the day and were observed to be less active within the sea-whip habitat at night (Brodeur, 2001). In deeper rocky bank areas with lower levels of ambient light, it is not known whether an overall change from high to low activity from day to night exists, as is observed in shallow temperate fish communities (Ebeling and Bray, 1976; Hobson and Chess, 1976; Moulton, 1977).

We hypothesized there would be differences in the day and night assemblages of fishes in deep temperate waters, but that the patterns and changes in abundance and activity would be less distinct than those observed in tropical and shallow temperate fish communities. Given its diverse range of habitats and water depths, Heceta Bank is an ideal location for studying day-night patterns of demersal fishes among different depths and habitat types.

Materials and methods

Study area

Heceta Bank is one of the largest of all submarine, rocky banks off the west coast of the United States, located approximately 60 km off the central Oregon coast, extending 50 km north to south (Fig. 1). The bank has been a primary focus of direct-observation studies of groundfishes, invertebrates, and habitat since the late 1980s (Pearcy et al., 1989; Stein et al., 1992; Wakefield et al., 2005; Whitmire et al., 2007; Hixon and Tissot[1]; Hixon et al.[2]). This bank comprises a wide range of benthic habitats from rock ridge and boulder to sand, and mud and extends from 70 m depth at the top of the bank to >500 m in water depth on its flanks (Figs. 1 and 2). The bank has been generally characterized as having three major habitat-depth profiles: 1) shallow rock ridge and boulder habitat from 70 to 100 m; 2) boulder and cobble habitat at mid-depth from 100 to 150 m; and 3) mud habitat in greater than 150 m of water depth (Hixon et al.[2]). Some portions of the bank show great habitat variability (Hixon and Tissot[1]).

Light levels

Ambient light levels on Heceta Bank were measured two weeks before the current study by the Plankton/Bio-Optics group at Oregon State University during a Global Ocean Ecosystems Dynamics (GLOBEC) study of meso- and fine-scale physical and biological fields (Whitmire and Cowles, unpubl. data[3]). In order to characterize the underwater light environment over the bank, the OSU group used *in situ* total absorption coefficient data. Absorption measurements (a_t[488 nm]) were collected with a dual-path absorption and attenuation meter (ac-9; WET Labs, Inc., Philomath, OR) that was mounted on a SeaSOAR, a towed undulating vehicle used to deploy a wide range of oceanographic monitoring equipment, and towed in an undulating fashion along east to west track lines over the bank during daylight hours on 5 and 6 June 2000. One percent light levels (in relation to surface light values), a commonly used oceanographic parameter for comparing light attenuation, were reached at approximately 20 m in high chlorophyll coastal waters (~3 to 6 mg/m), and at approximately 50 m in waters at the western end of the east–west transects. This empirical approach for light attenuation agreed well with theoretical relationships between depth and light attenuation as applied to coastal and offshore waters within the California Current (Morel, 1988; Barnard et al., 1999).

Survey transects

From 19 to 26 June 2000, an interdisciplinary group of scientists used the remotely operated vehicle (ROV) *ROPOS* (Remote Operated Platform for Ocean Science), managed and operated by the Canadian Scientific Submersible Facility (CSSF), to revisit five stations on Heceta Bank that were established in the 1980s (Figs. 1 and 2) (Pearcy et al., 1989; Stein et al., 1992; Hixon and Tissot[1]; Hixon et al.[2]) and to explore new sites on the bank. At each of five historical stations fish assemblages were compared between day and night.

The ROV *ROPOS* is well suited for deepwater demersal fish surveys. *ROPOS* is a 30-horsepower electrohydraulic ROV equipped with two video systems, a

[1] Hixon, M. A., and B. N. Tissot. 1992. Fish assemblages of rocky banks of the Pacific Northwest. Final Report supplement, OCS Study 91-0025, 128 p. U.S. Minerals Management Service, Camarillo, CA 93010.

[2] Hixon, M. A., B. N. Tissot, and W. G. Pearcy. 1991. Fish assemblages of rocky banks of the Pacific northwest, Heceta, Coquille, and Daisy Banks. OCS Study MMS 91-0052, 410 p. U.S.D.I. Minerals Management Service, 770 Paseo Camarillo, 2nd Floor, Camarillo, CA 93010.

[3] Whitmire, A. L., and T. J. Cowles. 2008. College of Oceanic and Atmospheric Sciences, Oregon State Univ., Corvallis, OR 97331.

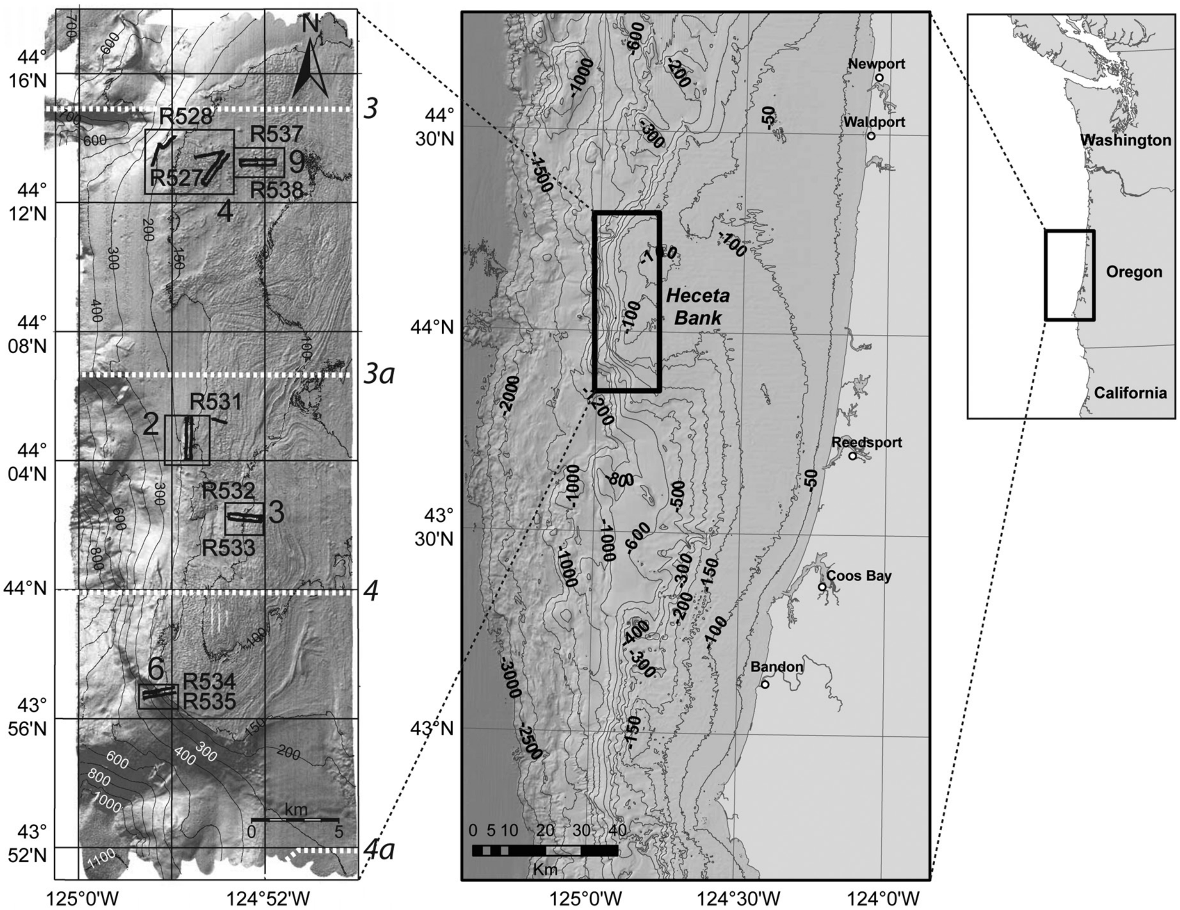

Figure 1

Location and depth (in meters) of the study area, Heceta Bank off the Oregon coast, and the area mapped with a multibeam sonar system in 1998 (MBARI 2201; modified from Whitmire et al., 2008). The leftmost panel shows the location of the ROV transects for areas surveyed during day and night periods for each station (boxes) on Heceta Bank, Oregon. Global Ocean Ecosystem Dynamics (GLOBEC) track lines for light levels (lines 3, 3a, 4, and 4a) are shown in white dashed lines and are labeled to the right of the map. Depth contours are given in meters.

broadcast-quality Sony DXC 950 three-chip color video camera (used for fish and habitat video analysis), a wide-angle low light black and white video camera, an obstacle avoidance sonar, a compass, three arc lights (250 W), four halogen lights with adjustable intensity (250 W), and a 10-hp cage with a separate light and video system (Wallace and Shepherd, 2003). One pair of scaling lasers (10-cm scale) mounted in parallel on the color video camera provided scale in the field of view of the video image for estimating the width of transects and the size of fishes and features on the seafloor. The distance surveyed was determined from smoothed navigation of tracklines obtained from ultra-short baseline tracking. Real-time audio commentary of habitat type and fish identification was overlaid on the videotape. The technical side of the ROV dive transects was managed and conducted by two four-member CSSF teams that worked in alternating 12-hour watches. Parallel interdisciplinary science teams worked in tandem with the ROV group to direct the scientific operations and ensure consistency in sampling effort.

Day and night complements were completed outside the two-hour twilight periods of dawn (0436 to 0636 PST) and dusk (2006 to 2206 PST) to avoid possible biases due to changes in the behavior of fishes during crepuscular periods (Yoklavich et al., 2000). Only daytime fish transects that overlapped geographically with, or were in close proximity to, corresponding night fish transects (stations 2, 3, 4, 6, and 9) were used in this analysis. Station 4 contained a night transect located approximately 1 nautical mile (nmi) away from the day transect but in a comparable depth range and over similar habitat, and therefore it was included in the analysis.

A total area of 5.5 hectares along a combined total transect distance of 40.9 km was surveyed during 45.6 hours (Fig. 2). Stations varied in habitat composition and depth (Fig. 2). Shallow areas (70–100 m) were dominated

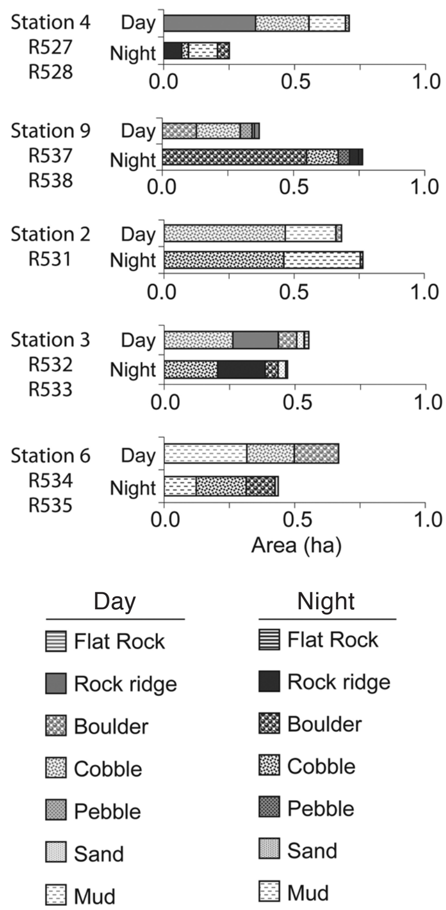

Figure 2

Bar graphs indicate the area and relative composition (in hectares) of each primary habitat surveyed along transects during day and night periods for each station on Heceta Bank, OR. ROV dives associated with each station are identified by an "R" followed by the dive number.

by rock ridge and boulder, mid-depth by cobble, and deeper areas by mud habitat with isolated patches of cobble and boulder. Rock ridge, boulder, cobble, and mud composed the four most dominant primary habitat types.

Videotape analysis

Videotape collected along all transects was analyzed for fish and habitat identification. Sunset, dawn, dusk, and nautical twilight times (Pacific daylight savings time) were derived from the U.S. Naval Observatory website (http://www.usno.navy.mil/, accessed June 2000) and calculated for the day of each dive by using the specific longitude and latitude coordinates (degrees and minutes) for each station.

Transects were subdivided into habitat patches**,** based on primary habitat types observed on the videotapes. Seafloor habitats were classified into seven standardized categories (Hixon and Tissot[1]; Stein et al., 1992): rock ridge (high relief where vertical rock was found to be >3.0 m); flat rock (low relief where vertical rock was found to be ≤3.0 m); boulder (300–25.6 cm rock); cobble (25.6–6.4 cm rock); pebble (6.4–0.2 cm rock); sand (2.0–0.06 mm); and mud (<0.06 mm). Only the primary habitat (≥50% of the seafloor) in the field of view was used in our analysis. The length of each habitat patch was determined by using the geographic position recorded at the start and end of each patch. With the scaling lasers, the width of each transect was estimated by selecting random frames every minute during each transect, measuring the width of these lasers on the video monitor, and extrapolating to the field of view. Transect width ranged from 1.3 to 2.1 meters. The area of each patch was determined by multiplying the patch length by the average patch width. Each transect consisted of a few to many habitat patches, depending on the variability of substrate.

Videotape analysis was performed by two technicians simultaneously in order to confirm fish identifications, counts, and fish activity. All fishes were identified to the lowest practical taxonomic unit (usually to species) and total fish length was estimated to the nearest 5 cm. For fish that could be identified to a taxonomic group, but not species, a generalized abbreviation was used (e.g., FF for unidentified flatfish), and in cases where the fish observed was one of two species, a new abbreviation was created to accommodate this situation. Fish were counted at the point where they passed through the level of the scaling lasers and were assigned a GMT time that became a permanent time and geographic reference point in a database. A single anatomical feature (eye) was used to determine whether or not a fish was considered within the transect to prevent underestimating transect width and overestimating abundance. We restricted our analysis to 31 identified species or taxonomic groups that were seen frequently enough to represent ≥0.1% of the total day and night fish density (number of fish per hectare). Exceptions to this rule were the inclusion of three rarely seen species: darkblotched rockfish (*S. crameri*), because this is an important commercial species; kelp greenling (*Hexagrammos decagrammus*); and bigfin eelpout (*Lycodes cortezianus*), because the day-night activity patterns of the latter two have been studied in shallow temperate areas (Moulton, 1977). Some categories of multiple taxa were created, such as "pygmy-Puget Sound rockfish complex" (*S. wilsoni* and *S. emphaeus*), where it was impossible to identify every individual in aggregations. Another common category was "unidentified rockfish," where it was not possible to classify a rockfish to species conclusively. "Unidentified juvenile rockfish" (abbreviation RRF) were categorized by size (<10 cm long), not by morphological features, because video resolution and inherent difficulty of *in situ* identification of young-of-the-year rockfishes precludes determinations at the level of species. Hagfishes (*Eptatretus* spp.) were not identified to species, but on the basis of depth of occurrence, the species observed was probably the Pacific hagfish (*Eptatretus stoutii*) (Barss, 1993).

All fish in the videotapes were counted and assigned an activity category ("active" or "inactive"). The two categories were developed in order to analyze the videotape efficiently and quantitatively, and all fishes were placed into one of the two categories. Active fish were off the bottom (or temporarily in contact with the substrate), and inactive fish were in contact with the substrate (e.g., in contact with the seafloor or were occupying crevices). All flatfish were excluded from the activity analysis because of our definition of "activity." We assumed that fish were counted only once and that the submersible did not influence the activity of fishes. When the ROV clearly affected the behavior of a fish, the activity of the fish observed before the ROV interruption was used in analyses.

Data analysis

Relative abundance was determined for each taxon on a broad scale over all stations (2, 3, 4, 6, and 9) and all habitat types, and on a finer scale within each of the four primary habitat types (rock ridge, boulder, cobble, and mud) over all stations. Fish abundance was first normalized by dividing the abundance for a given taxon in a habitat patch by the area swept in that habitat patch. Relative abundance in a daytime habitat patch was matched up with a relative abundance in a nighttime habitat patch of closest geographic proximity for a given taxon. These pairs were used to create the ranks in a Wilcoxon signed-rank test. For all taxa, 402 habitat patches were included in the analysis, and an average of 59 habitat patches were compared for each taxon (many taxa were in the same habitat patch). This enabled us to estimate if relative abundance trends were consistent at both scales. For the finer scale, some habitat types (e.g., flat rock) did not contain sufficient relative abundance for analysis.

The Wilcoxon signed-rank test was performed with S-Plus, vers. 3.2 software (TIBCO Software Inc., Palo Alto, CA) to determine significant differences in the activity of fishes during day and night (Ramsey and Schafer, 2002). This test involved estimating the percentage of fish active and inactive within each habitat patch for each taxon (raw abundance was used). These day and night pairs (percentage of fish active and percentage of fish inactive) were used to create the ranks in the test for a given taxon over primary habitat types. A total of 398 habitat patches were analyzed for all taxa, with an average of 64 habitat patches compared for each taxon.

We also used nonmetric multidimensional scaling (NMS) to examine associations between day and night fish abundance with depth and with primary habitat (McCune and Grace, 2002). PC-ORD software, vers. 5.0 (MjM Software, Gleneden Beach, OR), was used with a Monte Carlo test and Sørensen distance measure, starting with random configurations (Mather, 1976). We restricted the NMS to taxa that showed significantly greater abundance during day or night in the Wilcoxon signed-rank test ($P<0.05$), and to those that showed a strong correlation (Pearson and Kendall correlation) with depth ($R<-0.5$ or >0.5 on the second axis) during trial NMS runs with all 31 taxa. A total of 11 taxa met these criteria. The final species (taxa) matrix included columns of log-transformed abundance and rows of sample units grouped by primary habitat for each dive during day and night (e.g., boulder-night-R534). All primary habitat types were used because the NMS determines correlation strength along an environmental gradient and does not require paired plots as in the Wilcoxon signed-rank test. The final environmental matrix included two quantitative variable columns: primary habitat types (flat rock, rock ridge, boulder, cobble, pebble, sand, and mud) and average depth (meters). Sample units greater than 3.0 standard deviations were excluded from analysis. The final ordination had 166 iterations and 15 runs. This test enabled us to determine if marked differences in fish abundance were associated with depth and primary habitat, and whether taxa showing significantly greater abundance during day or night were distributed similarly on the bank.

Results

A total of 29,787 individual fish were counted on the ROV transect videotapes. During the day, we observed an average of 207 fishes per hectare, and at night we observed a lower average of 141 fishes per hectare. Fish taxa in greatest abundance were from the genus *Sebastes*. Dominant taxa (pygmy and Puget Sound rockfish, and unidentified juvenile rockfish) showed the largest differences in relative abundance between day and night (Fig. 3). Across all stations and primary habitat types, and within at least one primary habitat type, eight taxa showed significantly greater abundance during the day ($P<0.05$) and five taxa exhibited significantly greater abundance during the night ($P<0.05$, Table 1 , Fig. 3). Three taxa were found to be significantly greater in abundance during day (kelp greenling and unidentified mottled poacher [Agonidae]) and night (redstripe rockfish [*S. proriger*]) only in specific primary habitat types (Table 1). Several taxa showed apparent differences in abundance, but sample sizes were too small for statistical significance in the paired Wilcoxon signed rank test (e.g., kelp greenling). Harlequin rockfish (*S. variegatus*) was the only species we regularly encountered exclusively at night (darkblotched rockfish were rare but were also seen only at night), whereas kelp greenling were encountered only during the day at shallow depths.

NMS analysis of distribution

The NMS analysis showed significant correlations ($P=0.03$) among taxa, depth, primary habitat, and day and night (Fig. 4). The ordination explained 78% of the variation with an acceptable stress value (a lower value

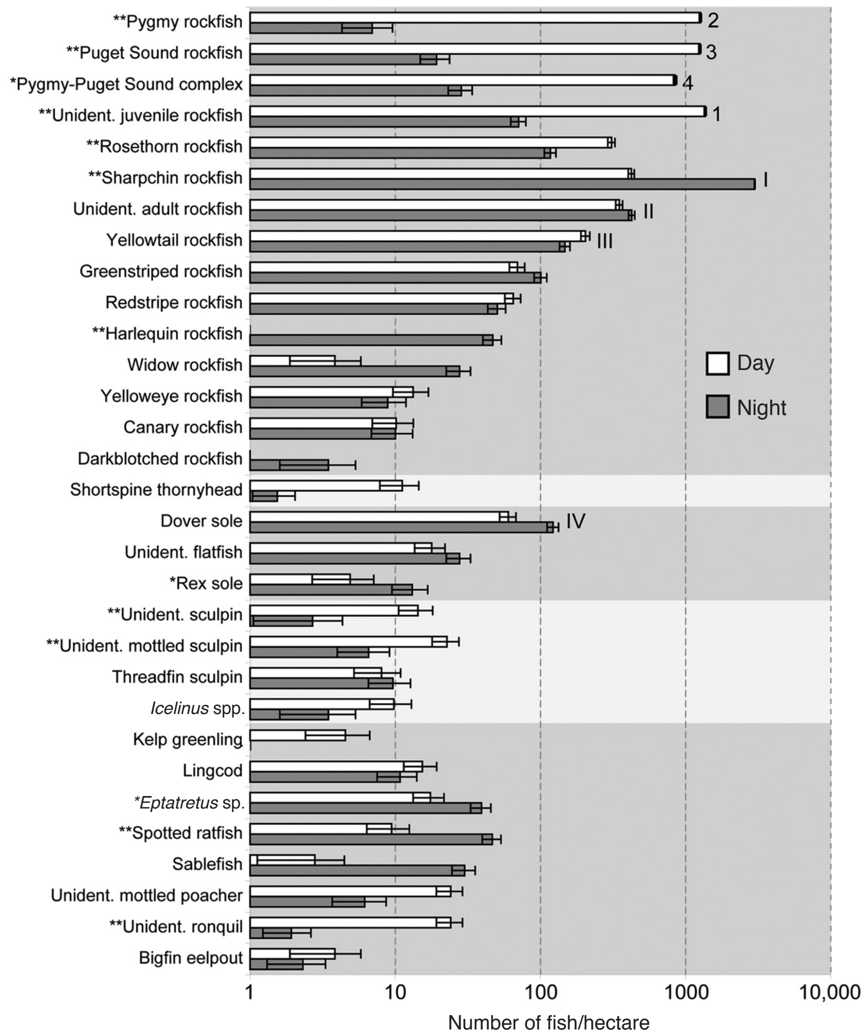

Figure 3

Total abundance (number of fish per hectare) of fish taxa as determined from the ROV during night and daytime transects over all habitat types. Wilcoxon signed-rank test was used to compare day and night abundance across stations and primary habitat types (*$P<0.05$, ** $P<0.01$). Arabic numerals indicate the most dominant taxa during day, and Roman numerals indicate the most dominant taxa during night. Error bars indicate standard error of the abundance for each taxon. White bars represent day abundance and gray bars represent night abundance for the following species groups: *Sebastes*, *Sebastolobus*, flatfishes, Cottidae, and other fish. Scientific names for all taxa include from top to bottom: pygmy rockfish (*S. wilsoni*), Puget Sound rockfish (*S. emphaeus*), unidentified juvenile rockfish less than 10 cm long (*Sebastes* spp.), rosethorn rockfish (*S. helvomaculatus*), sharpchin rockfish (*S. zacentrus*), unidentified adult rockfish (*Sebastes* spp.), yellowtail rockfish (*S. flavidus*), greenstriped rockfish (*S. elongatus*), redstripe rockfish (*S. proriger*), harlequin rockfish (*S. variegatus*), widow rockfish (*S. entomelas*), yelloweye rockfish (*S. ruberrimus*), canary rockfish (*S. pinniger*), darkblotched rockfish (*S. crameri*), shortspine thornyhead (*S. alascanus*), Dover sole (*Microstomus pacificus*), unidentified flatfish (Pleuronectidae), rex sole (*Glyptocephalus zachirus*), unidentified sculpin (Cottidae), unidentified mottled sculpin (Cottidae), threadfin sculpin (*Icelinus filamentosus*), *Icelinus* spp., kelp greenling (*Hexagrammos decagrammus*), lingcod (*Ophiodon elongatus*), unidentified hagfishes (*Eptatretus* spp.), spotted ratfish (*Hydrolagus colliei*), sablefish (*Anoplopoma fimbria*), unidentified mottled poacher (Agonidae), unidentified ronquil (Bathymasteridae), and bigfin eelpout (*Lycodes cortezianus*). Alternate shading of the background represents general taxonomic groups.

Table 1

Fish taxa exhibiting significantly greater relative abundance (number of fish per hectare) across all stations over primary habitat types at Heceta Bank, OR, (rock ridge, boulder, cobble, and mud) during daytime or nighttime. Wilcoxon signed-rank test was used (*$P<0.05$, **$P<0.01$) to compare day and night relative abundance between habitat patches in closest geographic proximity within primary habitat types over all stations. Taxa are listed in order of relative abundance from top to bottom; primary habitat is listed in decreasing order of size from left to right, and numbers in parentheses are relative abundance during day or night.

Taxon	Rock ridge	Boulder	Cobble	Mud
Significantly more abundant during day				
unidentified juvenile rockfish (*Sebastes* spp.)	(1498)**	(2123)*	(632)**	(150)*
Puget Sound rockfish (*S. emphaeus*)			(2235)**	(421)**
pygmy rockfish (*S. wilsoni*)	(4878)**	(46)*	(634)**	
pygmy-Puget Sound complex (*S. wilsoni* and *S. emphaeus*)	(3240)*			
rosethorn rockfish (*S. helvomaculatus*)	(249)**		(291)*	(124)*
unidentified ronquil (Bathymasteridae)	(16)**			(43)*
unidentified mottled sculpin (Cottidae)			(30)**	
unidentified sculpin (Cottidae)			(12)*	(28)**
unidentified mottled poacher (Agonidae)			(12)*	
kelp greenling (*Hexagrammos decagrammus*)		(6)*		
Significantly more abundant during night				
sharpchin rockfish (*S. zacentrus*)	(460)**	(1134)*	(5603)*	(1656)*
redstripe rockfish (*S. proriger*)	(90)*			
harlequin rockfish (*S. variegatus*)			(103)**	
spotted ratfish (*Hydrolagus colliei*)			(75)*	(56)*
unidentified hagfishes (*Eptatretus* spp.)			(45)*	(64)*
rex sole (*Glyptocephalus zachirus*)				(69)*

denotes a better "fit" of data) of 20.5 for three axes. After a +115° rotation, the first axis showed correlation with day (right side) and night (left side) sample units, explaining 22% of the variation in the data and revealed a mean stress of 49.8. The second axis explained an additional 30% of the variation in the data and showed a negative correlation with depth (Pearson's r=0.141) and a mean stress of 29.1. The second axis also showed a positive correlation with substrate, and larger-size primary habitat was found in the first and second quadrants of the graph and smaller-size primary habitat in the third and fourth quadrant. The third axis improved the cumulative coefficient of determination, r^2, to 0.777 with little additional stress; this axis enabled us to rotate the ordination in three dimensions to distinguish habitat and species and showed good correlations with the day-night and habitat-depth axes, but is not easily plotted. Higher dimensions showed little improvement in model fit.

Taxa more abundant during the day (rosethorn rockfish, pygmy rockfish, pygmy-Puget Sound rockfish complex, kelp greenling, and unidentified juvenile rockfish) showed a positive correlation along axes one and two and appear in the upper right quadrant of Figure 4. Puget Sound rockfish showed a correlation with the day-night axis, but this species was associated with greater depth and smaller-size substrate as primary habitat when compared to the other taxa that were more abundant during the day; this taxon appears in the lower right quadrant. Thus, this dominant day assemblage was observed mainly at shallow- to mid-depths over medium to large-size substrata. Taxa showing greater abundance during the night (spotted ratfish [*Hydrolagus colliei*], hagfishes, rex sole [*Glyptocephalus zachirus*], sharpchin rockfish [*S. zacentrus*], and harlequin rockfish) showed a negative correlation along axes one and two. Thus, the dominant night assemblage was generally over deeper areas of medium- to small-size substrata of cobble and mud.

Day and night species assemblages

During the day within all stations, large densities of mostly small-size rockfish taxa were primarily found over shallow rock ridge, boulder, and cobble substrata (Table 1, Figs. 3 and 4). The four most dominant day taxa (both active and inactive) were pygmy rockfish, Puget Sound rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish. Yellowtail rockfish (*S. flavidus*) were also an important component of the daytime assemblage, albeit less abundant and less dominant during night. Many of these taxa showed significantly greater abundance and activity over medium- to large-size habitat (cobble, boulder, and rock ridge) (Tables 1 and 2). Rosethorn rockfish showed the clearest diurnal pattern of all species (Table 2). Small rockfishes and yellowtail rockfish were more active during the day but did not exhibit clear inactivity during the night.

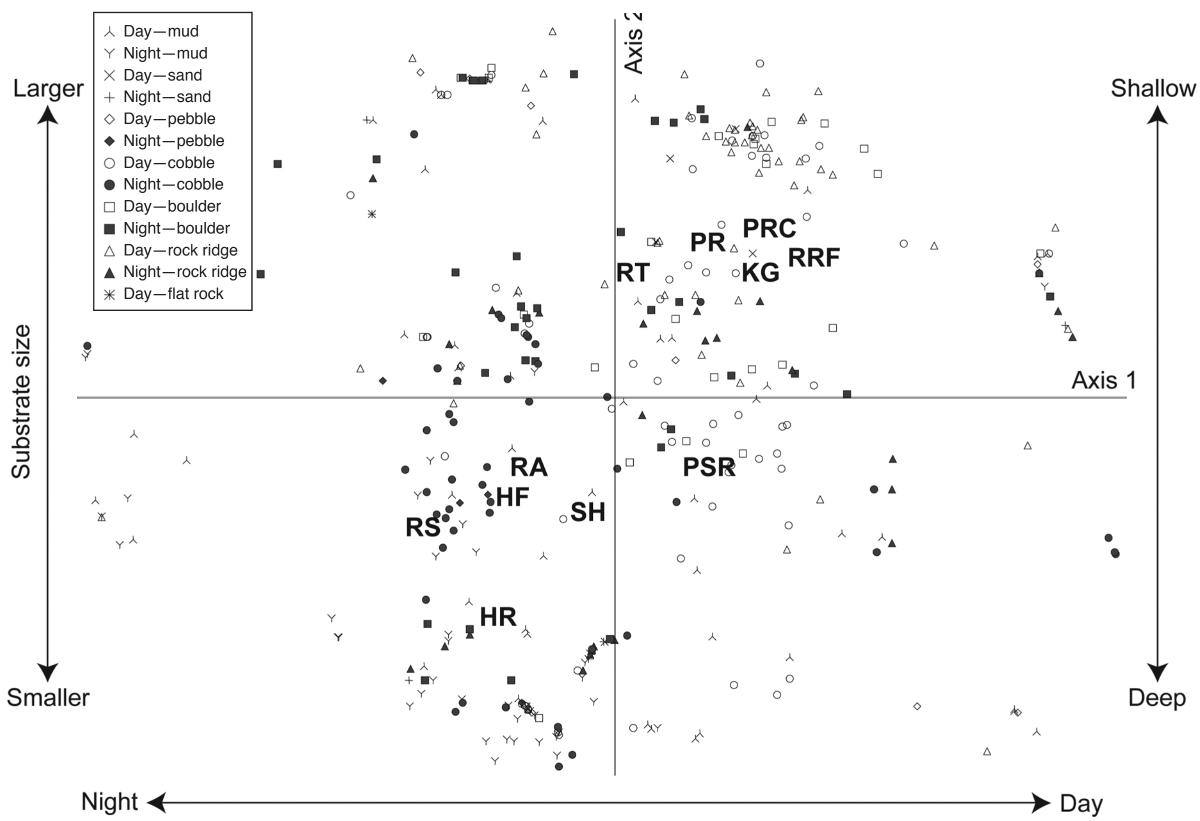

Figure 4

Nonmetric multidimensional scaling (NMS) ordination showing association between 11 taxa and habitat patches (different symbols) from all stations (2, 3, 4, 6, and 9). Taxa codes are: HF (hagfishes, *Eptatretus* spp.), HR (harlequin rockfish, *S. variegatus*), KG (kelp greenling, *Hexagrammos decagrammus*), PR (pygmy rockfish, *S. wilsoni*), PRC (pygmy-Puget Sound complex, *S. wilsoni* and *S. emphaeus*), PSR (Puget Sound rockfish, *S. emphaeus*), RA (spotted ratfish, *Hydrolagus colliei*), RS (rex sole, *Glyptocephalus zachirus*), RT (rosethorn rockfish, *S. helvomaculatus*), RRF (unidentified juvenile rockfish, *Sebastes* spp.), and SH (sharpchin rockfish, *S. zacentrus*). Environmental variables include the quantitative variable of depth (increasing depth from top to bottom), and the categorical variables (shape of symbols) of day, night, and habitat.

When compared to the dominant day assemblage, the night assemblage exhibited lower overall densities and consisted of less active, larger-size fish of fewer taxa, many of which were also seen during the daylight hours (Tables 1 and 2, Fig. 3). Dominant night taxa were sharpchin rockfish, yellowtail rockfish, Dover sole (*Microstomus pacificus*), and greenstriped rockfish (*S. elongatus*). Of the dominant night assemblage, sharpchin rockfish comprised over half of the fish encountered at night (Fig. 3) and was one of the only taxa that showed significantly greater abundance during the night ($P<0.05$) in most primary habitat types (Table 1). Hagfishes and spotted ratfish were significantly greater in abundance and activity during the night ($P<0.05$), and widow rockfish showed significantly greater activity during the night ($P<0.05$), despite being rarely observed (Table 2). Hagfishes were the only taxa that exhibited a distinct nocturnal activity pattern ($P<0.05$).

Discussion

The relative composition of fish taxa over all depths and habitat types on Heceta Bank did not show a broad replacement from day to night, as observed in shallow tropical areas. However, there were consistent patterns of abundance and activity that were species-, depth-, and habitat-specific. There was a considerable day-night change in the abundance of the four most dominant day taxa (pygmy rockfish, Puget Sound rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish) over shallower areas of rock ridge and boulder habitat. Active, small- to medium-size fish taxa tended to aggregate around shallow medium- to large-size habitat features during the day, and larger-size night taxa (sharpchin rockfish, yellowtail rockfish, Dover sole, and greenstriped rockfish) tended to aggregate around these features at night. Rosethorn rockfish

Table 2

Fish taxa (raw counts) exhibiting a significant difference in the percentage of fish found to be active and inactive during day and night within similar primary habitat types (rock ridge, boulder, cobble, and mud) over all stations at Heceta Bank, OR. Values represent the percentage of fish found to be active or inactive over each substrate type, and values in parentheses indicate *n* for each comparison. Wilcoxon signed-rank test was used (**P*<0.05, ***P*<0.01, not significant [ns], *P*>0.05). Taxa are listed in order of highest abundance (number of fish per hectare) within each category.

Taxon	Primary habitat	Day active fish	Day inactive fish	Night active fish	Night inactive fish
Diurnal					
rosethorn rockfish (*S. helvomaculatus*)	rock ridge	76% (246)**			ns
	boulder	74% (243)**			85% (123)**
	cobble	66% (405)*			92% (143)**
	mud	ns			93% (47)**
Nocturnal					
Eptatretus spp.	cobble		87% (23)*	69% (29)*	
Significantly more active during day					
unidentified juvenile rockfish	rock ridge	99% (855)**			
(*Sebastes* spp.)	boulder	98% (1214)**			
	cobble	96% (876)**			
	mud	91% (54)**			
Puget Sound rockfish (*S. emphaeus*)	boulder	71% (367)**			
	cobble	73% (2501)**			
	mud	87% (126)**			
pygmy rockfish (*S. wilsoni*)	rock ridge	99% (855)**			
	cobble	99% (235)**			
	mud	94% (34)**			
yellowtail rockfish (*S. flavidus*)	rock ridge	95% (259)**			
	boulder	96% (260)**			
Significantly more active during night					
spotted ratfish (*Hydrolagus colliei*)	boulder			87% (16)*	
	mud			92% (87)*	
widow rockfish (*S. entomelas*)	boulder	96% (45)*			

and hagfishes exhibited distinct diurnal and nocturnal activity, respectively. These day and night patterns were similar to those observed during day-time surveys from manned submersibles on Heceta bank (Pearcy et al., 1989; Stein et al., 1992; Hixon et al.[2]), day and night surveys on Stonewall Bank (Hixon and Tissot[1]), and are generally consistent with most patterns found in other shallow temperate day and night studies, but were much less distinct than those for fishes inhabiting tropical fish communities (Helfman, 1978). The overall marked decrease in abundance and activity of smaller-size taxa at night was similar to the decrease that Ebeling and Bray (1976) and Moulton (1977) observed, but our study did not provide evidence of a pronounced replacement of diurnally active taxa by exclusively nocturnal species as observed at Santa Catalina Island (Hobson and Chess, 1973; Hobson et al., 1981), Hawaiian tropical reefs (Hobson, 1972), and reefs in the Virgin Islands (Colette and Talbot, 1972).

It is possible that light illumination at the top of Heceta Bank during the day contributed to the higher abundance and activity of the three most dominant day taxa (pygmy rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish), as found in similar studies on temperate species. Fishes found at the top of Heceta Bank likely perceive and use the faint sun illumination during the day (Boehlert, 1979). On Heceta Bank, the photic zone generally extends down to approximately 50 m water depth and it is generally accepted that sun illumination affects behavior of fishes down to these depths (L. Britt, personal commun.[4]). This was confirmed by the GLOBEC survey, which measured one percent of surface light at 50 m, just above the shallowest fish survey depths (70 m) where most of the unidentified juvenile rockfish were present. Light illumination may be aiding the dominant day assemblage because these taxa stay close (perhaps within visual distance) to large features that provide refuge from larger, active piscivorous predators. In Puget Sound

[4] Britt, Lyle L. 2007. Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way N.E., Seattle, WA 98115.

(Moulton, 1977), on rocky kelp forests off Santa Barbara, California (Ebeling and Bray, 1976), and on Santa Catalina Island, California (Hobson and Chess, 1976; Hobson et al., 1981), the small-size adult and juvenile rockfish that remain exposed from refuge during the night stay close to the seafloor.

Only two taxa showed distinct day and night activity patterns (diurnal: rosethorn rockfish and nocturnal: hagfish), indicating that marked differences in day and night activity are not as prevalent as those found in shallow tropical coral reef and temperate fish communities (Table 2) (Hobson, 1972; Helfman, 1978). The diurnal activity pattern exhibited by rosethorn rockfish was independent of habitat, indicating that habitat type may not be a significant factor in determining differences between day and night activities for this species (Tables 1 and 2). The nocturnal activity pattern that hagfishes exhibited was similar to that observed by Ooka-Souda et al. (1985) of another hagfish species (*Eptatretus burgeri*), in the laboratory. During the day on Heceta Bank, most hagfish were observed coiled up over mud or sand, or around cobble, whereas during the night fish of this taxon was observed swimming above bottom or moving in contact with the bottom in a twisted manner. Like silver hake (*Merluccius bilinearis*) which use sand waves (transverse ridges of sand) for refuge during the day (Auster et al., 2003) and that forage during the night (Bowman and Bowman, 1980; Auster et al., 1995), hagfishes on Heceta Bank may use mid-depth cobble and mud habitats for resting during the day and may forage at night. Not all rosethorn rockfish and hagfishes strictly followed a diurnal or nocturnal activity pattern; however, the fish activity measure we used was not sensitive enough to detect subtle differences in behavior, such as resting individuals found hovering close to but not in contact with the seafloor.

Potential bias exists in observing and attempting to quantify activity in fishes when using video survey methods (Uzmann et al., 1977; Sale and Douglas, 1981; Wakefield and Smith, 1990). Our inability to identify many of the rockfishes to species is potentially problematic, and illustrates a limitation of this survey method. The majority of historical studies show that very few fishes exhibit changes in activity with the presence of an ROV or submersible, although a handful of taxa do show behavioral responses (High, 1980; Carlson and Straty, 1981; Pearcy et al., 1989). SCUBA-based video surveys of fish abundance and behavior indicate that although the majority of fishes show no noticeable reaction, some species may avoid or be attracted to divers outside the camera's field of visibility and may even follow divers (Moulton, 1977). It has been argued that SCUBA surveys do not significantly affect counts because most fishes that follow divers remain behind the field of view of the camera (Powles and Barans, 1980). In our study, anecdotal evidence indicated that the ROV had limited effect on fish behavior, except in cases where the ROV came in contact with the substrata. Further investigation is needed, however, to fully grasp the impacts of observational vehicles on fish responses (Stoner et al., 2008).

Implications for groundfish surveys

Day and night activity patterns in demersal fishes have been shown to dramatically change the catchability of some species on the West Coast (Hannah et al., 2005), in the Northwest Atlantic (Bowman and Bowman, 1980), in Newfoundland (Casey and Myers, 1998), and in the North Sea (Petrakis et al., 2001). In this study, we found that daytime surveys could underestimate the abundance of certain species that are more abundant or active at night, such as sharpchin rockfish. Highly significant differences in day and night abundance of schooling rockfishes found in this study indicate that daytime trawl surveys over small- to medium-size habitat features may be biased for some fish species. Migration of fishes into the overlying water column, horizontally off the bank, or into hiding among medium- to large-size features is likely the most common day and night behaviors that would decrease the availability of fishes to the ROV. Specifically, Puget Sound rockfish may be more available over deeper, smaller-size rock structures, whereas other dominant day taxa (pygmy rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish) and sharpchin rockfish are likely less available to trawl surveys over large-size features in shallower portions of the bank. We speculate that the reduction in abundance of the four most dominant day taxa is due to fish seeking refuge around medium- to larger-size structures because of the potential presence of large piscivores (Wilkins, 1986; Adams, 1987), rather than to schooling in the water column.

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