



Abstract—We used scuba over fixed-width strip transects to monitor seasonal abundances of brown rockfish (*Sebastes auriculatus*) and copper rockfish (*S. caurinus*) on a nearshore artificial reef in Puget Sound, Washington, over a 7-year period. Spring and fall abundances were intermediate and marked transitional phases between seasons of highest (summer) and lowest (winter) abundance for both species. Analyses of length classes indicated that the numbers of seasonal juvenile recruits were not sufficient to account for the marked differences in abundance between summer and winter. For both species, the proportion of large fish (≥ 20 cm in total length) to the total number observed in summer and winter was significantly greater during the winter. Late-stage gravid brown rockfish occurred in greatest abundance during the spring and late-stage gravid copper rockfish were observed only in the summer. We examined auxiliary data from a genetics study of brown rockfish that was conducted concurrently at the reef and interpreted the results, along with our survey findings, as providing compelling evidence of seasonal migrations on and off the reef.

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Seasonal changes in abundance and compelling evidence of migration for 2 rockfish species (*Sebastes auriculatus* and *S. caurinus*) inhabiting a nearshore, temperate-water artificial reef

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Understanding fish movement is paramount to the design and implementation of effective resource conservation and management strategies. Movement influences the dynamics, demographics, and genetics of populations; the structure and function of ecosystems; species interactions; modes of energy transfer; and biodiversity (Rothschild, 1986; Frank, 1992; Merz and Moyle, 2006; Clark et al., 2009; Condal et al., 2012). Known patterns of movement are often key considerations in the development of harvest management plans established to protect fish populations from overexploitation. For example, in the northeast Pacific Ocean, lingcod (*Ophiodon elongatus*) are widely believed to participate in seasonal nearshore–offshore spawning migrations (Jagiello, 1990, 1995), and in some regions (e.g., Puget Sound), recreational fisheries that target lingcod are managed to protect nearshore spawning fish (Palsson et al.¹). Pacific halibut (*Hippoglossus stenol-*

epis) also undergo seasonal migrations (St-Pierre²), and establishment of the commercial fishery season by the International Pacific Halibut Commission is designed in large part to protect offshore spawning populations (Loher, 2011).

Fish movement also has crucial implications for the design of scientific sampling strategies and stock assessments, and movement poses both operational and conceptual challenges for the selection of appropriate temporal and spatial scales in ecological studies. Inferences about the ecological processes under investigation may be constrained or confounded when, as is often the case, scales of operational convenience, rather than ecological relevance, are incorporated into study designs. Failure to identify and integrate fish movement into study designs can lead to the selection of temporal or spatial scales of observation that are ill-fitted to the study objectives, particularly when movement occurs over multiple habitat types. Sampling strategies that

¹ Palsson, W. A., T. J. Northup, and M. W. Barker. 1998. Puget Sound Groundfish Management Plan, 48 p. Washington Dep. Fish Wildl., Olympia. [Available at [website](#).]

² St-Pierre, G. 1984. Spawning locations and season for Pacific halibut. Int. Pac. Halibut Comm., Sci. Rep. 70, 46 p. [Available at [website](#).]

focus on single habitat types are also subject to bias when based on untested assumptions about habitat use, extent of home range, and site fidelity, as reviewed by Pittman and McAlpine (2003). These authors assert that if information on movement is not available, the assumption of single habitat use should be considered carefully or rejected entirely. They advocate for an assumption of the use of multiple habitats because it allows for the consideration of broader-scale movement and potential linkages among habitat types. Movement patterns, whether over short (e.g., diel) or long (e.g., seasonal, annual) temporal scales, rank as one of the most important behavioral sources of bias in fish stock assessments (Gayanilo and Pauly, 1997; Sparre and Venema, 1998). Statistical methods for incorporating patterns of fish movement into stock assessments are advancing (Hilborn and Walters, 1992; Methot, 2011), and the integration of known fish behavior parameters, such as diel and seasonal movements, will likely lead to substantial improvements in the accuracy of stock assessment models (Fréon et al., 1993).

Although the potential conservation benefits of individual marine protected areas (MPAs) have been discussed for decades, there is currently a growing worldwide interest in establishing coordinated networks of MPAs that are ecologically joined over broad geographic regions, and this approach has been advocated for rockfishes in the northeast Pacific Ocean (Yoklavich, 1998; Parker et al., 2000). Further, understanding migrations and other movement patterns of adult rockfishes has been identified as critical for formulating effective recovery plans that may include MPAs for rockfishes in Puget Sound (Wyllie-Echeverria and Sato, 2005). The trend toward MPAs, however, is not without controversy—much of it centering on how to choose and configure MPA sites into mosaics that are adequately sized and placed to achieve prescribed conservation goals. The related and equally critical issue of how best to assess the performance of such networks once established is also a topic of considerable debate. The size and placement controversy owes much of its genesis to attempts at applying theories of island biogeography to the design of nature reserves (Diamond, 1975) and continues under what is widely known as the SLOSS (single large or several small) debate (Simberloff and Abele, 1982). Fundamental to the debate is the concept of source-sink dynamics (Pulliam, 1988) whereby, under optimal MPA performance conditions, increased regulatory protection is expected to result in a net export of individuals to unprotected habitat or to marginally suitable habitat within an MPA through larval advection, density-dependent displacements of later life history stages (spillover), or both. Many criteria for MPA design and site selection lack robust scientific justification and most established temperate-water MPAs are not subjected to systematic, or even periodic, performance evaluations relative to fishery enhancement, species recovery, biodiversity preservation, or other desired outcomes. Although the number of theoretical MPA performance models is proliferating (Willis et al.,

2003), and presumably improving, these models rarely incorporate fish movement (but see Attwood and Bennett, 1995; Roberts and Sargant, 2002; Berezansky et al., 2011). Understanding the frequency, periodicity, and scale of fish movement will aid modelers and resource managers in choosing and scaling MPA sites, and in constructing MPA networks that adequately serve the ecological needs of species targeted for conservation.

In this study, we seasonally monitored the abundance of 2 demersal rockfish species, brown rockfish (*Sebastes auriculatus*) and copper rockfish (*S. caurinus*) over a 7-year period on an artificial reef in Puget Sound, Washington. Counts for each of the 2 species were obtained by using scuba-based underwater visual censuses (UVCs) conducted over fixed-width strip transects. Brown and copper rockfish belong to the subgenus *Pteropodus* and occur sympatrically in many regions of the northeast Pacific Ocean, including much of Puget Sound. They share similar life history attributes, habitat affinities, behavioral characteristics, and food preferences (Washington et al.³; Lea et al., 1999; Stout et al., 2001; Love et al., 2002) and, in Puget Sound there is evidence of hybridization between the species (Seeb, 1998; Schwenke, 2012). In Washington State, they are managed as “bottomfish” and brown rockfish stock status throughout Puget Sound is classified as “precautionary,” whereas copper rockfish are classified as either precautionary (north Puget Sound) or “vulnerable” (south Puget Sound), as defined by Palsson et al.⁴

Although tagging studies involving brown or copper rockfish have occurred throughout much of the range of these species and have encompassed a variety of investigative objectives (Miller et al., 1967; Miller and Geibel, 1973; Dewees and Gotshall, 1974; Hallacher, 1977; Walton⁵; Laufle⁶; Gowan, 1983; Mathews and Barker, 1983; Hueckel et al.⁷; Matthews, 1985; Matthews et al., 1987; Hartmann, 1987; Matthews, 1990a; Matthews, 1990b; Lea et al., 1999; Eisenhardt, 2004; Lowe et al., 2009; Tolimieri et al., 2009; Reynolds et al., 2010; Longabach, 2010; Starr et al.⁸; Hannah and

³ Washington, P. M., R. Gowan, and D. H. Ito. 1978. A biological report on eight species of rockfish (*Sebastes* spp.) from Puget Sound, Washington, 50 p. Northwest Alaska Fish. Cent. Proc. Rep. Northwest Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle. [Available at [website](#).]

⁴ Palsson, W. A., T.-S. Tsou, G. G. Bargmann, R. M. Buckley, J. E. West, M. L. Mills, Y. W. Cheng, and R. E. Pacunski. 2009. The biology and assessment of rockfishes in Puget Sound. Wash. Dep. Fish Wildl. FPT-09-04, 208 p. [Available at [website](#).]

⁵ Walton, J. M. 1979. Puget Sound artificial reef study. Wash. Dep. Fish., Tech. Rep. 50, 130 p.

⁶ Laufle, J. C. 1982. Biological development and materials comparisons on a Puget Sound artificial reef. Wash. Dep. Fish. Tech. Rep. 72, 183 p.

⁷ Hueckel, G. J., R. M. Buckley, and B. L. Benson. 1983. The biological and fishery development on concrete habitat enhancement structures off Gedney Island in Puget Sound, Washington. Wash. Dept. Fish. Tech. Rep. 78, 67 p.

⁸ Starr, R. M., D. Wendt, K. T. Schmidt, R. Romero, J. Dur-yea, E. Loury, N. Yochum, R. Nakamura, L. Longabach, E.

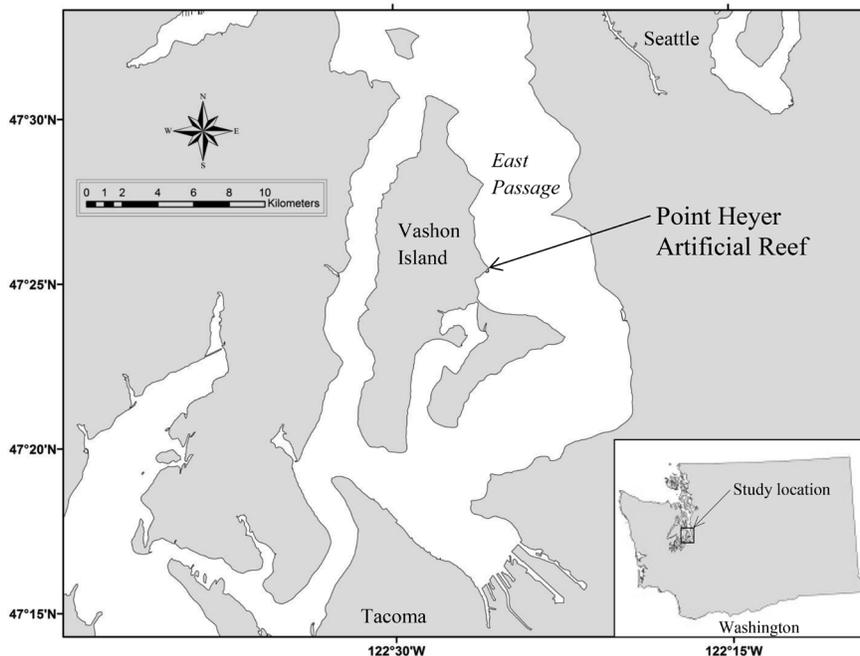


Figure 1

Location of Point Heyer Artificial Reef in central Puget Sound, Washington, where 2 rockfish species (brown rockfish [*Sebastes auriculatus*] and copper rockfish [*S. caurinus*]) were monitored over a 7-year period to determine seasonal changes in abundance and to find evidence of seasonal migrations.

Rankin, 2011; Hanan and Curry, 2012; Rankin et al., 2013), long-term trends in seasonal abundance have not been specifically addressed, and drawing informed conclusions from these studies about potential seasonal changes in abundance or movement patterns is hampered by the temporal or spatial scales over which they were conducted, numbers of fish tagged, or insufficient information (e.g., mark and recapture dates). Collectively, the studies indicate that most adults of both species maintain high site fidelity, although some exceptions have been observed; that habitat type (e.g., high-relief, low-relief, natural, artificial) may influence site fidelity and movement behavior; and that some level of homing ability from beyond their putative home range is likely. Estimates of home range for brown and copper rockfish vary widely, from <math><10\text{ m}^2</math> over high relief habitat to 4656 m^2 over low relief habitat (Matthews 1990b; Tolimieri et al., 2009; Rankin et al., 2013).

The goal of our study was to determine whether there were patterned seasonal changes in abundance on the reef for either species, and if so, whether the observed patterns differed between species. In order to gain further insight into our monitoring results, we examined auxiliary data from a genetic study of brown

rockfish that was conducted concurrently at our study site. These data, along with our findings, are discussed in the context of providing compelling evidence of rockfish migratory behavior. Migrations are well known for many temperate-water marine fishes (e.g., cods, herrings, and sharks) and are often associated with changes in seasonally variable resources, such as food supply or shelter, or with spawning or mating behaviors (Harden Jones, 1968; McCleave et al., 1984; McKeown, 1984; Smith, 1985).

Materials and methods

Point Heyer Artificial Reef (PHAR) is a high-relief, insular reef located along the eastern shore of Vashon Island in the hydrographically defined “main basin” (Ebbesmeyer et al. 1984) of central Puget Sound (Fig. 1). Puget Sound is a glacially formed saltwater estuary fjord characterized by mixed semidiurnal tides. It is connected to the Pacific Ocean through one, approximately east-west running strait (Strait of Juan de Fuca) that is bounded to the north by Canada’s Vancouver Island, and by a north-south running inland waterway between Vancouver Island and the Canadian mainland. It consists of 5 sub-basins that are separated by shallow-water sills. The bathymetry of Puget Sound extends to depths of nearly 300 m (all depths reported herein are corrected to mean lower low water depths).

Nakada, D. Rasmussen, N. Hall, K. Green, and S. McMillan. 2010. Baseline surveys of nearshore fishes in and near central California marine protected areas 2007–2009. Final project report submitted to the Ocean Protection Council, 124 p. California Sea Grant College Program, La Jolla, CA. [Available at [website](#).]

The reef was constructed in 1983 by the Washington Department of Fisheries (now the Washington Department of Fish and Wildlife) for the purpose of increasing the number of productive recreational fishing sites in the region (Buckley 1982). It covers an area of approximately 5400 m² and is constructed of various-size quarried boulders and cobble interspersed with long horizontally placed concrete beams. The near- and offshore margins of the reef lie at a depth of about 4 and 36 m, respectively. The surrounding seafloor consists primarily of unconsolidated sand, shell hash, and gravel, as well as widely dispersed small glacially deposited boulders. The reef is situated on a steeply sloping bottom that descends to depths of nearly 240 m over a distance of about 3 km to the approximate center of the passage that separates Vashon Island from the mainland (East Passage, Fig. 1). Large year-round patches of eelgrass (*Zostera spp.*) occur in the shallow water shoreward of the reef and dense growths of perennial nonfloating macroalgae (e.g., laminarians, ulvas, palmarials) form over the shallower portions of the reef during the summer and fall. Bull kelp (*Nereocystis leutkeana*), the predominant canopy-forming floating kelp in Puget Sound, does not grow on or near the reef. Twenty-two years had elapsed between the construction of the reef and the commencement of our study and we presume that sufficient time had passed for ecological succession to have occurred.

In 2005, 3 permanent straight-line 60-m transects (T-1, T-2, and T-3), each running due east–west (as per standard compass) and separated by a distance of at least 10 m, were established on the reef. The transects ran perpendicular to shore and were strategically placed in order to capture the dominant micro- and macrohabitat features of the reef (e.g., boulder, cobble, beams, sandy bottom, high and low relief, reef margins, crevice and overhang space). The nearshore ends were positioned in 4.5, 4.0, and 6.0 m and the offshore ends in 21.5, 21.0, and 20.5 m for T-1, T-2, and T-3, respectively. The offshore ends of each transect were semipermanently marked with a buoyed line of about 1 m in length fastened to a hollow-core cinder block of approximately 40×20×20 cm affixed to the seafloor with 2 steel bars. Coordinates (based on the North American Datum of 1983) for the offshore markers were as follows: T-1, 47.420040°N, 122.427145°W; T-2, 47.420082°N, 122.427182°W; T-3, 47.420579°N, 122.426947°W. Real-time coordinate-corrected positions were obtained by connecting a line between the transect marker to a surface buoy and registering the position with a GeoExplorer 6000 Centimeter Edition⁹ GPS receiver (Trimble Navigation Ltd., Sunnyvale, CA).

The transects were divided into twelve, 5-m segments each and were surveyed by scuba divers swimming in tandem along the bottom from deep to shallow

and pausing briefly at each segment marker. During surveys, divers counted fish in each segment on their respective sides of the transect centerline to a width of 2 m (total bottom coverage per transect=240 m²) and as high into the water column as visibility permitted. Hand-held lights were used to search beneath overhangs, in crevices, and in other poorly lit areas. In order to ensure consistent effort among surveys, the slowest practical swimming speed was maintained over each transect as governed by the maximum allowable safe bottom-time using conventional scuba.

All species of fish that were conspicuous to the divers were recorded and enumerated. Highly cryptic species or species that remain very small into adulthood, though occasionally noted, were not targeted in the search effort. Careful written and hand-signal communication between divers reduced the risk of counting fish twice when they were swimming across transect from one survey lane to the other. Individual fish from the 3 most visually dominant taxonomic families (Sebastidae, Embiotocidae, and Hexagrammidae) were recorded to species and their length (all fish lengths herein are reported as total length [TL] in centimeters) was estimated into length classes, which varied among species. The occurrence of apparent late-stage gravid brown and copper rockfish, evidenced by their prominently distended abdomens, was also noted. Cooper (2003) showed that bulging abdomens can be a reliable means for identifying late-stage gravid copper rockfish when they are viewed underwater.

In 2005, surveys were conducted on all 3 transects during the summer, but only on T-2 in the fall, and no surveys were conducted during the spring of 2005 or the winter of 2005–2006. Beginning in the spring of 2006, each transect was surveyed at least once during each season through summer of 2012. In most instances, multiple transects were not surveyed on the same day. The order in which transects were surveyed during any given season was randomly determined. No attempt was made to synchronize the surveys to the cycle of the tides; therefore the surveys occurred over a broad range of tidal conditions. Strong tidal currents are not generally encountered over the reef and current velocities rarely exceed 1.5 knots. The mean range of the tide at PHAR is approximately 2.4 m. Temperature data loggers (HOBO[®] Pro v2, Onset Computer Corporation, Bourne, MA) were deployed at the near- and offshore margins of the reef (4.5 m and 28 m, respectively) and they recorded water temperature every 4 hours for a period of one year beginning 8 December 2006.

In order to mitigate the potential effects of observer variation, only 5 divers were used throughout the entire course of the study and all surveys on the south side of the transect center-lines were conducted by the same diver. Four different divers conducted surveys on the north side of the transect center-lines; but nearly all (~96%) of those surveys were conducted by just 2 divers. All scuba divers had extensive experience in surveying rockfish on Puget Sound rocky reefs prior to

⁹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the Washington Department of Fish and Wildlife or the National Marine Fisheries Service, NOAA.

Table 1

Number of surveys, by season and tide cycle, conducted over a 7-year period (from summer 2005 through summer 2012) at Point Heyer Artificial Reef, Puget Sound, Washington.

Transect	Flood tide	Ebb tide	Slack water before flood tide	Slack water before ebb tide	Total surveys by transect
Spring					
T-1	4	4	1	3	12
T-2	2	5	0	1	8
T-3	3	4	1	0	8
Summer					
T-1	0	6	1	0	7
T-2	2	6	0	0	8
T-3	3	7	0	0	10
Fall					
T-1	3	3	1	0	7
T-2	7	0	0	1	8
T-3	6	1	0	0	7
Winter					
T-1	2	3	0	1	6
T-2	2	4	0	0	6
T-3	1	5	0	0	6
Grand totals	35	48	4	6	93

participating in this study, and they periodically used hand-held graduated staffs to calibrate their visual estimates of fish length.

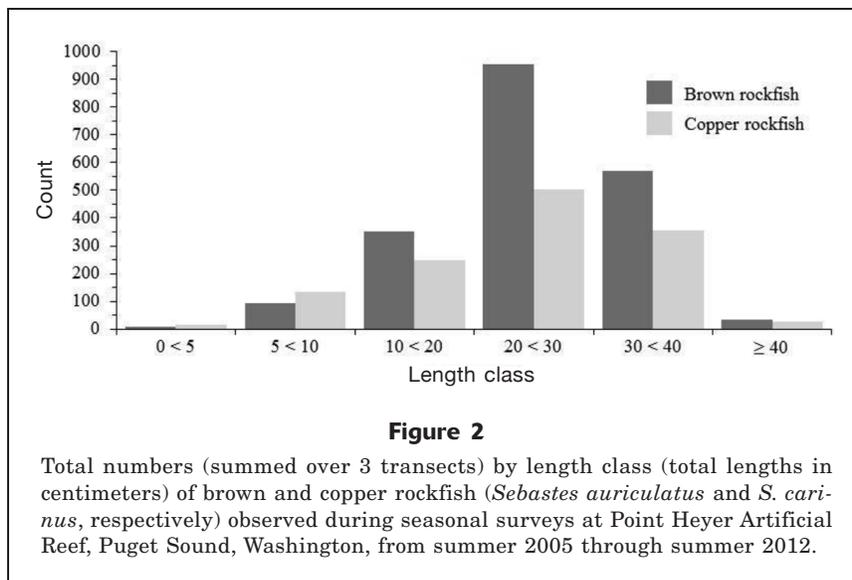
The genetic data were compiled from a study in which molecular markers had been used to estimate genotyping error rates from brown rockfish captured at PHAR (Hess et al. 2012). In that study, 718 brown rockfish ranging in length from 10 to 37 cm (M [mean]=22; SD [standard deviation]=7.1) were sampled and returned alive to their point of capture during all seasons between spring of 2004 and summer of 2009. The genetic data were used to identify individuals that were recaptured in multiple years.

Results

A total of 93 survey dives were conducted between 30 June 2005 and 18 September 2012. All surveys commenced between 1.5 and 7 hr after sunrise (M=4 hr, SD=1.2), and the mean survey time per transect was 28 minutes (SD=7.8). In no case was diver-estimated visibility less than twice the width of a survey lane. The numbers of surveys by tide cycle are presented in Table 1. The total numbers of brown and copper rockfish observed by length class summed over all 3 transects are presented in Figure 2. A list of all species recorded on transect over the course of the study (a subjective appraisal of how often the species were observed) and length classes for species from the 3 visu-

ally dominant taxonomic families are presented in the [Supplementary Table](#).

We fitted a generalized linear mixed model (GLMM) to the data by maximum likelihood by using the Laplace approximation and a Poisson link with the lme4 package, vers. 1.1-8 (Bates et al., 2015) and statistical software R, vers. 3.1.1 (R Core Team, 2014). For each of the 2 species, we ran a random effects only (null) model with count as the response variable, and year and transect as random effects. We then added season as the explanatory variable to produce a full model. We used ANOVA to compare the null and full models and for both species the results were significant ($\chi^2=386.64$ and 214.09 [3 df] for brown and copper rockfish, respectively, $P<0.001$). The full model was selected over the null model by both Akaike information criteria (Akaike, 1974) and Bayesian information criteria (Schwarz 1978). The log-likelihood increased, and the deviance, which in linear models is equal to the residual sum of squares, decreased with the full model, further indicating that the full model provided a better fit to the data (Table 2). The GLMM back-transformed seasonal mean counts with 95% confidence intervals (confidence intervals were computed before back-transformation) are presented in Figure 3. We conducted a multiple means comparison of counts between seasons with Bonferroni corrected alpha (0.0042 from 0.05) to test the null hypothesis of no difference in mean counts between seasons. For both species, spring was not significantly different from



summer, fall, or winter; summer was significantly different from fall and winter; and fall was significantly different from winter.

For each species and for any given year, the summer fish density summed over all length classes was more than twice that for winter, and the densities did not vary greatly over time. To evaluate the potential impact of seasonal juvenile recruitment on overall seasonal abundances, we combined the 2 smallest length classes (<5 and 5<10 cm) and examined the relative proportion of these fish to the overall counts, by season, and summed over all surveys for both brown and copper rockfish. The number of juveniles encountered was greatest during the summer for both species, as was the relative proportion of juvenile copper rockfish to the total number of copper rockfish encountered (14%). Brown rockfish juveniles, however, represented the greatest proportion during the winter (9%) (Fig. 4). We used a two-tailed z-test for comparison of 2 proportions

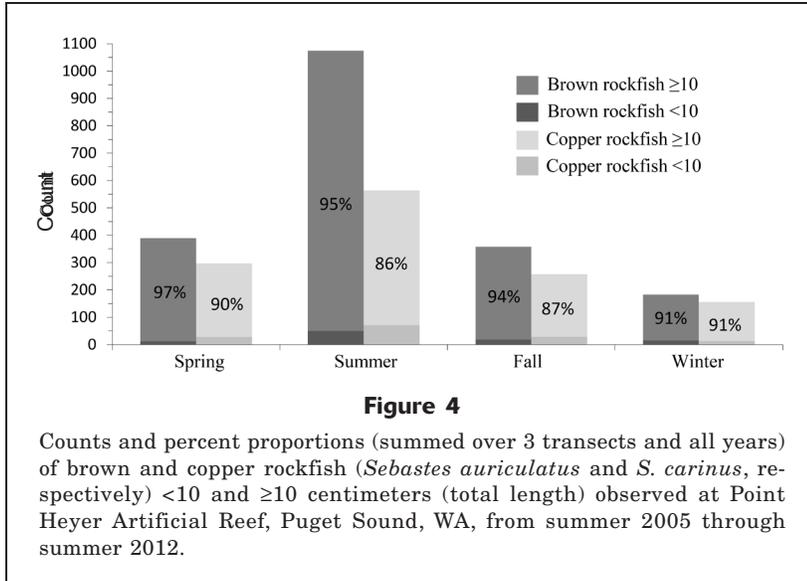
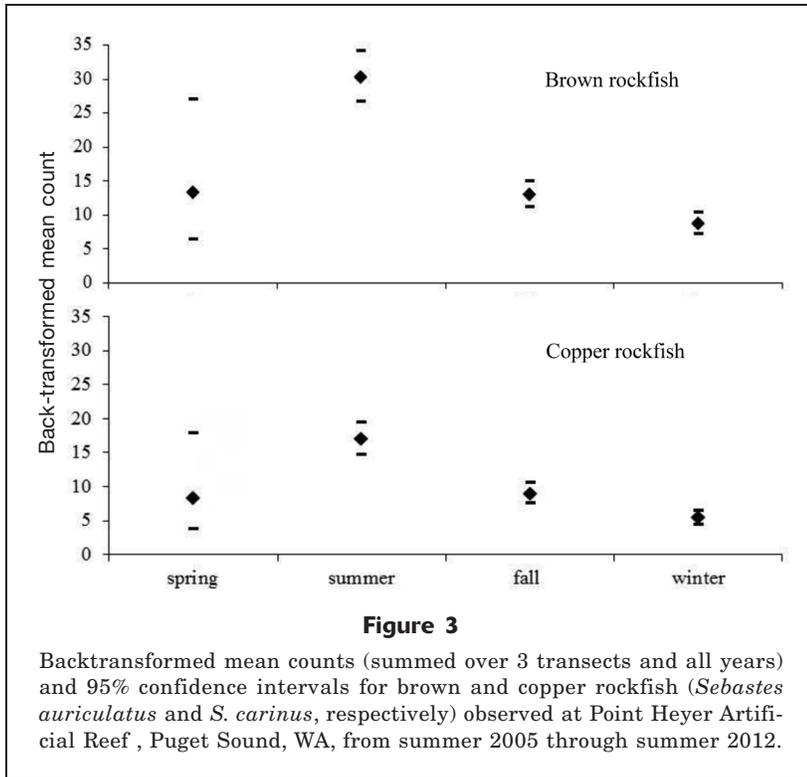
to determine whether juvenile rockfishes composed a significantly greater proportion of the total number of fish observed during either summer or winter. The proportion of juvenile brown rockfish was significantly greater in the winter ($z=2.2, P<0.05$), but the proportions did not differ significantly between summer and winter for copper rockfish ($z=1.6, P>0.05$) (satisfactory $n \cdot p_i > 5$ and $n[1-p_i] > 5$ sample-size tests where n =sample size and p =proportion).

To determine whether there were qualitative differences between brown and copper rockfish that occupied the reef in the summer and winter we divided them into 2 length classes, small (<20 cm) and large (≥ 20 cm). Summed over all surveys, the densities of both small and large fish were greatest during the summer, and large fish were more abundant than small fish year round (Fig. 5). For both species, the proportion of large fish to the total numbers observed was significantly greater in the winter ($z=2.5$ [brown rockfish] and 4.2

Table 2

Summary of analysis of variance (ANOVA) comparisons between generalized linear mixed model (GLMM) null models (fish count as the response variable, and year and transect as random effects) and full models (season added as explanatory variable) for seasonal counts of brown and copper rockfish at Point Heyer Artificial Reef, Puget Sound, WA.; AIC=Akaike information criteria; BIC=Bayesian information criteria; df =degrees of freedom.

Model	df	AIC	BIC	Log-likelihood	Deviance	χ^2	χ^2 df	$P(>\chi^2)$
Brown rockfish Null model	3	1032.33	1039.93	-513.17	1026.33			
Brown full								
Full model	6	651.69	666.89	-319.85	639.69	386.64	3	<0.001
Copper rockfish Null model	3	1003.44	1011.04	-498.72	997.44			
Copper rockfish								
Full model	6	795.36	810.55	-391.68	783.36	214.09	3	<0.001



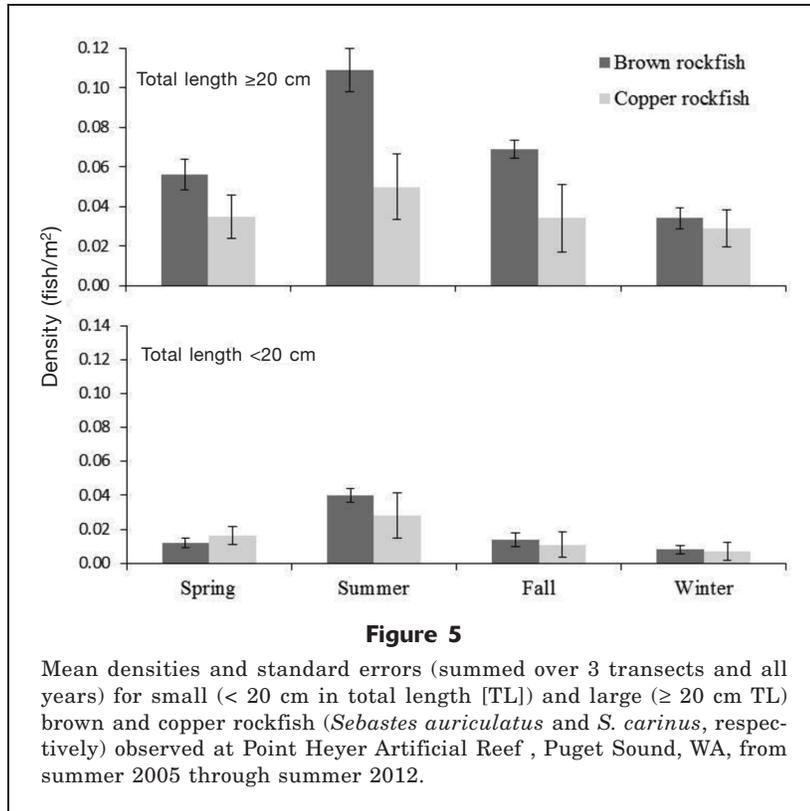
[copper rockfish], $P < 0.05$; two-tailed z-test for comparison of 2 proportions; satisfactory $n \cdot p_i > 5$ and $n[1 - p_i] > 5$ sample size tests) (Fig. 6).

Summed over all surveys, a total of 70 late-stage gravid brown and copper rockfish were observed, all of these in the spring and summer. Of the total number of brown rockfish ≥10 cm observed in the spring ($N = 377$) and summer ($N = 998$), 9% and 2%, respectively, were noted as late-stage gravid (we assume that no

female rockfish reach maturity at <10 cm [Washington et al.³; Gowan, 1983]). Late-stage gravid copper rockfish were only observed during the summer, and of the total number of copper rockfish ≥10 cm observed (493), 3% were noted as late-stage gravid (Fig. 7). If we assume a population sex ratio of 1:1, the percentages double with respect to the total number of potential female spawners. In order to determine whether there were differences in time of spawning by length, we grouped the late-stage gravid brown rockfish into 2 length classes (10 < 30 and ≥30 cm) on the basis of 50% maturity at approximately 30 cm TL (Love et al., 2002). The proportion of late-stage gravid brown rockfish ≥30 cm to the total numbers of late-stage gravid fish observed in the spring and summer was significantly greater in the spring ($z = 2.4$, $P < 0.05$; z-test for comparison of 2 proportions; satisfactory $n \cdot p_i > 5$ and $n[1 - p_i] > 5$ sample-size tests).

Fifty-one (7%) of the 718 brown rockfish ≥10 cm sampled by Hess et al. (2012) were fish that had been recaptured (2 of these were recaptured twice) according to genotype matching. The number of days at liberty between first and final capture ranged from 1 to 1518 ($M = 615$; $SD = 448.8$). Thirty-one fish (4%) ranging in length from 17 to 35 cm ($M = 27$; $SD = 4.1$), including the 2 fish that were recaptured twice, were at liberty for more than one year between first and final capture. A total of 136 (19%) of the 718 samples were from late-stage gravid fish and 12 of those were captured twice in late-stage gravid condition in different years. The number of days at liberty between captures for these fish ranged from 328 to 1469 ($M = 635$; $SD = 447.2$). Overall, the lengths of the late-stage gravid brown rockfish sampled ranged from 21–35 cm ($M = 27$; $SD = 3.28$; includes only the length at time of first capture for fish that were captured twice).

Minimum and maximum recorded temperatures during 2006–2007 at the near- and offshore margin of the reef ranged from 7.5° to 14.6°C and from 8.1° to 13.4°C, respectively. Mean daily temperature changes were at least twice as great in the spring and summer as they were in the fall and winter at both locations, and daily temperature fluctuations tended to be slightly greater at the nearshore margin year-round (Table 3, Fig. 8). The mean monthly air temperatures during the 12-month water temperature recording period were all within 2% of the aver-



age monthly air temperatures summed over a 12-year period beginning in 2000 and recorded at a weather observation station located less than 10 km from PHAR. Our water temperature data were therefore deemed to be an acceptable proxy for trends in seasonal temperature at PHAR during the study.

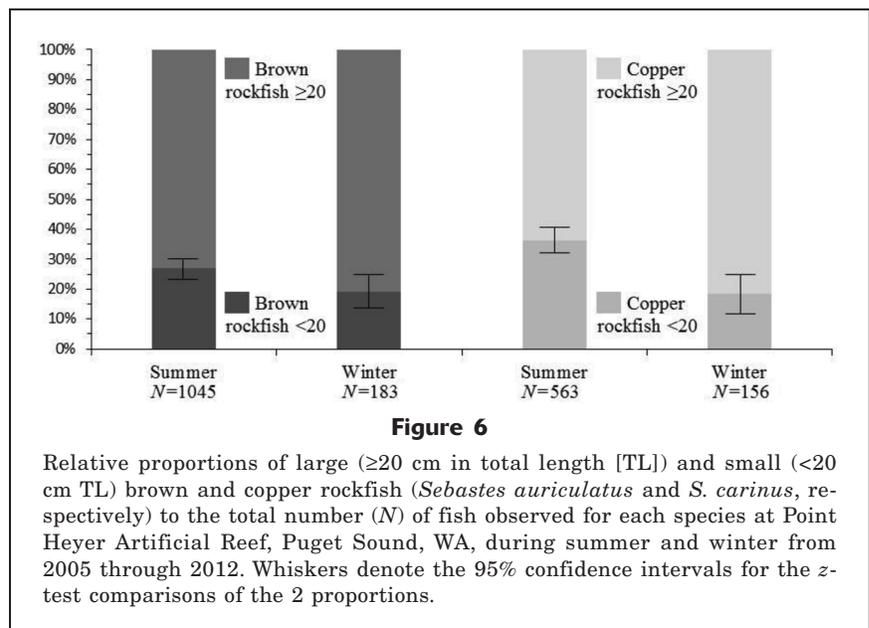
Discussion

The different sensory inputs that motivate animals to move and the variety of spatiotemporal scales over which movements may occur has led to some blurring among specialists over what constitutes migration (Dingle and Alistair Drake, 2007). The most broadly accepted definitions of fish migration include some element of to-and-fro movement during the life cycle of a fish, and some predictability of occurrence. Heape (1931) described migration as, "...that class of movement which impels migrants to return to the region from which they have migrated." Harden Jones (1984) defines fish migration as "...a coming and going with the seasons on a regular basis..." Migration

is usually distinguished from emigration (a form of dispersal), whereby return to an area does not occur (Lidicker and Stenseth, 1992), or occurs only by chance. Adding confusion (or clarity, depending on one's perspective) to characterizing fish movement is the concept of home range (Burt 1943). According to McLoughlin and Ferguson (2000), home range is established once the cumulative area that is used ceases to increase over time (i.e., an asymptote is reached). However, and consistent with Burt (1943), it is generally accepted that home ranges comprise only those areas within which routine activities occur over finer temporal scales, and that they do not include infrequent spatially broad-scaled movements, migration corridors, or the movements of planktonic life history phases for which the total area used may not reach an asymptote over time.

We have shown that both brown and copper rockfish exhibited pronounced changes in abundance between summer and winter at PHAR, that the changes occurred with regularity over a broad time span, and that the observed patterns were similar for both species.

Whether the seasonal changes in abundance reflect migratory behavior hinge on whether the same fishes return to repopulate the reef during the summer. If, for instance, fish populations disperse over broad geographic areas while overwintering in deeper water and return to shallower water without predilection toward



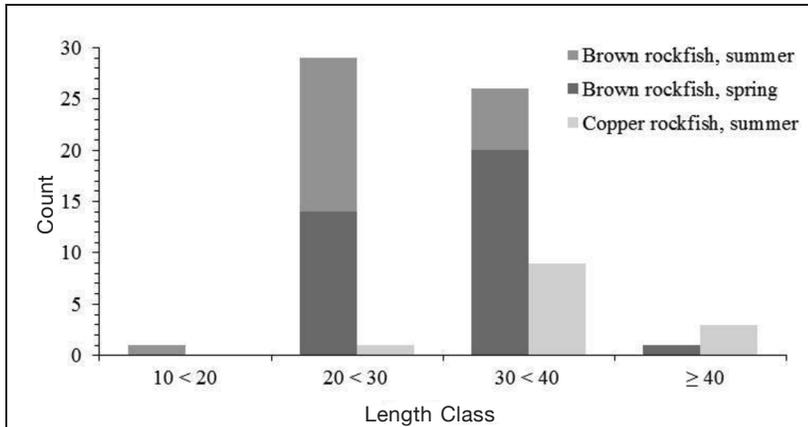


Figure 7

Total numbers (summed over 3 transects) of visually apparent late-stage gravid brown and copper rockfish (*Sebastes auriculatus* and *S. carinus*, respectively) by length class (total lengths in centimeters) observed during seasonal surveys at Point Heyer Artificial Reef, Puget Sound, WA, from summer 2005 through summer 2012. Note: Late-stage gravid copper rockfish were observed only during the summer, and late-stage gravid brown rockfish were observed only in the spring and summer.

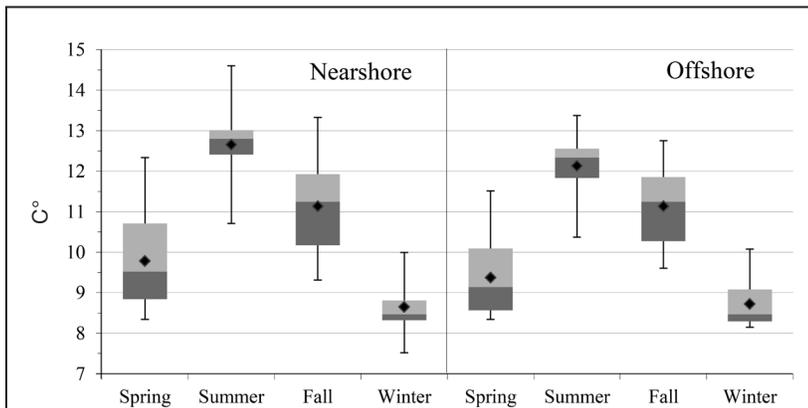


Figure 8

Temperatures at the near- and offshore reef margin, by season, at Point Heyer Artificial Reef, Puget Sound, WA, during 2006–2007. Whiskers indicate the minimum and maximum temperatures recorded, boxes capture the first and third quartiles, and the mean is denoted by a diamond shape.

their nearshore point of departure, then the behavior may be characterized as emigrative (Heape, 1931). Moreover, if emigrant populations lose their cohesiveness once they leave the reef, the seasonal return of itinerant individuals to the nearshore environment would result in an annual shuffling of members among geographically proximate, or possibly even distant, populations. Whether emigrants wander as groups or individuals, their return to the nearshore environment could serve to replenish local populations with harvest-size fishes, and may provide a buffer against

localized overfishing provided they arrive from populations that are capable of sustaining a net export of individuals (i.e., source populations sensu stricto Pulliam, 1988). Conversely, local populations made up predominantly of seasonal migrants may be more vulnerable to depletion because replenishment would be less dependent on harvest-sized immigrants and more dependent on reproductive success and juvenile recruitment, both of which are known to be highly variable for rockfishes (Leaman and Beamish 1984; Ralston and Howard 1995; Ralston et al., 2013). We note here that the aforesaid statement lies in contrast to Mathews and Barker's (1983) view that local populations of "migratory" rockfishes would be less vulnerable to depletion; however, their opinion appears to have been formed around an implied working definition of migration that includes any type of movement beyond a narrowly defined geographic area, and without regard to whether the same fish are coming and going. This contrast in conclusions serves to underscore the importance of adequately defining the terms used to characterize fish movements.

We could not determine whether the brown rockfish recaptures identified by Hess et al. (2012) that were at liberty for more than one year remained on the reef year-round or left the reef in the winter and returned during the summer (i.e., migrated), although only one of the fish was recaptured in the winter. The recapture data indicate some degree of reef fidelity for some brown rockfish at PHAR. The relatively low abundance of brown rockfish on the reef during the winter, the year-round sampling effort, and the high rate of recapture in relation to effort lend substantial credence to the notion of seasonal movements by individuals on and off the reef over spatial scales that exceed reported maximum home ranges. Further, the 12

genetically identified brown rockfish that were encountered as late-stage gravid individuals in multiple years indicate that more than one spawning by the same fish occurred at the same location (assuming the fish carried their larvae through to parturition).

Diver effects on fish behavior can be a significant source of bias when producing estimates of standing stock or community structure by using noninstantaneous UVCs (i.e., strip transects) (see Bozec et al., 2011 and references therein). In this study, we assumed that bias due to diver effects remained constant over time

Table 3

Maximum and mean daily temperature (t) (°C) changes (Δt) by season recorded at the near- and offshore reef margins of Point Heyer Artificial Reef, Puget Sound, WA, during 2006–2007. SD=standard deviation.

Reef margin	Spring		Summer		Fall		Winter	
	24 hr max. Δt	Mean daily Δt (SD)	24 hr max. Δt	Mean daily Δt (SD)	24 hr max. Δt	Mean daily Δt (SD)	24 hr max. Δt	Mean daily Δt (SD)
Nearshore	2.2	0.7 (0.44)	2.1	0.8 (0.44)	1.1	0.3 (0.21)	1.1	0.2 (0.22)
Offshore	1.6	0.4 (0.31)	1.7	0.6 (0.32)	0.6	0.2 (0.14)	0.8	0.2 (0.19)

and thus was not a factor in assessing relative changes in abundance. Tides were also not judged to be a factor because the numbers of summer and winter surveys by tide cycle were not substantially different. Although rockfish are popular among Puget Sound anglers, recreational harvest was considered an unlikely source of bias, and commercial rockfish harvest is prohibited in central Puget Sound. From spring of 2005 through fall of 2006 the reef was closed to all rockfish retention. From fall of 2006 through spring of 2010, the rockfish season and retention rules were highly restrictive in Puget Sound, and PHAR attracted very few anglers. The minimal harvest that did occur took place during the summer, when rockfish abundance was highest. Since May of 2010, recreational rockfish retention throughout nearly all of Puget Sound, including PHAR and adjacent waters, has been prohibited. Effects from potential diel movements were also dismissed as a source of bias in estimating rockfish densities because all surveys were conducted approximately halfway between sunrise and mid-day.

Moulton (1977) observed a winter decrease in copper rockfish densities over the course of scuba surveys of nearshore rocky reefs in north Puget Sound. On the basis of seasonal density differences, over multiple depth strata, he concluded that over-wintering in deeper water beyond the survey range of his study was the most likely explanation. Richards (1987), observing a similar trend over rocky habitats, offered an alternative explanation. She postulated that reduced activity and more cryptic behavior by copper rockfish during winter months can lead to lower abundance estimates from scuba surveys over rocky habitat. This hypothesis is consistent with Patten's (1973) observation that copper rockfish on a small low-relief rocky reef in Puget Sound were more thigmotactic in the winter and spring. Similar behavior has been noted for dusky (*S. ciliates*) and yellowtail (*S. flavidus*) rockfish surveyed by scuba divers in southeast Alaska (Carlson and Barr, 1977). In reference to Richards' (1987) observation, Matthews (1990c) noted that winter decreases in brown and copper rockfish abundance had been observed in the nearshore environment of Puget Sound over sparsely vegetated low-relief reefs and sandy-bottom habitat, where hiding space is limited or nonexistent. The same

author, however, also reported that brown and copper rockfish were more reclusive on high-relief reefs during the winter (Matthews, 1990a).

To ensure that our observed winter decreases in abundance were not due to fish moving into the interstices of the reef and beyond our vision, divers equipped with digging and prying tools searched for fish by excavating several off-transect boulder and cobble sites during the winter months. The excavations occasionally revealed rockfish that could have gone unnoticed with the use of our standard survey method, but the encounters were rare and we do not believe that they occurred with enough frequency to explain the marked decreases in abundance we observed during the winter. Also, several surveys, with roving divers covering distances of up to 2.5 km of the nearshore waters adjacent to and on either side of PHAR, were conducted during the winter in order to ascertain whether winter decreases in abundance might have been due to fish moving off the reef but remaining nearby within the same depth strata. No rockfish were encountered during any of these off-reef surveys. It was also possible that fish may have been crowding the deepest parts of the reef (beyond our maximum survey depth) during the winter. We conducted several winter dives along the deep offshore margin of the reef and found no evidence to indicate that fish remained, though at greater depths than those surveyed, on or near the reef during the winter.

For some fish species, seasonal changes in abundance may be attributed to an influx of juveniles that leads to higher counts during certain times of the year (Allen and Horn, 1975; Relini et al., 1994, Allen et al., 2002, Barreiros et al., 2004). In our study, although the proportion of juvenile brown rockfish was significantly greater in the summer, juveniles of both species (length <10 cm) accounted for a very small proportion of the overall counts by season. Young-of-the-year fish made up an even smaller proportion because the <10 cm length class would have included some fish that were greater than 1 year in age. We conclude that the seasonal changes in abundance that we observed were not due to juvenile recruitment. The higher overall number of copper than brown rockfish juveniles observed during the spring, summer, and fall is likely due to

the highly successful recruitment of juvenile copper rockfish observed in Puget Sound in 2006 (LeClair et al., 2007; Palsson et al., 2012). Although the numbers of juveniles did not influence the overall pattern of change in seasonal abundance for either species, juvenile recruits during one or more years may have been plentiful enough to account for the overall statistically significant greater proportion of small fish (< 20 cm) observed in the summer. Other potential explanations for the disproportion include seasonal mortality, predation, and movement.

Washington et al.³ and Gowan (1983) reported female first-spawning lengths for both brown and copper rockfish in Puget Sound to be in excess of 20 cm (age 3–4 years) and our observations at PHAR are in general agreement, although a single late-stage gravid brown rockfish less than 20 cm was encountered in our study and we have observed late-stage gravid brown rockfish elsewhere in Puget Sound as small as 18 cm (determined by cannulation). All of the late-stage gravid brown rockfish sampled by Hess et al. (2012) were in excess of 20 cm. In our study, the percentages of late-stage gravid rockfish in relation to the number of potential female spawners are conservative because some fish ≥ 10 cm would not have reached maturity. The higher numbers of late-stage gravid brown rockfish encountered by Hess et al. (2012) than the numbers we observed reflect an intentional sampling bias toward gravid rockfish in their study.

We observed more late-stage gravid brown rockfish in the spring ($N=35$) than in the summer ($N=22$). The larger length classes comprised a statistically significant greater proportion of the spring observations, and this is consistent with Bobko and Berkeley (2004) and Love et al. (1990), who found that parturition occurs earlier for older black (*S. melanops*) and yellowtail rockfish. Cooper (2004) also found the same to be true for copper rockfish in Puget Sound. Because of sampling bias, we did not examine length-by-season for the late-stage gravid brown rockfish sampled by Hess et al. (2012). Nevertheless, the mean length of the late-stage gravid fish sampled in that study falls near the center of the length class that accounted for most of our observations of late-stage gravid brown rockfish. In Puget Sound, peak parturition is known to occur earlier in the year for copper rockfish than for brown rockfish (DeLacy et al.¹⁰; Washington et al.³). Curiously, we did not observe any late-stage gravid copper rockfish in the spring at PHAR. Of the 13 late-stage gravid copper rockfish observed, 10 were encountered during the final 2 years of the study and only 2 of those were in the largest length class. On the basis of length-frequency changes over time and a substantial increase in copper rockfish abundance over

the study period after 2006, we surmise that most of the observed late-stage gravid copper rockfish belonged to the strong 2006 year class noted above. If so, they were just reaching maturity during the final years of the study and may have been spawning later in the season, as has been noted for black, yellowtail, and copper rockfish (see above).

Consistent with many habitat selection models, the results of Matthews (1990a, 1990b) indicated that the apparent homing ability of some rockfish species may enable them to embark on periodic exploratory excursions in response to unfavorable changes in habitat, allowing them to assess other environments but return to their point of departure if more suitable surroundings are not encountered. Matthews (1990c) further noted that the winter disappearance of canopy-forming bull kelp, with the structure and associated prey it provided, may have explained the seasonal exodus of brown and copper rockfish she observed on naturally formed low-relief reefs. Although bull kelp does not occur at PHAR, the seasonal presence of non-floating seaweeds may provide similar levels of refuge and prey. The study areas of Matthews (1990c) included a high-relief artificial reef (Boeing Creek Artificial Reef) also located in the main basin of Puget Sound. The reef is comparable in age, size, depth, and construction to PHAR; is subject to similar wave energy, current, and temperature regimes; and supports a similar ichthyofauna and flora that is devoid of canopy-forming kelp. However, the highest densities of >20 cm brown and copper rockfish recorded by Matthews at that site occurred during the fall and winter, not during the summer as observed in our study.

Resiliency to temperature fluctuations is not known for copper rockfish. However, Wilson et al. (1974) studied metabolic compensation in response to temperature in brown rockfish, and vermilion rockfish (*S. miniatus*). This latter species resides below the thermocline and is therefore not exposed to the same seasonal temperature fluctuations experienced by brown rockfish residing above the thermocline. Wilson et al. concluded that there are metabolic differences between the 2 species that correlate with differences in depth distribution, and that brown rockfish have a higher capacity to acclimate over a wider range of temperatures. Both brown and copper rockfish have a similar biological range, occurring from the subtropics to the subarctic (Horn et al., 2006) and are found in warmer inland seas, as well as colder oceanic waters (Love et al., 2002). The mean daily recorded temperature changes at PHAR were highest during the spring when both species began appearing on the reef, and during the summer when they appeared on the reef in their greatest abundance. Although we do not have temperature data beyond the offshore perimeter of the reef, water column data (available at [website](#)) in East Passage conducted by the Washington State Department of Ecology indicate that diurnal and seasonal temperature regimes become less labile with increasing depth. If, as noted by Neill and Gallaway 1989, fish move in response to the totality of

¹⁰DeLacy, A. C., C. R. Hitz, and R. L. Dryfoos. 1964. Maturation, gestation, and birth of rockfish (Sebastes) from Washington and adjacent waters. Wash. Dep. Fish. Fish. Res. Rep. 2:51-67.

their environment and not to any single environmental factor in isolation (e.g., temperature), we consider it unlikely that either species moved on and off the reef in direct response to temperature alone, especially given that they would be leaving the relatively stable thermal environment of deeper water for the more broadly fluctuating temperatures encountered over the reef during the spring and summer.

We hypothesize on the basis of our survey findings and the evidence gleaned from Hess et al. (2012) that the observed changes in abundance of brown and copper rockfish at PHAR are the result of seasonal relocations of these species to different migratory destinations beyond their home ranges; most likely in response to reduced refuge space and prey density (e.g., due to reduced macroalgal cover and associated prey) during the winter months. Behaviors associated with spawning and mating may also play a crucial role in determining the seasonal movements and spatial distributions for these 2 rockfish species. The statistically significant greater proportion of large brown and copper rockfish present on the reef during the winter could be attributed to an overall suboptimal year-round habitat that is interspersed with enclaves of microhabitats suitable for year-round occupancy and that are held more successfully by larger territorial fishes.

The applicability of our hypothesis to brown and copper rockfish populations elsewhere in Puget Sound is unclear. If habitat quality is correlated with rockfish movement, behavioral variability among local populations is likely to be high and our observed seasonal changes in abundance would not be conserved across sites. If, as proposed by Matthews et al. (1987), there is a relationship between habitat quality and rockfish movement on and off reefs, determining the timing and magnitude of seasonal variability in rockfish abundance at different sites could prove to be a useful means for ranking the relative importance of those sites for rockfish conservation efforts. This research could be critical for establishing MPAs and for determining the spatial scales over which protection should be afforded.

Exploitation of aggregating behavior by fisheries, such as often occurs with cods, forage fish, and other species, may be detrimental to the recovery of declining rockfish stocks if the aggregations are composed of migrant adults. Fishery managers may wish to consider the potential for, and management implications of, local rockfish migratory behavior. Concentrating fisheries in the nearshore environment during times of year when migratory rockfish are present could result in the depletion of local populations, particularly if aggregations are linked to spawning, courtship, or mating behavior.

Generalized linear mixed-effects models, parameterized with spatially and temporally explicit habitat, prey availability, and movement data could aid researchers in identifying the key habitat attributes and environmental indicators that characterize essential habitat for these and other fish species.

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