

Effect of hypoxia on rockfish movements: implications for understanding the roles of temperature, toxins and site fidelity

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ABSTRACT: We used a high-resolution acoustic telemetry array to study the effect of seasonal hypoxia (defined as dissolved oxygen concentration [DO] < 2 mg l⁻¹) on the movements of quillback rockfish *Sebastes maliger* and copper rockfish *S. caurinus* at Cape Perpetua Reef, Oregon, USA. Over 18 weeks in summer 2010, a period with both normoxic and hypoxic conditions at the reef, both species showed high site fidelity. Home range was variable within species, was much larger than previously shown, and was influenced by foray and relocation behavior. Several quillback rockfish forayed well off of the reef into sand and gravel areas. Foray departure time was synchronous among individuals and related to time of day (sunset). Hypoxic conditions reduced home range for copper rockfish by 33%, but home range was variable for quillback rockfish, with no change in foray behavior. We propose that the origin, chemistry, and temperature of the hypoxic water mass and the species' innate behavioral tendencies must be considered, along with DO, in determining the effects of hypoxia on fish.

KEY WORDS: *Sebastes* · Hypoxia · Acoustic telemetry · Home range · Behavior · Temperature

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INTRODUCTION

Evaluating species' ecology within an ecosystem exposed to complex and dynamic environmental conditions requires a comprehensive understanding of both the species' natural history and the conditions to which it may be responding. Changing ocean conditions illustrate this challenge and may affect species' movements and fitness in broad- and fine-scale ways. One environmental phenomenon which can influence the health and distribution of marine life is a change in oxygen availability. Episodes of decreasing oxygen concentration in marine waters have been reported worldwide and are caused by a variety of anthropogenic and natural conditions (Gray et al. 2002, Grantham et al. 2004, Newton 2008). Hypoxia—defined here as dissolved oxygen concentration (DO) < 1.4 ml l⁻¹ or < 2 mg l⁻¹—is found

naturally in the oxygen minimum zone (OMZ) where its marine residents are evolutionarily adapted to a low oxygen environment (Vetter & Lynn 1997).

Large-scale hypoxic water masses exist naturally in the deeper marine waters of the US Pacific Northwest (Grantham et al. 2004, Connolly et al. 2010). In the summer, strong NW winds create upwelling which can advect this cold, high-nutrient water mass inshore into the shallower (< 70 m) waters of the inner continental shelf. As the nutrients become available within the photic zone, plankton populations flourish, contributing to the high primary productivity of the area (Pauly & Christensen 1995). However, the cycle of intense productivity, decomposition and oxygen consumption can further reduce oxygen levels. If NW winds continue in strength and duration, this increasingly hypoxic water mass may move into nearshore areas and even enter bays and estuaries where the

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marine life may not be adapted to low oxygen conditions (Grantham et al. 2004, Brown & Power 2011, Roegner et al. 2011).

There is strong historical (1950 to 1975) evidence of episodic, seasonally occurring hypoxia in Pacific NW coastal waters (Brown & Power 2011). Since 2002, areas of seasonal hypoxia have been well-documented in the nearshore waters of Oregon (Chan et al. 2008). The movement of hypoxic water masses is influenced by bathymetry, as well as other oceanographic conditions, and certain locales off the Oregon coast have been repeatedly exposed to low oxygen water (Grantham et al. 2004). One area, a small, isolated rocky reef located 5 km southwest of Cape Perpetua, Oregon (see Fig. 1), has been exposed to several known hypoxic events since 2002, but in 2006 an episode of severe hypoxia ($\text{DO} < 0.5 \text{ ml l}^{-1}$, $< 0.7 \text{ mg l}^{-1}$) occurred (Chan et al. 2008). This reef had been surveyed in prior years with a video-equipped remotely operated vehicle (ROV) and showed a diverse community of mobile and encrusting invertebrates, as well as many species of fishes including various rockfishes *Sebastes* spp., lingcod *Ophiodon elongatus* and kelp greenling *Hexagrammos decagrammus* (Weeks et al. 2005). When this video survey was repeated in August 2006 (after the severe hypoxia event), mortality of many forms of invertebrates was observed. Rockfishes, which had previously dominated the fish fauna at the reef, were absent (Chan et al. 2008). Rockfishes were subsequently observed during each annual ROV survey of the Cape Perpetua reef from 2007 to 2009 (M. Donnellan pers. comm.).

Rockfishes comprise a large (102 species), diverse group of long-lived, late-maturing fishes, with many species exhibiting substantial niche overlap in nearshore areas (Love et al. 2002). Recent findings using acoustic telemetry have shown considerable variability in behavior and site fidelity among and within the rockfishes of the NE Pacific (Lowe et al. 2009, Tolimieri et al. 2009, Hannah & Rankin 2011). However, these species' responses to changes in environmental conditions, such as hypoxia, are not well known and have only recently been reported for a few areas (Palsson et al. 2008). Oxygen tolerances for NE Pacific rockfishes have not been established, and experimental results for many other types of fishes indicate varying thresholds (Nakanishi & Itazawa 1974, Gray et al. 2002, Vaquer-Sunyer & Duarte 2008).

Changes in oxygen availability can significantly influence behavior in fish, with laboratory experiments showing fish sensing and avoiding areas of low oxygen (Herbert et al. 2011). However, little

research has been conducted with reef-dwelling, refuge-seeking fishes, nor with fishes that may be strongly territorial, have strong site fidelity, or small home ranges. These behavioral traits may lead to hiding or remaining within an area as conditions deteriorate, particularly if there is no nearby safe habitat (Palsson et al. 2008, Herbert et al. 2011), making fish particularly vulnerable to deteriorating water quality. These fishes may subsequently incur greater harm than other, more mobile fishes.

High site fidelity, small home ranges and a strong affinity for substrate have been documented for several species of reef-dwelling, nearshore rockfish, increasing their potential vulnerability to detrimental environmental conditions (Lowe et al. 2009, Tolimieri et al. 2009, Hannah & Rankin 2011). Knowledge of their physical and behavioral responses to environmental stress is critical to a basic understanding of their ecology. We report here on our use of acoustic telemetry in a high-resolution positioning system (VPS) to study the behavior and movements of 2 species of rockfishes inhabiting Cape Perpetua Reef. The area encompassing the Cape Perpetua Reef was recently designated as a marine reserve site (Oregon Ocean Information www.oregonocean.info), with rockfishes being a taxon of interest. The primary study objective was to determine the home range, site fidelity, and movement patterns for these species living on this type of low-relief reef, during the summer, when seasonal hypoxia can develop. An additional objective was to observe and describe any changes in movement behavior in response to changing oceanographic conditions.

MATERIALS AND METHODS

Cape Perpetua Reef is located 5 km southwest of Cape Perpetua, Oregon (Fig. 1) and ranges in depth from 47 to 53 m (Fox et al. 2004). The reef is small, approximately 0.07 km^2 , and consists of rock patches with low vertical relief within a large expanse of gravel and coarse sand. Rock patches are variable, and range in size from 1 m^3 boulders to 1.6 ha benches (Fox et al. 2004). Our study focused primarily on 2 species of nearshore rockfish—quillback *Sebastes maliger* and copper rockfish *S. caurinus*. These demersal species are relatively abundant at Cape Perpetua Reef (Weeks et al. 2005), allowing us to increase sample size by species to better capture variability in individual behavior. We also opportunistically tagged a single brown rockfish *S. auriculatus*, a demersal species which is rarely captured in

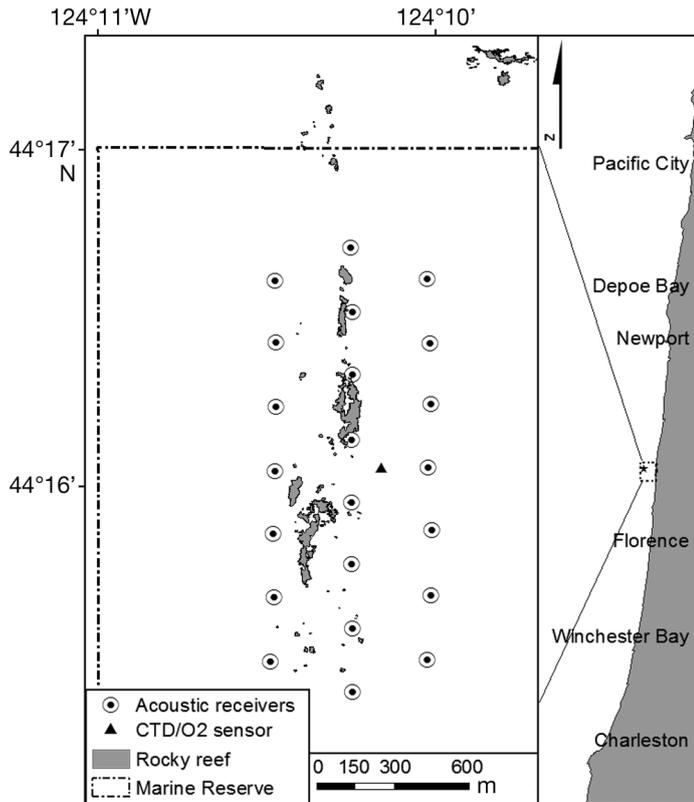


Fig. 1. Study area showing rocky reef, location of acoustic receivers and CTD/O₂ sensor, and marine reserve boundary line

Oregon, but is commonly encountered in Hood Canal, Washington—another area of recurring hypoxia in the Pacific Northwest (Newton 2008, Palsson et al. 2008).

Rockfish were captured in May 2010, using recreational hook-and-line fishing gear. Each fish was evaluated for barotrauma, measured for length (cm, total length), and vented using an 18-gauge hypodermic needle inserted through the body wall to remove excess gas from the swim bladder. Fish were surgically tagged as per methods outlined in Parker et al. (2007). Implanted tags were Vemco V13-P coded acoustic transmitters (69 kHz, 158 dB power output, 13 × 45 mm, pressure-sensing 100 m, accuracy ± 5 m, resolution 0.44 m) which transmit a unique identification number and the depth of the tagged fish. All tags were tested prior to deployment. After tagging, fish were immediately returned to depth in a video-equipped underwater release cage (Hannah & Matteson 2007) at the point of original capture, as per methods outlined in Hannah & Rankin (2011).

To track tagged fish, we used a Vemco VPS positioning system, which utilized moored VR2W sin-

gle-channel acoustic receivers (Vemco) in a grid, in combination with moored 'synctag' transmitters. With precise position information on receiver and synctag locations, environmental parameters (to determine the speed of sound in water) and synchronized clocks within all receivers, very precise fish location information can be obtained for each individual (Andrews et al. 2011). The receiver grid was designed based on range-testing in the area which showed 350 m spacing to be optimal for maximizing acoustic reception. This spacing generally allowed tagged fish to be detected by 3 or more receivers for accurate position triangulation. Downloaded detection data was sent to Vemco for data processing. For each download, Vemco provided a fish ID code, the time of detection, precise position information (latitude and longitude), depth (m), and an estimate of horizontal position error (HPE) for each triangulated position.

Our VPS system used a grid of 22 receivers with collocated V16 synctags (random delay 700 to 1100 s) and was deployed from 13 April through 21 September 2010, encompassing an area of roughly 1.4 km² (Fig. 1). Three additional V16 synctag transmitters were separately moored within the grid. These 'reference tags' were left in place throughout the study period, without being brought to the surface, to provide a stable locational 'fix' for the rest of the array, which had to be pulled and redeployed monthly to download telemetry data.

We recorded conductivity, temperature, depth and DO at our study site using a Sea-Bird SBE16plus V2, equipped with an SBE43 oxygen sensor (Sea-Bird Electronics). The unit was moored within the acoustic receiver array from 28 May through 21 September 2010. It was positioned 1 m off the bottom and was programmed to sample every 15 min.

Data analysis

To allow for a recovery period following tagging, we disregarded the first 48 h of fish locations for all analyses. We estimated home range for each tagged fish as the 95% kernel utilization distribution (KUD) from all remaining locations for the complete study duration, using the program AdehabitatHR, as implemented in R (Calenge 2006). We defined core area similarly, but based on the 50% KUD. To estimate the use of space for shorter time periods or subsets of the data, we also used the 95% KUD, but use the term 'activity space' to avoid confusion with home range or core area. To examine how activity

space changed in relation to the diel cycle, we divided all positional fixes into either day, night or the crepuscular period, which was defined as from 1 h before to 1 h after either sunrise or sunset. Sunrise and sunset at the study site were determined from tables provided by the United States Naval Observatory (<http://aa.usno.navy.mil/data/>). We evaluated site fidelity by analyzing how frequently tagged animals made 'relocations' or 'forays'. A relocation was defined as a tagged specimen with a spatial distribution encompassing 2 or more distinct activity spaces that were each persistent for more than 1 wk. In contrast, we defined a foray as a movement of at least 100 m away from the calculated center of activity that lasted for more than 1 h, consisted of a pattern of sequential movements (in time and space) as opposed to just a single positional fix, and ended in a return to a spot within 100 m of the activity center. We estimated the duration of each foray based on when the tagged fish left and returned to a location less than 100 m from its center of activity. We also calculated the maximum distance of the foray based on the positional fix that was most distant from the center of activity. In some instances, this was considered a minimum estimate because the tagged fish completely left the study area and then later returned. The maximum foray distances are also approximations because the accuracy of position data using VPS is influenced by the tagged fish's position relative to the receivers.

To quantify how hypoxia influenced movements of these demersal rockfish, we examined how fish locations and movements changed as the oxygen concentration reached levels generally considered 'hypoxic'. To make a quantitative comparison of the effect of oxygen concentrations on space use, we selected 2 equal time periods (11 d each), one encompassing the lowest continuous oxygen concentrations encountered during the study and a second period of much higher (non-hypoxic) oxygen levels. We then compared, by species, the 95 % KUD for these 2 equal time periods using a paired *t*-test (Sokal & Rohlf 1981).

RESULTS

Fish tagging and receiver array

We tagged 8 copper, 9 quillback and 1 brown rockfish between 06 May and 16 May 2010 (Table 1). The time from capture until release at depth ranged from 3 to 12 min (average = 7 min). All fish survived the tagging process, remained in the study area, and were consistently detected for the 18 wk of the 2010 array deployment (13 April to 21 September). The VPS acoustic receiver array remained in place and functioned well throughout the study. Due to the depth of the array (50 m), an error minimization algorithm was applied to the calculated receiver positions which served to calibrate the system. Transmission propagation times for synctags were somewhat variable, likely due to changing environmental conditions. The precision of the system was estimated at about ± 15 m (Vemco VPS Results Report). The high resolution data generated by the VPS system allowed

Table 1. *Sebastes maliger*, *S. auriculatus*, *S. caurinus*. Kernel utilization density (KUD, m²) for Pacific rockfish by species and tag ID. 95 % KUD = home range; 50 % KUD = core area. Normoxia KUD (mean DO = 5.9 mg l⁻¹) spanned 11 d (30 May to 9 June 2010). Hypoxia KUD (mean DO = 1.8 mg l⁻¹) spanned 11 d (9 July to 19 July 2010). Forays were defined as beginning 100 m beyond the calculated center of the activity space. Relocations were defined as 2 or more distinct activity spaces, persisting for more than 1 wk

Rockfish species/ tag ID	Fish length (cm)	KUD (m ²)		95 % KUD (m ²)		Forays (n)	Reloca- tions (n)
		95 %	50 %	Normoxia	Hypoxia		
<i>S. caurinus</i>							
100	40	8017	1221	9996	7156	–	–
103	44	2774	320	2286	2224	–	–
104	42	1966	269	2538	1007	–	–
249	47	2866	434	3903	2459	–	–
252	46	13834	2873	3485	1699	–	6
254	39	2637	350	3306	1656	–	–
255	46	1874	275	2074	1584	–	–
256	34	3283	579	3567	2972	2	–
Mean KUD	–	4656	790	3894	2595	–	–
<i>S. maliger</i>							
101	42	2175	240	2034	2033	–	–
102	45	3274	447	2149	23624	20	–
105	41	2231	278	2279	1870	5	–
223	36	2877	483	3046	2930	–	–
225	40	1232	190	1211	899	–	–
227	43	24164	1263	2711	4835	34	–
250	40	1645	185	1779	851	4	–
251	38	2932	588	2916	2890	–	–
253	36	7493	1671	10057	7949	–	–
Mean KUD	–	5336	594	3131	5320	–	–
<i>S. auriculatus</i>							
226	42	3272	501	979	904	–	1

us to differentiate a variety of movement patterns, including relocation, habitat utilization, foray behavior away from the reefs and daily activity patterns. The CTD/O₂ sensor acquired pressure, temperature, salinity and oxygen data from a depth of 50 m from the date of deployment until 31 July. The unit was recalibrated by the manufacturer at the end of the study and there was no significant sensor drift.

Development of seasonal hypoxia

As the upwelling season progressed, hypoxia developed at 50 m of water depth in the study area. Early in the study period, southerly winds generated downwelling conditions off Cape Perpetua which resulted in seafloor DO ranging from 3.9 to 8.9 mg l⁻¹ and a temperature range of 8.9 to 12.9°C at the study site (Fig. 1). By 15 June, NW winds had produced strong coastal upwelling, and the resulting oceanographic conditions reduced seafloor DO to 1.6–3.2 mg l⁻¹ and the temperature to 6.8–8.2°C for the rest of the sensor sampling period (Fig. 2). Oxygen saturation levels ranged from 42 to 102% during the initial downwelling period and dropped to 17–34% during the subsequent upwelling. A period of hypoxia (DO range = 1.62–1.97 mg l⁻¹) began on 7 July and lasted until 25 July when DO rose to >2 mg l⁻¹ (average = 2.5 mg l⁻¹) for 6 d. Seafloor water temperature remained cold, and averaged 7°C during the hypoxic period (Fig. 2). DO levels <3 mg l⁻¹ continued to be present off Cape Perpetua at 70 m depth for the remainder of the study period (Adams et al. in press).

Site fidelity and home range

All of the tagged fish maintained high site fidelity to the reef area throughout a wide range of oceanographic conditions for the duration of the study, including a prolonged period of low oxygen, and a period of hypoxia (Figs. 2 & 3). Home range was variable among individual fish and was influenced by foray behavior (excursions away from the reef) and by some individual's use of multiple, distinct core areas (Table 1, Fig. 3). Home ranges for 8 of 9 quillback rockfish ranged from 1232 to 7493 m², but forays conducted by quillback 227 resulted in a very large home range of 24 164 m² (Table 1, Fig. 3a). The home range of quillback 227 was comprised of 2 separate areas;

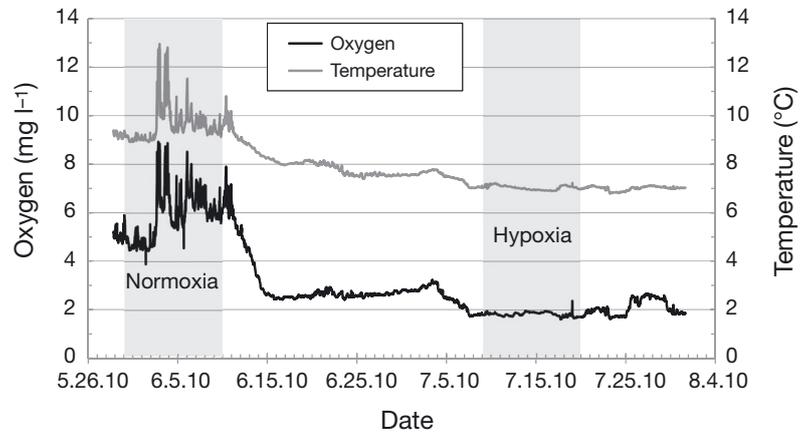


Fig. 2. Oxygen and temperature at the study site at 50 m water depth from 28 May to 31 July 2010. The 11 d comparison periods chosen were 30 May to 9 June 2010 for normoxia conditions (average DO = 5.9 mg l⁻¹), and 9 July to 19 July 2010 for hypoxia conditions (average DO = 1.8 mg l⁻¹). Dates are mm.dd.yy

however, this fish did not actually have a 'center of activity' in the western area. It simply passed through this area repeatedly as it traveled away from and back to its center of activity, located in the eastern area of the reef (Table 1, Fig. 4). Home ranges for 7 of the 8 copper rockfish ranged from 1874 to 8016 m², but copper 252 relocated alternately to 1 of 2 distinct areas 6 times throughout the study, generating a larger home range of 13 833 m² (Table 1, Fig. 3b). The single brown rockfish had a home range of 3272 m², comprised of 2 distinct areas (Table 1, Fig. 3a).

Habitat utilization and movement patterns

Relocation

Copper 252 repeatedly (6 times) moved between 2 activity centers, located 535 m apart (Fig. 3b). The time interval between relocations ranged from 9 to 39 d. Once initiated, relocations were direct and rapid, with the fish leaving one area, swimming directly towards the other area and arriving (on average) in about 1 h. Brown 226 relocated only once during the study to a new activity center 211 m away from the original area (Fig. 3a). The fish's path was indirect and meandering, and the time to relocate (6 h) was much longer than for copper 252.

Habitat utilization and foray behavior

Most tagged fish remained within the rocky reef area; however, quillback 227 and quillback 102 con-

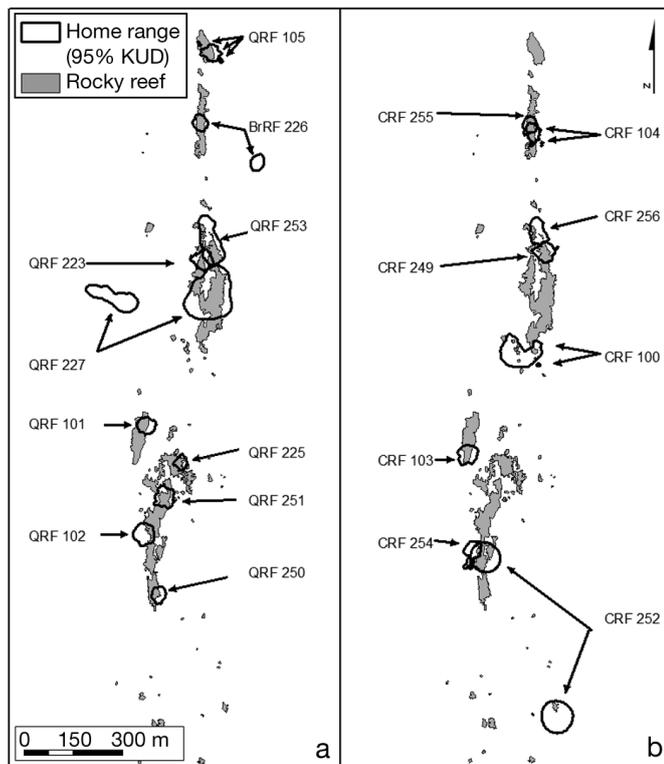


Fig. 3. *Sebastes maliger*, *S. auriculatus*, *S. caurinus*. 95% KUD (black line) and rocky reef for (a) quillback rockfish (QRF) and brown rockfish (BrRF) and (b) copper rockfish (CRF). KUD: kernel utilization density

ducted repeated, extensive nightly forays well beyond the reefs to the west, in an area comprised of large expanses of sand interspersed with gravel patches (Goldfinger et al. 2012). Foraging quillback rockfish generally completed a roughly elliptical route, returning to the reefs close to their center of activity. Rarely, fish returned to the reefs well away from their center of activity, but once within the reef area, they traveled directly home.

Five fish exhibited foray behavior: 4 of 9 quillback rockfish and 1 of 8 copper rockfish. Variability among individuals' foray behavior was evident in many aspects of the fish's travel: frequency, distance, duration and direction. Quillback 227 had the highest frequency of forays ($n = 34$) (Fig. 4), followed by quillback 102 ($n = 20$), quillback 105 ($n = 5$), quillback 250 ($n = 4$), and copper 256 ($n = 2$) (Table 1). Forays ranged from 105 m to 1124 m from the designated activity center (Fig. 5) and lasted from 30 min to 12.5 h (Fig. 6). The maximum measurable path travelled was over 3000 m, but at times quillback 227 appeared to have moved completely out of acoustic range west of the array (>1 km), returning into range some hours later, suggesting a longer path than

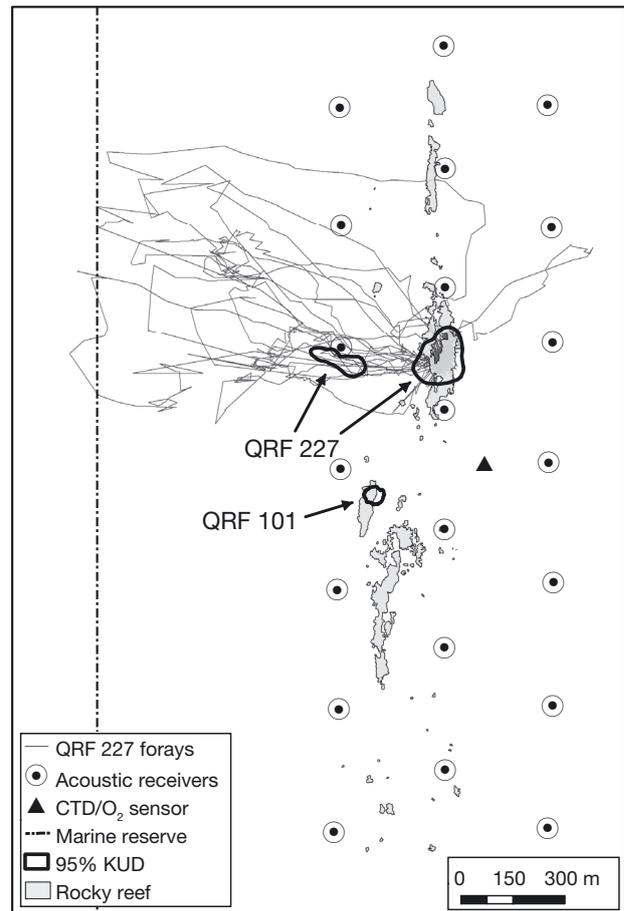


Fig. 4. *Sebastes maliger*. Foray tracks (grey line) for quillback rockfish 227 (QRF 227) for September 2010, and 95% KUD (solid outline) for QRF 227 and comparison fish QRF 101

measured (Fig. 4). In contrast, quillback 105 had 5 forays, all less than 200 m from its activity center and traveled to the east, southeast or south. The only copper to foray was copper 256. This fish had 2 forays (Table 1), both to a rock patch 120 m to the north.

Intriguingly, some movement patterns were repeated within individuals, and on several occasions the timing of the patterns was synchronous among individuals, and related to time of day. For example, most (31 of 34) of quillback 227's forays were west of the reef area (Fig. 4) and occurred close to sunset (Fig. 7). Quillback 102 also exhibited this behavior, travelling exclusively to the west of the study site and leaving the core area within 1.5 h of sunset (Fig. 7). Although core areas for these 2 fish were separated by 738 m (Fig. 3a), on 8 occasions their foray departure times were within minutes of each other (Figs. 5 & 7). Synchronous foray timing was a prevalent aspect of foray behavior. In total, 53 of 65 rockfish foray departure times were within 1.5 h of sunset.

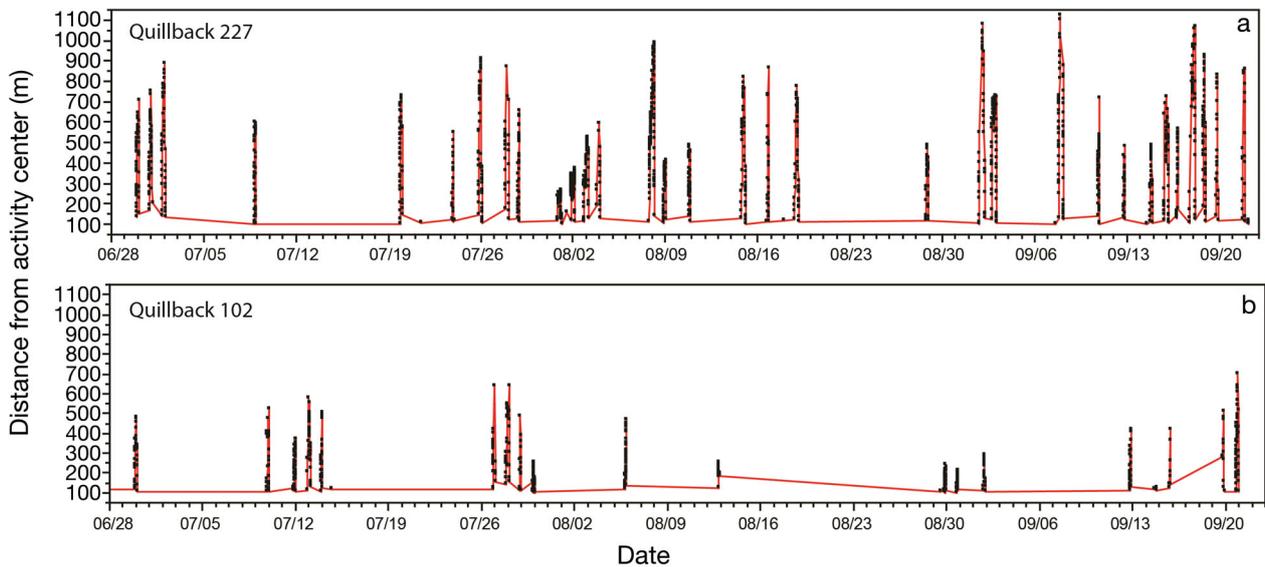


Fig. 5. *Sebastes maliger*. Foray date and foray distance from activity center for (a) quillback 227 and (b) quillback 102. Dates are mm/dd. Black dots are individual detections. Red line indicates the time series of detections

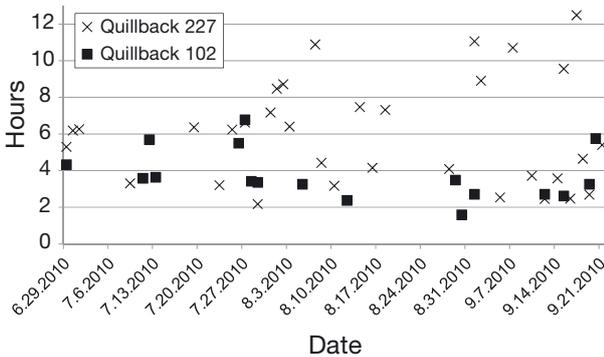


Fig. 6. *Sebastes maliger*. Foray date and foray duration for quillback 227 and quillback 102. Dates are mm.dd.yy

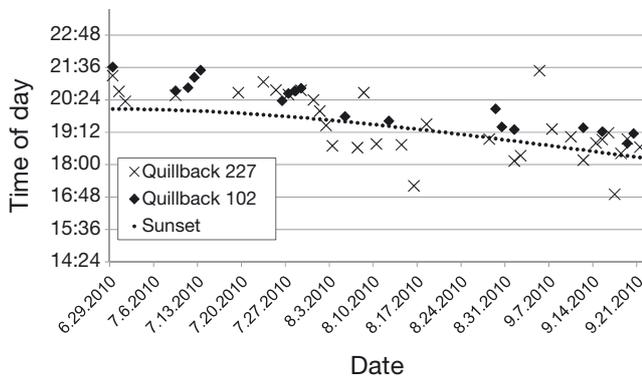


Fig. 7. *Sebastes maliger*. Foray date and time of departure from activity center for quillback 227 and quillback 102, showing synchrony of timing between rockfish and relationship to time of sunset. Dates are mm.dd.yy

Daily activity patterns

We found little difference in the activity space used by tagged fish during day, night and crepuscular periods for all but 2 fish (Fig. 8) — quillbacks 227 and 102. The frequent nighttime foray behavior exhibited by these fish resulted in markedly larger home ranges at night (both fish) and during the crepuscular period (quillback 227) (Fig. 8b).

Comparison of hypoxic and normoxic conditions

Although all fish remained in the study area and within their previously established home ranges during the hypoxic period, the hypoxic water mass did influence the size of the activity space used by most fish. For copper rockfish, the 95% KUD was 33% smaller during the hypoxic period ($p < 0.01$; Fig. 9a). The response of quillback rockfish to the onset of hypoxia was more variable (Table 1). Seven quillback averaged a 14% reduction in 95% KUD during the hypoxic period, and quillback 253 reduced its very large ($>10\,000\text{ m}^2$) activity space by 21%. In contrast, quillbacks 102 and 227 increased their 95% KUDs 1099% and 178%, respectively during the hypoxic period due to foray behavior (Table 1, Fig. 9b). The single brown rockfish showed a small ($<1\%$) reduction in 95% KUD during the hypoxic period.

Other than the effect on the size of the activity space, the onset of hypoxia had little effect on fish

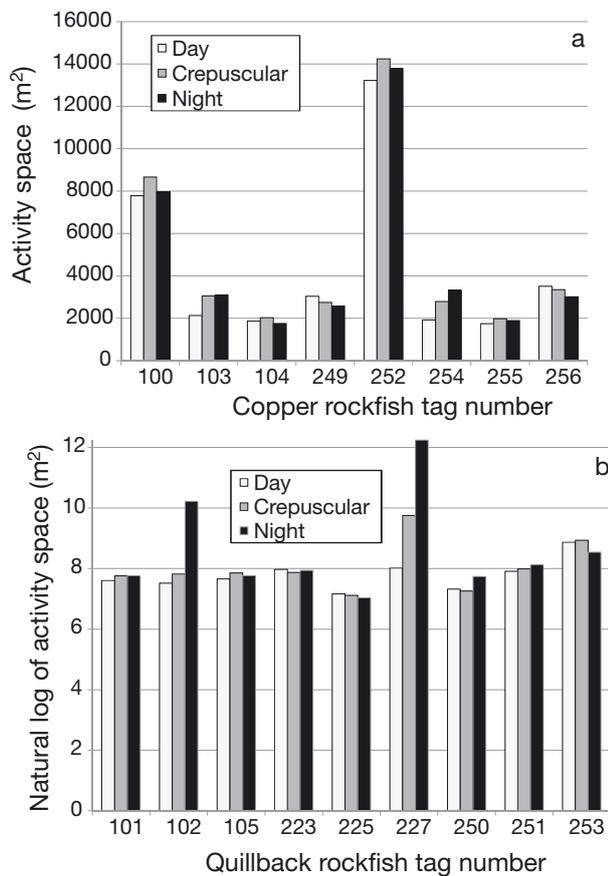


Fig. 8. *Sebastes caurinus*, *Sebastes maliger*. Activity space (95% KUD, m²) compared by day, crepuscular and nighttime periods for each (a) copper rockfish and (b) quillback rockfish. Forays by quillback rockfish 102 and quillback rockfish 227 resulted in larger nighttime activity spaces for both fish and a larger crepuscular activity space for quillback rockfish 227 (note log scale for quillback rockfish)

movement. Copper 252 and brown 226 each utilized 2 distinct home ranges throughout the varied environmental conditions of the study period (Table 1, Figs. 3a,b), but relocations did not appear to be initiated by the change in temperature and oxygen concentration. Copper 252 relocated during the normoxic period before upwelling (22 May), again 39 and 66 d later in periods of low oxygen (DO range = 2.6 to 2.8 mg l⁻¹, O₂ saturation = 26 to 29%), but not during the hypoxic period. Brown 226 relocated 211 m from its previous home on 22 August, well after (44 d) the hypoxic period.

Foray behavior was evaluated in relation to the presence of hypoxic water and did not appear to be initiated by changes in DO. One foray was observed during the initial downwelling (normoxic) phase of the study, and forays were observed with equal frequency during the low-oxygen and hypoxic periods.

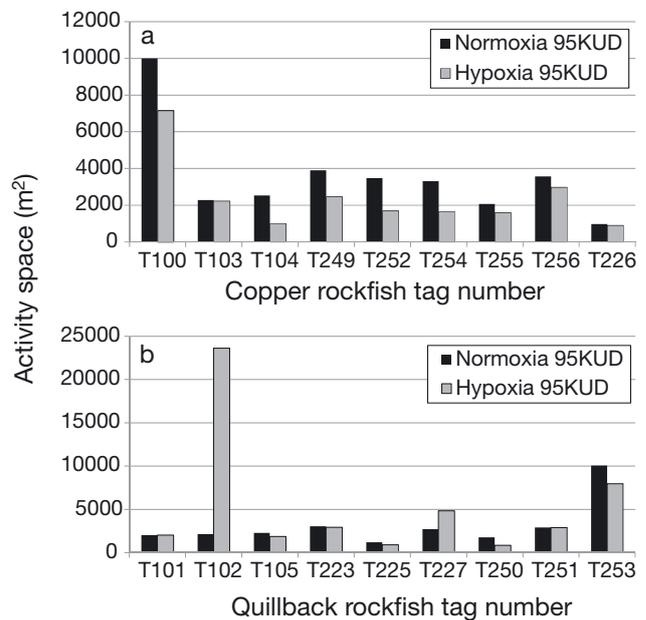


Fig. 9. *Sebastes caurinus*, *Sebastes maliger*. Comparison of activity space (95% KUD, m²) for normoxia and hypoxia periods for each (a) copper rockfish and (b) quillback rockfish

DISCUSSION

By combining a VPS system with a larger sample size of tagged animals from each of 2 rockfish species occupying the same reef area, our study provided high-resolution data on fish movements that showed both between- and within-species variation in the use of space and the response to hypoxia. The precision of the system and a high frequency of tag transmission allowed the description of both intra-seasonal variation and variation among individual fish in the use of areas away from the rocky reefs. The on-site moored CTD/O₂ sensor allowed us to relate changes in water chemistry to fish behavior, providing a very complete picture of how these species of rockfish use the reef and surrounding areas as conditions changed over time.

Mean home range sizes for copper and quillback rockfish in our study were larger than those previously described by Tolimieri et al. (2009) for a summer study in Puget Sound, Washington. The larger sample sizes in our study revealed substantial behavioral variability within species. Home ranges were 3.6 times larger for quillback rockfish (mean = 5336 m² vs. 1463 m²; our study vs. Tolimieri et al. 2009, respectively) and 1.9 times larger for copper rockfish (mean = 4656 m² vs. 2448 m²), due primarily to foray behavior and relocations of a few fish. Our

findings support previous work showing that habitat type and habitat quality influence the scale of movement with larger home ranges being associated with lower relief habitat for rockfishes (Matthews 1990). However, the scale of movements for quillback rockfish in our study is far larger than previously reported.

Relocation to a different activity center by copper 252 supports previous findings for 2 copper rockfish studied at Siletz Reef, Oregon, showing fish moving repeatedly between 2 primary locations (Hannah & Rankin 2011). Lowe et al. (2009) reported highly variable detectability rates and low site fidelity for copper rockfish (detected <30% of days at liberty), and one specimen was shown to move between 2 oil platforms. The relocations exhibited by copper 252 and the brown rockfish provide an interesting contrast in relocation behavior. The copper rockfish's quick (1 h), direct and repeated relocation to 1 of 2 core areas suggests knowledge of the habitat and recollection of a suitable home. The 6 h of meandering behavior leading to the brown rockfish's new home suggests the fish was investigating or foraging in the area, versus travelling directly to a known location.

The quillback rockfish foray behavior described in this study is also novel. Our study is not the first report of foray-like behavior, as Tolimieri et al. (2009) described 'wandering' for 1 of 5 quillbacks tracked in Puget Sound. In that study, wandering was defined as 'extensive movements that occur only during a particular portion of the day, but which are not substantial enough to result in a core area seen only nocturnally or diurnally.' Our study differs in that the movements revealed were repeated and extensive enough to result in substantially larger activity space at night and/or in the crepuscular period. Our findings also conflict with the contention by Love et al. (2002) that quillback rockfish are likely 'inactive at night'. Four of our quillback rockfish were also shown to consistently utilize open sand and gravel areas, spending considerable time off the reef in this open area with a combined total of 64 forays, ranging as far as 1000 m off the reef, and sometimes traveling more than 3 km in transit. One fish was off the reef for over 12 h. These fish would seem to be in a remarkably vulnerable position in terms of lack of suitable refuge from predators. The ecological advantage of such potentially risky behavior suggests a substantial gain in fitness. Reproductive maturity data support neither mating nor parturition for quillback rockfish off Oregon during our study period (Hannah & Blume 2011). The timing and repeated nature of this behavior, with the majority of forays commencing at sunset, strongly suggests foraging upon nocturnally active benthic

prey such as the smooth bay shrimp *Lissocrangon stylirostris* (Wakefield 1984, Marin Jarrin & Shanks 2008) and Dungeness crab *Metacarcinus magister*. Prey transitioning into or out of the sand, such as sand lance *Ammodytes hexapterus* (Love 2011), or vertically migrating pelagic invertebrates (Murie 1995) may also be potential prey. Juvenile fish are another known food item for quillback rockfish (Murie 1995), and have been shown to reside within rippled scour depression habitat, defined in part as depressions in the seabed comprised of sediments coarser than the surrounding area (Hallenbeck et al. 2012). Multibeam and sidescan sonar data from the foray areas show gravel beds recessed up to 0.5 m below the surrounding sand, which may similarly provide juvenile fish habitat and prey for quillback rockfish in an otherwise featureless area (Goldfinger et al. 2012).

Although hypoxia was present for an extended time period in our study, the tagged fishes' minimal response to these conditions would seem to indicate that low oxygen levels are well-tolerated by these species. In contrast, tolerance was not indicated in the 2002 hypoxia event ($DO < 2.24 \text{ mg l}^{-1}$) at Cape Perpetua Reef, where Oregon Department of Fish and Wildlife (ODFW) ROV video footage at this same site showed numerous dead sculpins (family Cottidae; ODFW unpubl. data) and no visible rockfish (Grantham et al. 2004). A likely scenario for this difference is that DO may have reached much lower levels at the reef proper in 2002. Our results are also contrary to other published studies, the most relevant of which is Palsson et al. (2008) who reported on hundreds of copper rockfish monitored in Hood Canal during seasonally-occurring hypoxia from 2001 to 2006. In that study, copper rockfish made dramatic, definitive changes in their behavior and distribution with the onset of hypoxia, moving towards the shore and into shallow water, moving to new reef areas, and forming dense schools in shallow water. Over time, these fish became physically compromised, showed weight loss, lethargy and scale loss. Another significant study which also conflicts with our findings is that of Vaquer-Sunyer & Duarte (2008). The authors reviewed 872 publications to conduct a comparative analysis of experimentally derived oxygen thresholds for 4 taxa, including fish. They found that the conventional definition of $DO = 2 \text{ mg l}^{-1}$ was actually well below the lethal and sublethal oxygen thresholds for fish, which exhibited sublethal responses to DO levels as high as 4.8 mg l^{-1} .

Our fishes' minimal response to these low oxygen concentrations suggests other factors must be considered in understanding the effects of hypoxia on fish

in the wild. We propose these factors include origin of the source water mass, its physical and chemical properties, and the species' innate behavioral tendencies within their specific habitat.

The source water for hypoxia at Cape Perpetua differs from hypoxic water in other areas. In many coastal waters, eutrophication and resulting hypoxia can be caused by anthropogenic addition of nitrogen and phosphate, conditions not applicable to our source water (Gray et al. 2002). In coastal Oregon, summertime NW wind advects deep (>600 m) naturally oxygen-poor waters onto the lower shelf and into the photic zone (Wheeler et al. 2003, Grantham et al. 2004). This source water is characterized by lower temperatures (e.g. 7°C) and higher salinity than wintertime nearshore waters. Although the oxygen concentration is reduced further through primary production processes and respiration (Wheeler et al. 2003), temperature remains low. In contrast, summertime hypoxia in Hood Canal is formed by a combination of factors which include intrusion of low-oxygen ocean water, but is confounded by stratification of fresh and saltwater, creating a barrier to mixing. Bathymetry limits flushing in the system and contributes to mid-level hypoxic water moving towards the surface (Newton 2008). Resulting temperatures in Hood Canal were considerably warmer in rockfish habitat, between 9 and 11°C below 7 m depth, while surface waters (<3 m depth) were over 14°C (Palsson et al. 2008). The lower metabolic rate of a fish species residing in the colder temperatures of its natural temperature range (e.g. Cape Perpetua), versus the upper range of temperature tolerance (e.g. Hood Canal) could better enable fish to withstand the physiological challenge of hypoxia, as oxygen demand is lowered (Kim et al. 1995, Graham 2005).

An additional factor that contributes to a fish's fitness and respiratory capacity includes exposure to the toxic byproducts of decaying organic matter, which may be concentrated in near-bottom environments (Gray et al. 2002). Low doses of these compounds can be lethal to many species of fish and invertebrates (Gray et al. 2002). Bacteria residing in sediment generate hydrogen sulfide (H₂S) in the absence of oxygen, and ammonia is formed by mineralization of organic nitrogen as organic matter decays. The 2006 ODFW ROV video footage at Cape Perpetua showed decomposition of crabs and sessile benthic organisms and the presence of bacterial mats during a time of severe hypoxia (DO < 0.5 mg l⁻¹), when (as in 2002) no rockfish were visible (Chan et al. 2008). Although no testing was conducted to de-

tect the presence of these compounds, it is reasonable to expect that they were present. The level of decomposition would further reduce oxygen concentration in the immediate area. Diaz & Rosenberg (1995) note that the effects of hypoxia and H₂S are difficult to separate and may be, at a minimum, additive for fauna not evolutionarily adapted to tolerate them. Video observations at Cape Perpetua during our 2010 study showed no evidence of dead or dying benthic fauna, nor bacterial mats, suggesting physiological challenges from ammonia or hydrogen sulfide compounds were not present at high concentrations.

Fishes' innate behavior and specific habitat may also influence any tendency to avoid low oxygen conditions. Although the quillback forays reveal this species is not as tightly associated with rocky habitat as previously thought, both species demonstrated very high site fidelity during hypoxia in an area with no other nearby reefs. One interesting aspect of hypoxia avoidance behavior of copper rockfish was observed in Hood Canal with fish moving 170 m horizontally to another hypoxic reef area, versus 39 m to a shallow reef with higher oxygen concentration (Palsson et al. 2008). One explanation for this behavior was that the route to the shallow reef was over non-consolidated substrate, suggesting the fishes' behavioral affinity for rocky habitat may compete with their physiological need for oxygen (Palsson et al. 2008). Cape Perpetua fish may also have strong behavioral incentive to remain associated with their isolated reef, as rocky habitat is very limited in the area. Evaluating hypoxia in light of species' site fidelity could greatly assist in spatial management for certain species. For instance, 2 rockfish species classified as overfished in Oregon vary greatly in their site fidelity tendencies: canary rockfish *Sebastes pinniger* are highly mobile, show very low site fidelity and a high range of vertical movement (up to 27 m), while yelloweye rockfish *S. rubberimus* may remain in one small area near the bottom (3 to 7 m vertical range) for many months or even years (Hannah & Rankin 2011). Although both these fish are found in association with rocky habitat, the difference in their tendencies is not subtle. The study showed most acoustically tagged canary rockfish were semi-pelagic, and left the reef area entirely and rapidly; one moving over 13 km in a 14 h period (Hannah & Rankin 2011). Exposure to hypoxia for these fish could have very different effects based on site fidelity alone, with the behavioral tendency for canary rockfish to simply leave the same area in which a yelloweye would remain. Utilizing knowledge of site fidelity and/or other behavioral tenden-

cies, such as refuge-seeking, in addition to hypoxia tolerance could greatly enhance our understanding of these species ecology and responses to changing oceanographic conditions.

Although our study animals showed remarkable tolerance to hypoxia, some physical and ecological effects can still be expected. The reduced movements by the copper rockfish could interfere with foraging opportunities or could be caused by a decrease in prey availability. Reproductive success may be influenced as well. Hopkins et al. (1995) used oxygen consumption rates to determine metabolic rates of yellowtail rockfish *Sebastes flavidus*. They found that females incubating larvae had an 82 to 101 % higher metabolic rate than spent females and males (Hopkins et al. 1995). This study also calculated the maternal nutrient contribution to the embryo. Results show that yellowtail rockfish had lower embryonic energy requirements than other rockfish species (3.4% for yellowtail, 11.5% for copper and 69.2% for black rockfish *S. melanops*) (Dygert & Gunderson 1991, Hopkins et al. 1995). These data suggest gestational metabolic demands for rockfish species could compromise incubating larvae in areas of low oxygen availability.

The broader ecological impacts of hypoxia are not insignificant for rockfish stocks. For instance, McClatchie et al. (2010) predicted significant habitat loss (18%) for *Sebastes* spp. in the Southern California Bight if the trend of shoaling of hypoxic waters does not reverse. Recurring hypoxia may fundamentally change the characteristics of a mature reef which include high levels of species diversity, abundance, biomass and larger body sizes of the associated fauna—all factors contributing to increasing reproductive opportunities and reproductive fitness of a stock (PISCO 2007). At Cape Perpetua, many species of fishes and invertebrates did not survive hypoxia in 2002 (Weeks et al. 2005). Although some rockfish returned to Cape Perpetua Reef in subsequent months and years, their abundance was reduced (Weeks et al. 2005) and the reef continues to be exposed to periodic seasonal hypoxia (PISCO hypoxia updates 2012: www.piscoweb.org/research/science-by-discipline/coastal-oceanography/hypoxia/hypoxia-updates). Although these conditions may degrade reef maturity, it is possible our fish may have an ecological advantage in the lack of competition with species which may not be as tolerant of hypoxia, particularly if prey is a limiting resource. In light of this, our quillback's potentially prey-seeking forays into open sand and gravel beds may support re-characterization of fish habitat for this species.

Although our study period encompassed a wide range of oxygen concentrations on the reef, severe hypoxia was not observed in the area in 2010, so we were not able to monitor fish movements during this greater physiological challenge; nor did we conduct the study during wintertime, when other studies have reported a seasonal component of habitat use for these species (Matthews 1990, Tolimieri et al. 2009, Hannah & Rankin 2011). It is possible that a study that captured anoxic conditions would reveal additional broad-scale movements for these and other species at Cape Perpetua.

The variability of behaviors described here and in other studies reiterates the complexity of evaluating fishes' responses to changing environmental conditions. Interacting factors including the origin, chemistry, and temperature of the hypoxic water mass and the species' innate behavioral tendencies must be considered—along with dissolved oxygen—in determining the effects of hypoxia on fish.

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