



Home range size and patterns of space use by lingcod, copper rockfish and quillback rockfish in relation to diel and tidal cycles

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ABSTRACT: The estimation of home range size of marine fish has received attention because of its application to the design of marine reserves. How individuals use space may also be important to the management of the species and for understanding behavioral processes like optimal foraging or territoriality. We used an acoustic tracking system (VRAP) to examine patterns in home range size and movement behavior for 3 demersal fishes in Puget Sound: lingcod *Ophiodon elongatus*, copper rockfish *Sebastes caurinus* and quillback rockfish *S. maliger*. Data were collected over 8 wk in the summer of 2006 and 3 wk in the winter of 2007. Home ranges were relatively small (~1500 to 2500 m²) and did not differ among species. During the summer, lingcod had larger home ranges during the day than at night. Movement in all 3 species was in some way related to diel and tidal cycles, although individuals within species differed, and there was no general pattern. About half of the lingcod used portions of their home ranges only during the day and on the flood tide. Other individuals made similar movements on the ebb tide. Some copper rockfish moved to specific areas of their home range on the day ebb tide, while others made these movements on the night flood tide; others showed no pattern. Similar results were seen for quillback rockfish. While the arena of resource management often requires us to simplify complex systems, our results illustrate that such simplification may be difficult, and will depend ultimately on detailed behavioral data.

KEY WORDS: VRAP · Acoustic tracking · Rockfish · Lingcod · Home range

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INTRODUCTION

As ecosystem approaches to managing marine fisheries are adopted, it is becoming increasingly necessary to consider spatial aspects of population dynamics. Rational design of networks of marine protected areas (MPAs) requires an understanding of the relationship between the spatial extent of a reserve, home ranges of fish, and resource distribution. As a result, understanding movement patterns of fishes is of central importance to measuring MPA effectiveness. In part, this is due to 2 potentially conflicting objectives of MPAs: (1) to conserve a breeding stock, adult movement out of MPAs should be minimal, but (2) to augment local fisheries, some flux outside the MPAs to

harvested areas is desirable, i.e. 'spillover' (Zeller & Russ 1998, Kramer & Chapman 1999, Cole et al. 2000).

Well-defined home ranges appear to be common among the coral- and rocky-reef associated fish species that MPAs are typically intended to protect (Matthews 1990b, Kramer & Chapman 1999, Lowe et al. 2003, Topping et al. 2005). For these fishes, home range area can vary considerably among species targeted by fishers from as little as <10 m² for some rockfishes in high relief habitat (Matthews 1990c) to over 55 000 m² for New Zealand snapper *Pagrus auratus* (Sparidae) (Parsons et al. 2003). There can also be considerable variation within species in home range area based in particular on type or shape of habitat (Matthews 1990c, Topping et al. 2005).

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Examining how individuals use space can reveal the diversity of behaviors within a species. Such diversity may be important for management of species and for understanding basic behavioral ecological processes such as optimal foraging, predator avoidance, habitat preference, shelter use, territoriality, reproductive behavior, etc. (Fretwell & Lucas 1969, Fretwell 1972, Kramer & Chapman 1999, Parsons et al. 2003, Austin et al. 2004, Morgan & Kramer 2004, Lindholm et al. 2007). In species like New Zealand snapper *Pagrus auratus* (Willis et al. 2001, Willis & Millar 2005) and possibly lingcod *Ophiodon elongatus* (Jagiello 1990), some portion of the population makes annual onshore/offshore migrations potentially reducing the effectiveness of reserves as these individuals move out of the unfished area. At smaller spatial scales, individuals within the same species may use their home ranges differently. For example, in the sparid *Salpa salpa*, some individuals have separate diurnal and nocturnal areas of residence while others do not (Jadot et al. 2006). In other species, diel patterns are more general with all individuals seeking shelter at night (Topping et al. 2005, Jorgensen et al. 2006).

We examined movement and home range sizes of 3 temperate fish species: lingcod *Ophiodon elongatus* (Hexagrammidae), copper rockfish *Sebastes caurinus* (Sebastidae) and quillback rockfish *S. maliger* (Sebastidae). All 3 species are demersal and generally associated with rocky reefs (Eschmeyer et al. 1983, Love et al. 2002). Lingcod are found from the Gulf of Alaska to Baja California from the intertidal to 475 m depth (Allen & Smith 1988). Lingcod are generally resident on rocky reefs but do occasionally leave specific sites for periods of up to 2 wk (Starr et al. 2004). They can disperse more than 50 km over the course of several years, although most stay within 8 km of their initial tagging site (Jagiello 1990). Their dispersal rates are high enough that in areas like the Strait of Georgia they can be considered a single stock (Smith et al. 1990). Copper rockfish are found from central Baja California to the northern Gulf of Alaska from barely subtidal waters to 183 m depth (Love et al. 2002). Quillback rockfish are found from central California to Alaska and occur from subtidal to 274 m depth (Love et al. 2002). These 2 rockfish species are among the most common rockfish in Puget Sound in the nearshore (Love et al. 2002). Copper and Quillback rockfish have been the subjects of previous tracking studies in Puget Sound (Matthews et al. 1986, Matthews 1990a,b,c). On complex, high relief reefs they tend to have home ranges as small as 10s of m² while on low relief reef their home ranges are much larger, though still relatively small (4000 m²). Historically, all 3 species have been important components of the nearshore recreational fishery in Puget Sound. Copper and Quillback together averaged 71.3% of the

total recreational rockfish catch in Puget Sound from 1980 to 1999 (Data from the National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD; Marine Recreational Fisheries Statistics Survey, www.st.nmfs.gov/st1/; pers. comm.)

However, overexploitation has resulted in severe restrictions on fishing. At present, the lingcod fishery is limited to 1 May to 15 June, and there is a one/first fish bag limit for rockfish from 1 May to 30 September in some areas of Puget Sound, but in much of the Sound, rockfish can be taken only during lingcod season (WDFW 2007).

In this study, we used high-resolution ultrasonic telemetry to examine patterns of space use and movement of lingcod *Ophiodon elongatus*, copper rockfish *Sebastes caurinus* and quillback rockfish *S. maliger*. Specifically, we investigate the degree to which environmental variables (e.g. season, diel phase, or tidal phase) influence use of space and patterns of movement. For the copper and quillback rockfish, the basic calculation of home range to some extent replicates previous work (Matthews 1990c, b). However, our work has larger sample sizes and includes a detailed analysis of individual movement.

MATERIALS AND METHODS

Study site. We conducted all field-work for this study at the southern end of Whidbey Island in Puget Sound (47° 54.308' N, 122° 26.072' W) (Fig. 1). The study area ranges in depth from approximately 8 to 19 m chart datum with 3 m tides. This site is primarily low relief sandstone composite with strong east–west tidal flow of at least 1.4 m s⁻¹ (2.7 knots, measured with acoustic Doppler current profiler; N. Tolimieri unpubl. data). In the approximate center of the study area and running from the southwest to the northeast, there is an uplifted ridge, which ranges in height from ca. 10 cm to as much as 8 m (Fig. 1). This ridge is the primary physical structure in the study area. Although not visible on the multibeam map in Fig. 1, a cave-like area several meters deep extends horizontally under the eastern, uplifted side of the ridge. The higher, eastern fringe of the uplifted area generally supports brown macroalgae *Pterygophora californica* and *Agarum fimbriatum* from the ridge margin to ca. 10 m to the east in the shallower areas. Small rocks (up to ~0.3 m diameter) and several large boulders (~2.0 m diameter) are scattered throughout the area, especially to the east. To the northwest and just out of the VRAP buoy triangle (Fig. 1) is a depression approximately 2 to 3 m deeper than the surrounding area.

Tagging and tracking methodology. SCUBA divers caught all fish at approximately 15 to 20 m depth using

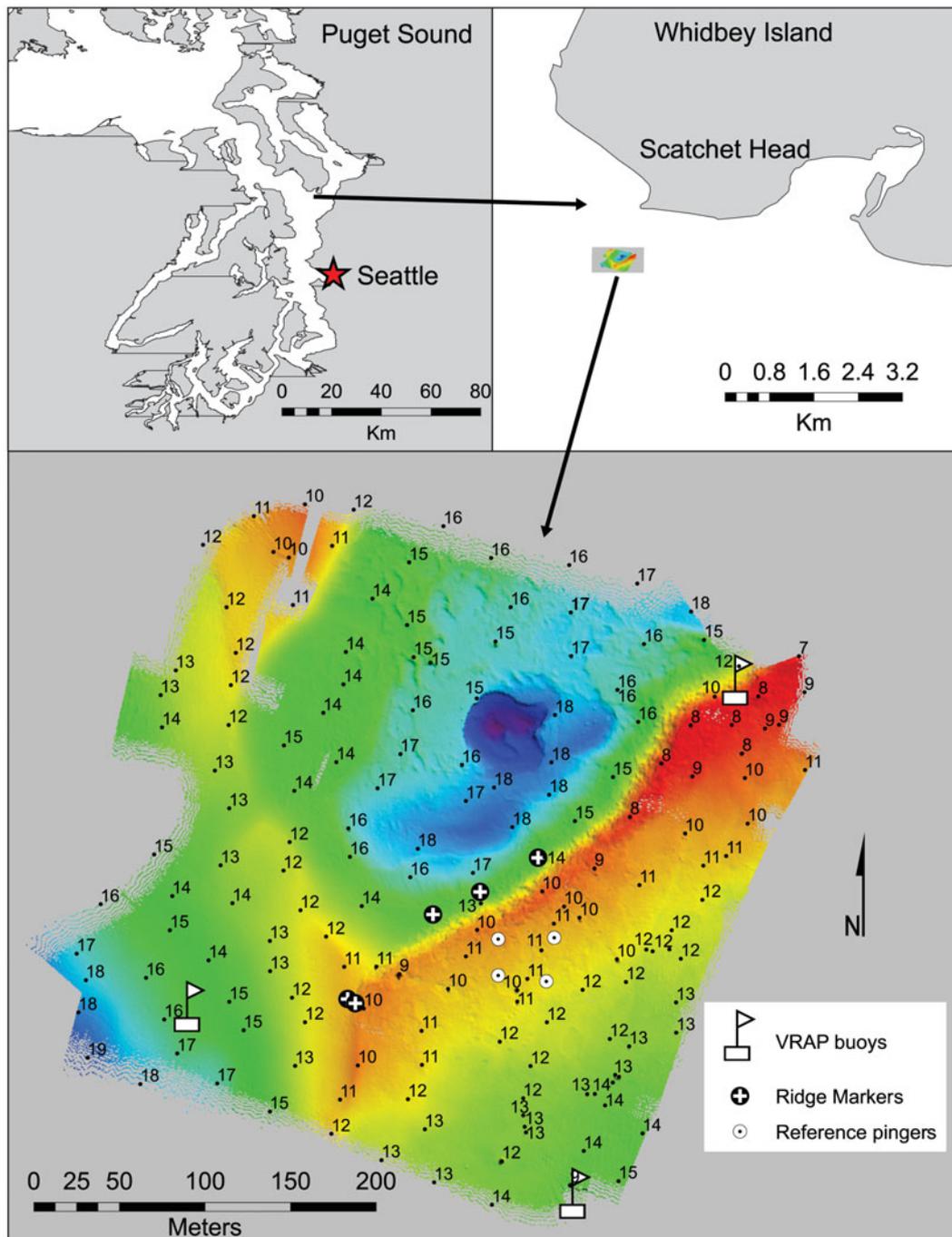


Fig. 1. Multibeam bathymetric map showing the ridge line and location of the VRAP sonobuoys, ridge markers and reference pingers. Ridge markers refer to pingers placed along the ridge line. Reference pingers were used to correct fish positions for buoy swinging due to tides. Numbers: depth soundings (m)

large hand nets (lingcod *Ophiodon elongatus*, copper rockfish *Sebastes caurinus* and quillback rockfish *S. maliger*). Individuals were placed in a wire mesh enclosure (2 to 4 per enclosure), brought slowly to the surface to minimize barotraumas (for the rockfishes), and then moved to holding containers aboard prior to surgery. aboard prior to surgery. To insert an acoustic

tag (VEMCO® , V13, 13 mm diameter, 36 mm length, weight: 12 g in air, 6 g in water; 20 to 60 s random on/off time, power output: 150 dB re 1 μ Pa at 1 m), an individual was placed on its back (i.e. dorsal side down) in a chamois-lined, v-shaped foam 'bed', which was placed within a larger, water filled plastic container to allow for irrigation of the gills during surgery.

After approximately 1 min in this position, the fish entered a state of tonic immobility (Henningsson 1994, Holland et al. 1999, Wells et al. 2005) and became non-responsive. A small 2 to 3 cm long incision was made anterior of the anus and the acoustic tag inserted. The incision was closed using either surgical thread or surgical staples. We used surgical thread on the rockfish because the size and prevalence of scales made staples difficult to use. We used surgical staples for the lingcod because their smoother skin did not interfere with staple use, and because we were able to close the incision wounds more rapidly with staples. A Floy[®] tag (Floy Tag & Mfg., Seattle) was inserted into the epaxial musculature to allow for external identification of individuals if necessary. Individuals were then placed in a separate holding container until they regained equilibrium (5 to 10 min) after which they were returned to the water in the general vicinity of their capture.

We monitored fish movements using VEMCO's[®] Radio Acoustic Positioning system (VRAP, VEMCO, Nova Scotia). The system consists of 3 radioacoustic buoys (VRAP buoys), and a computer controlled base station. The positions of the acoustic tags ('pingers') are calculated via triangulation of the arrival times of the tag signal at the 3 buoys (VEMCO 2003). Once deployed the VRAP system monitors fish position at a potential scale of 1 to 2 m precision with relocations received at a time scale of minutes (O'Dor et al. 1998). We used the locations of 5 acoustic tags placed in the array to mark the ridge line to estimate the system precision near the center of the array. The SD in the locations for these 5 pingers over 3 d was 2.6 m on the x-axis and 3.3 m on the y-axis. Error is least in the middle of the VRAP triangle and increases quickly as one moves outside (VEMCO 2003). In particular it becomes large directly behind the buoys. Most of our tracks were near the center of the VRAP array. While there are portions of some home ranges that are outside the triangle (see 'Results'), we feel that the accuracy is sufficient for the hypotheses tested here. The rate at which fish locations are recorded is dependent upon a number of factors including the ping rate of the tag, interference between tags, background acoustic noise and interference with the habitat (VEMCO 2003).

Individuals were monitored for approximately 8 wk during summer 2006 (31 July to 25 September) and 3 weeks during winter 2007 (9 to 28 February). As battery life of the VRAP buoys was ca. 10 d the study required 5 deployments in summer 2006 (31 July–7 Aug, 14 Aug–26 Aug, 28 Aug–5 Sept, 5 Sept–9 Sept, 14 Sept–25 Sept) and 2 in winter 2007 (9 Feb–16 Feb, 16 Feb–28 Feb).

The 3 VRAP buoys were moored in place using two 90 kg concrete blocks at the end of 30 to 40 m of mooring line. Strong tidally driven currents (primarily

east–west) produced large movements of the buoys at the surface over the tidal cycle (ca. 30 m). The relative positions of the buoys at the surface create a relative coordinate system in which the tagged fish are located. As the buoys shift with the tidal flux, the VRAP coordinate system also shifts relative to the fixed coordinate system that one might measure with GPS. To correct for tidal movements of the VRAP buoys and the coordinate system they define, we placed 4 fixed pingers in known locations on the bottom (Fig. 1). These were deployed in a square ca. 30 m apart on a side. When post-processing the data, fish locations were calculated relative to the most recent fixed pinger location. Specifically, we first calculated the position (the mean of the locations) of the fixed pingers during the initial few hours of each deployment when the position of the surface buoys was known (measured with a GPS) and before the tide changed. The apparent displacement from this initial mean position was then calculated for each fixed pinger location. Fixed pinger locations that were clearly erroneous based on trilateration with the other fixed pingers, or did not follow the tidal cycle, were excluded. The most recent displacement was then subtracted from each fish location. Fish locations received more than 10 min from the most recent fixed pinger location were excluded from the data set. The apparent movement of the fixed pingers was also used to define the time of change in tidal currents at the site so that fish behavioral patterns could be compared in relation to ebb, slack and flood tides.

Home range and core area. Home range is the area generally used by an individual during normal activities like food gathering and does not imply territoriality (Burt 1943). It is commonly defined as the area in which an individual spends 95% of its time (e.g. Anderson 1982, Parsons et al. 2003, Jadot et al. 2006, Katajisto & Moilanen 2006). The core area is an area of more intense use often defined as the area in which an individual spends 50% of its time (e.g. Jadot et al. 2006). We do not calculate a general home range based on all of the data for an individual. Instead we calculate home range for specific periods such as 'summer' home range or 'diurnal' home range. In these instances, home range refers to where an individual spent 95% of its time during that time period, e.g. diurnal, nocturnal, winter, summer. Thus summer home range would be the area where an individual spent 95% of its time during the summer sampling period; 'diurnal home range' would represent where an individual spent 95% of its time during the day ignoring data from other time periods. We use the term 'activity space' when referring to a portion of a fish's home range used during a particular time period but for which we did not actually calculate a home range.

We calculated core area and home range based on the 50 and 95 % kernel utilization density distributions (UD) respectively (Worton 1989, Katajisto & Moilanen 2006). Kernel UDs provide a probabilistic measure of space use. With standard kernel UD methods, the relocation data need to be regularly spaced in time. However, relocation data from the VRAP system are irregularly spaced in time because of a number of factors including the random ping rate of the tag, interference between tags, and behavior of the fish in relation to the habitat. To account for spatial and temporal autocorrelation in the data, we used spatiotemporal kernel methodology (Katajisto & Moilanen 2006), which accounts for temporal aggregation of observations by weighting observations based on their proximity in time and in space. Observations close in time are given less weight unless they are also distant in space. We calculated the 50 and 95 % UD for fishes using the program B-Range (available at: www.helsinki.fi/science/metapop/). The calculation requires choosing both the space kernel (h_s) and time kernel (h_t). Choice of these values should be based on the biology of the species, the accuracy of the location measurements and the desired spatial resolution of the estimate (Katajisto & Moilanen 2006). We first calculated h_{opt} (also referred to as h_{ref})—an ad hoc but simple and effective method of producing a reference value for h_s —from the distribution of the data (Bowman 1985, Worton 1989). Median h_{opt} across all individuals was 3.89. We also examined the SD in the locations of 5 pingers placed in the array for 3 d to mark the ridge line ($SD_x = 2.6$, $SD_y = 3.3$). Because h_{opt} tends to over-smooth when the distribution is not bivariate-normal, we set h_s at 3.0. We allowed the B-Range program to choose h_t based on $h_t(N_{min})$ (where N_{min} is the minimum effective number of observations) above which all observation become correlated to some degree (Katajisto & Moilanen 2006). Unless otherwise specified, we use 'home range' to refer to the 95 % UD calculated using the spatio-temporal kernel method.

We used linear mixed models (LMMs; Littell et al. 1996, Verbeke & Molenberghs 1997, McCullagh & Searle 2001) to make a number of comparisons among home range sizes, among species and within species at different times, e.g. winter versus summer or night versus day. We chose LMMs because they allowed us to account for and specifically estimate autocorrelation due to repeated measures on individuals and as well as directly estimate variance, i.e. assume heterogeneity of variance (Littell et al. 1996, McCullagh & Searle 2001). Choice of covariance parameters and autocorrelation structures was based on comparing Akaike's Information Criteria (AIC) among candidate models. We evaluated either first-order autocorrelation when there was only 1 time step between observations (e.g. winter ver-

sus summer) or an unstructured covariance structure where there were 3 time periods without an obvious order (e.g. night, crepuscular, day). We assessed the normality of the residuals for all models using QQ-plots and Kolmogorov-Smirnov tests. Further details of statistical comparisons are given in the results.

Behavioral patterns in relation to diel phase, tide, and season. To better examine behavioral patterns, we examined activity spaces for each fish in relation to diel phase (day, crepuscular, night), tidal period, deployment within season and deployment between seasons (winter versus summer). For diel phase, the crepuscular period was defined as 1 h from sunrise or sunset. Deployment within season was an arbitrary classification based on when the VRAP positioning buoys were replaced because of low battery power. Thus there were 5 'deployments' in 2006 and 2 in 2007 (see 'Methods') lasting an average of 8.7 d (range: 4 to 12 d). Coverage was not continuous in the summer primarily due to power losses at the onshore base station.

We defined a number of characteristics of each fish's behavior and home range. First we determined whether a fish had single or multiple core areas. A fish could have >1 core area if there were geographically distinct portions in its 50 % UD. An individual had a 'nocturnal', 'diurnal' or 'crepuscular' activity space if it used a particular portion of its summer 95 % UD exclusively or primarily during one of those periods. We then examined this space use in relation to the tidal cycle (ebb, flood, slack). Between deployments within the summer and between summer and winter, we determined whether the above behaviors changed as well as whether the home range shifted in location or the fish was absent for long periods of time.

RESULTS

Core area and home range size

We tagged a total of 24 fish between 06 July and 15 August 2006: 6 copper rockfish, 8 quillback rockfish and 10 lingcod. Of these, 2 copper and 2 quillback rockfish disappeared prior to the deployment of the VRAP system and were never recorded (2 copper and 2 quillback). One lingcod and 1 quillback were recorded for only 1 to 2 days following their initial tagging and then were no longer recorded in the array. These 6 fishes were excluded from the analyses. For this study we followed 18 fishes starting 31 July 2006: 4 copper rockfish, 5 quillback rockfish and 9 lingcod. Of these, all 4 copper rockfish were recorded in the array in February of 2007. Four of the 5 quillback and 5 of the 9 lingcod were also recorded in the array as of the February 2007 deployments.

We wanted to compare home range size in the winter to that in the summer, but the overall length of the winter (ca. 3 wk) and the summer (ca. 8 wk) sampling periods differed. Therefore, we first tested whether the length of the sampling period in the summer affected the estimate of home range size. We calculated home ranges for the 3 wk period of the summer that corresponded to the same portion of the lunar cycle for the 3 wk of winter sampling. We then compared these home ranges to the ones estimated from the full 8 wk sample. The length of the summer sampling period did not affect home range size (LMM, 'Period' and 'Species' as main effects, first order autocorrelation, $\rho = 0.98$; Period effect: $F_{1,15} = 1.91$, $p = 0.19$). Therefore, we used the home ranges estimated based on the full 8 wk summer deployment in the winter-summer comparison.

The mean size of a fish's core area (the 50% UD) differed among species and seasons (LMM, species \times season, $F_{2,25} = 3.47$, $p = 0.047$) and overall variance \pm SE was higher in the summer ($49\,724 \pm 18\,157$ m²) than in the winter (7931 ± 3547 m²). This result was driven by lingcod, which had larger core areas in the summer than in the winter (Tukey's test, $p = 0.036$, Table 1). There was no overall difference among species ($F_{2,25} = 1.07$, $p = 0.36$) nor among seasons ($F_{1,25} = 1.72$, $p = 0.20$) in mean size of the 50% UD. Autocorrelation was not important to the model fit.

Home range size (95% UD) did not differ between seasons (Table 1, $F_{1,25} = 2.471$, $p = 0.12$) or among species (LMM, $F_{2,25} = 0.56$, $p = 0.58$), and there was no interaction between the main effects (LMM, $F_{2,25} = 2.06$, $p = 0.15$). However, variance \pm SE in home range was much higher in the summer ($2\,547\,478 \pm 930\,207$ m²) than in the winter ($315\,343 \pm 141\,026$ m²). Autocorrelation was not important to model fit.

We next analyzed patterns in home range size among diurnal, nocturnal and crepuscular periods separately for each species. In these analyses, diel phase and season were the main effects in the LMM. Model fitting evaluated heterogeneous variances and an unstructured autocorrelation structure for the variance-covariance matrix. For lingcod, home range size differed among diel periods ($F_{2,26} = 6.36$, $p = 0.0056$) and seasons ($F_{1,13} = 7.34$, $p = 0.0018$) and there was a significant interaction ($F_{2,26} = 6.16$, $p = 0.0065$) (Fig. 2a,b). During the summer (Fig. 2a), home range was greater during the day than at night (Tukey-Kramer test, $p = 0.038$), and in the winter (Fig. 2b) crepuscular home range was smaller than the diurnal ($p = 0.04$) or nocturnal ($p = 0.01$) one. Crepuscular home range was lower in the winter than the summer ($p = 0.016$). The best model fit was achieved with an unstructured variance covariance matrix grouped by season. That is, there was autocorrelation between the diel periods, but levels of autocorrelation and variance

Table 1. *Ophiodon elongatus*, *Sebastes caurinus* and *S. maliger*. Home ranges (m²) during an 8 wk summer deployment and a 3 wk winter deployment expressed as 50 and 95% utilization distributions (UD). UDs were calculated using a spatio-temporal kernel method (Katajisto & Moilanen 2006). Means and SEs are model output from linear mixed models (Species \times Seasons, run separately for the 50 and 95% UDs). SL: standard length

ID	SL	Summer		Winter	
		50%	95%	50%	95%
Lingcod					
13	63	234	900	189	1080
15	55	513	1584	–	–
16	57	675	3573	108	495
17	50	918	3888	–	–
32	47	648	2952	–	–
35	68	369	1953	342	1944
44	65	729	2790	162	603
741	49	135	684	306	1575
745	45	225	1044	–	–
Mean		494	2820	221	1139
SE		74	532	39	251
Copper rockfish					
11	35	171	630	315	1755
18	33	198	783	333	1683
46	36	477	2628	234	1602
49	30	594	5751	378	2430
Mean		360	2448	315	1868
SE		111	798	44	280
Quillback rockfish					
14	32	135	621	–	–
34	26	108	612	351	2169
41	29	243	2475	396	2196
47	30	351	2394	270	1593
48	32	261	1215	171	864
Mean		220	1463	297	1706
SE		99	713	44	280

were higher in the summer than in the winter (results not shown).

For copper rockfish, there was no effect of diel phase on home range size (Fig. 2, $F_{2,18} = 1.85$, $p = 0.19$); there was no difference among seasons ($F_{1,18} = 0.76$, $p = 0.39$); and there was no interaction between main effects ($F_{2,18} = 0.13$, $p = 0.88$). While there were no overall differences in mean home range size, the best model fit was achieved by estimating separate variances by season and period. The highest variance was seen during summer nocturnal periods and variance in home range size was much lower in the winter than in the summer overall. Autocorrelation was not important to the model fit. Home range size for quillback rockfish did not differ among diel phase (Fig. 2, $F_{2,21} = 2.14$, $p = 0.14$), or seasons ($F_{1,21} = 1.02$, $p = 0.32$), and there was no interaction ($F_{2,21} = 0.09$, $p = 0.92$).

Neither winter nor summer home range size was correlated with body size for any of the 3 species for both

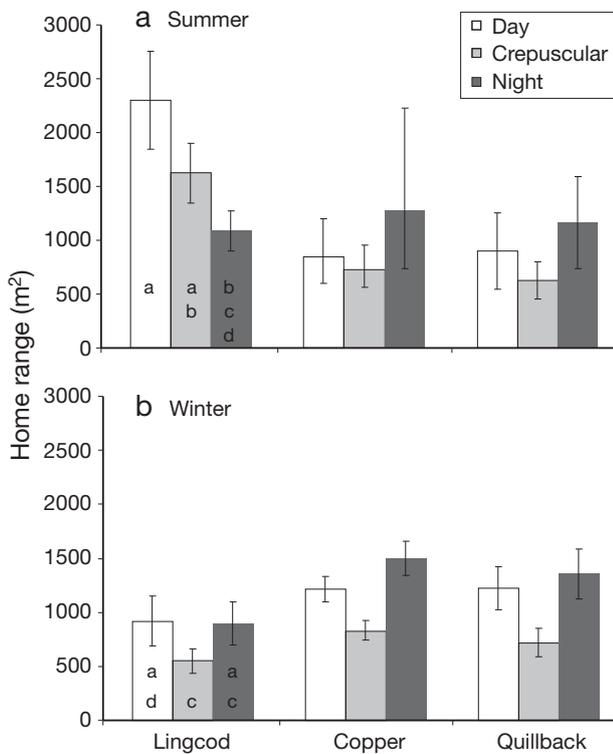


Fig. 2. *Ophiodon elongatus*, *Sebastes caurinus* and *S. maliger*. Mean home range size for diel period in (a) summer and (b) winter. Data are the 95% utilization distribution for that time period calculated using a spatio-temporal kernel. Error bars: ± 1 SE. For lingcod, letters indicate home ranges that could not be distinguished statistically (Tukey-Kramer test $p > 0.05$). No differences were found for copper and quillback; comparisons were not made among species

the 50% UD and the 95% UD ($p > 0.5$ in all cases). However, given the small sample sizes, especially for the rockfishes, this result should not be over-interpreted.

Behavior patterns in relation to diel phase, tide and season

For most individuals the ridge appeared to represent an important boundary (Fig. 3 & 4). Most of the lingcod operated primarily on one side of the ridge (Fig. 3), as did all of the copper rockfish (Fig. 4a,b), although the side varied among individuals for both species. Four of the 5 quillback rockfish operated almost exclusively to one side of the ridge boundary (Fig. 4c,d). Those fish that did move across the uplifted ridge tended to do so in the southwestern section where there was less of a difference in depth between the east and west side of the ridge. At the peak of tidal flow, vertical velocities above the ridge can reach 0.30 m s^{-1} (measured with

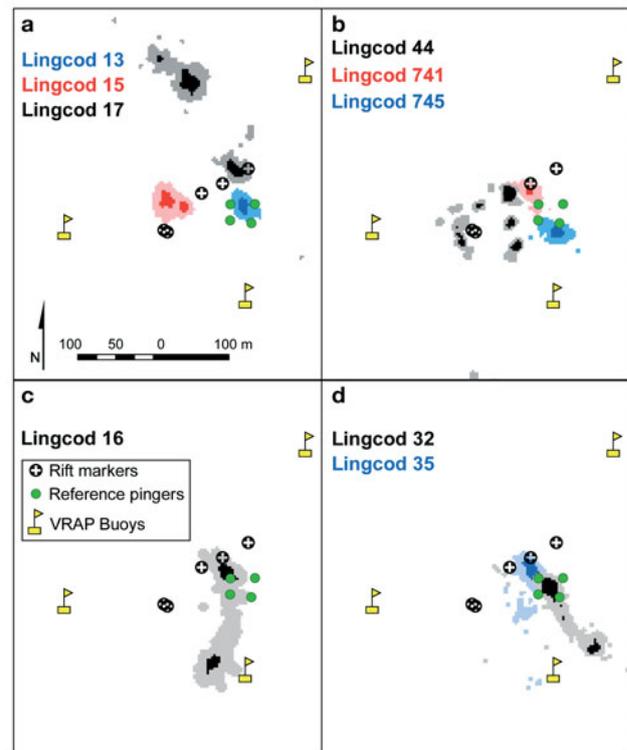
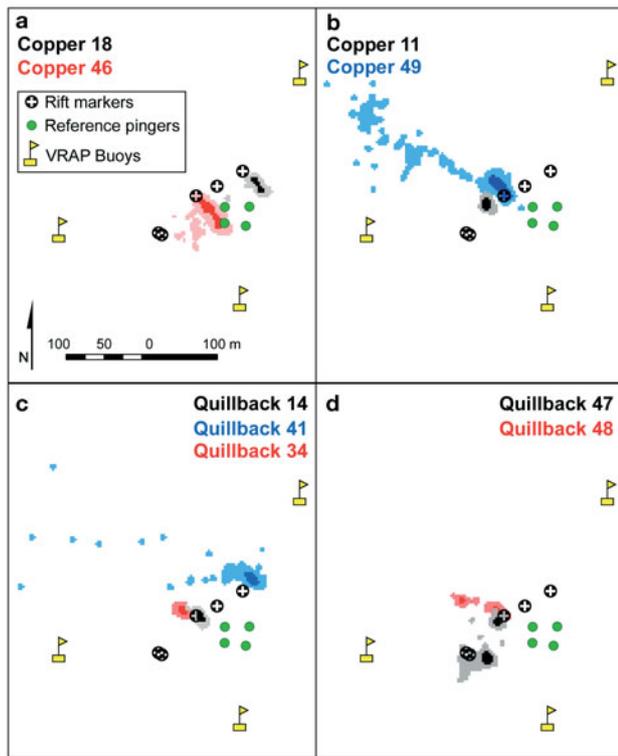


Fig. 3. *Ophiodon elongatus*. Summer (8 wk) home range for the 9 lingcod tagged in the study. For each fish, the darker shade is the 50% utilization distribution (UD); the lighter shade represents the 95% UD

Acoustic Doppler Current Profiler; N. Tolimieri pers. obs.) with a curtain of turbulent eddies that reach the surface. In this location it seems likely that hydraulic structures may reinforce observed behavioral boundaries set by physical habitat.

Five of the 9 lingcod and 2 of the 5 quillback rockfish had >1 core area during the summer (Table 2, Figs. 3 & 4c,d). None of the copper rockfish had >1 core area (Fig. 4a,b). For most of the fish with multiple core areas (1 of the 2 quillback, and all the lingcod), at least one was used either primarily nocturnally or diurnally and generally on a specific tide (Fig. 5). Five of the 9 lingcod had areas of their home range that they utilized primarily or exclusively during the day, although there was generally some crepuscular presence in these areas as well. Four of the 5 moved to these diurnal activity spaces on the daytime flood tide, while the fifth moved on the ebb tide. For example, lingcod 16 (Fig. 5a) and lingcod 32 (Fig. 5b) both made daily movements from the area of the ridge to other areas approximately 150 m distant. In the summer, the area of the ridge was occupied during all periods (day, crepuscular, night), but the areas distant from the ridge were occupied generally only during daylight hours on a flood tide (Fig. 6a,b). Fish made repeated daily move-



ments to these areas, but along with these daily movements were periods of several days when individuals did not make the daily movement away from the trench. Since these periods of inactivity were not the same, it does not seem likely that they were related to environmental factors (like lunar phase) in a general way across individuals.

Copper and quillback rockfish also showed diel patterns of movement. Unlike the lingcod, which primarily moved to certain areas during the day, the rockfishes showed this behavior both during the day and at night. For example, copper 49 occupied a small area near the ridge at all times (Fig. 5d). However at night it generally moved about 50 m off from the ridge to more open habitat, and on some nights it wandered up to several hundred meters from its daytime position. The smaller distance excursions do not appear to be partic-

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 Fig. 4. *Sebastes caurinus* and *S. maliger*. Summer (8 wk) home range for the (a,b) 4 copper and (c,d) 5 quillback rockfish tagged in the study. For each fish, the darker shade is the 50% utilization distribution (UD); the lighter shade represents the 95% UD

Table 2. *Ophiodon elongatus*, *Sebastes caurinus* and *S. maliger*. Summary of home range behaviors, by individual. SL: standard length; Multiple core: multiple core areas; Wandering: 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; Tide: tide during which an individual made tidally related movements. Y: presence of behavior; N: absence of behavior

ID	SL	Multiple core	Activity space		Wandering	Tide	Home range shift		Long absence	Winter presence	Winter diel movements
			Diurnal	Nocturnal			Within season	Between seasons			
Lingcod											
13	63									Y	
15	55	Y	Y		Y	Flood				Y	N
16	57	Y	Y		Y	Flood				Y	N
17	50	Y	Y		Y	Flood	Y				
32	47	Y	Y		Y	Flood					
35	68		Y			Ebb		Y		Y	
44	65	Y			Y	Ebb				Y	N
741	49									Y	
745	45							Y			
Copper rockfish											
11	35									Y	
18	33									Y	
46	36		Y			Spring ebb		Y		Y	
49	30			Y		Spring flood		Y		Y	
Quillback rockfish											
14	32									Y	
34	26									Y	
41	29					Flood				Y	
47	30	Y	Y			Ebb				Y	N
48	32	Y		Y	Y	Flood				Y	N

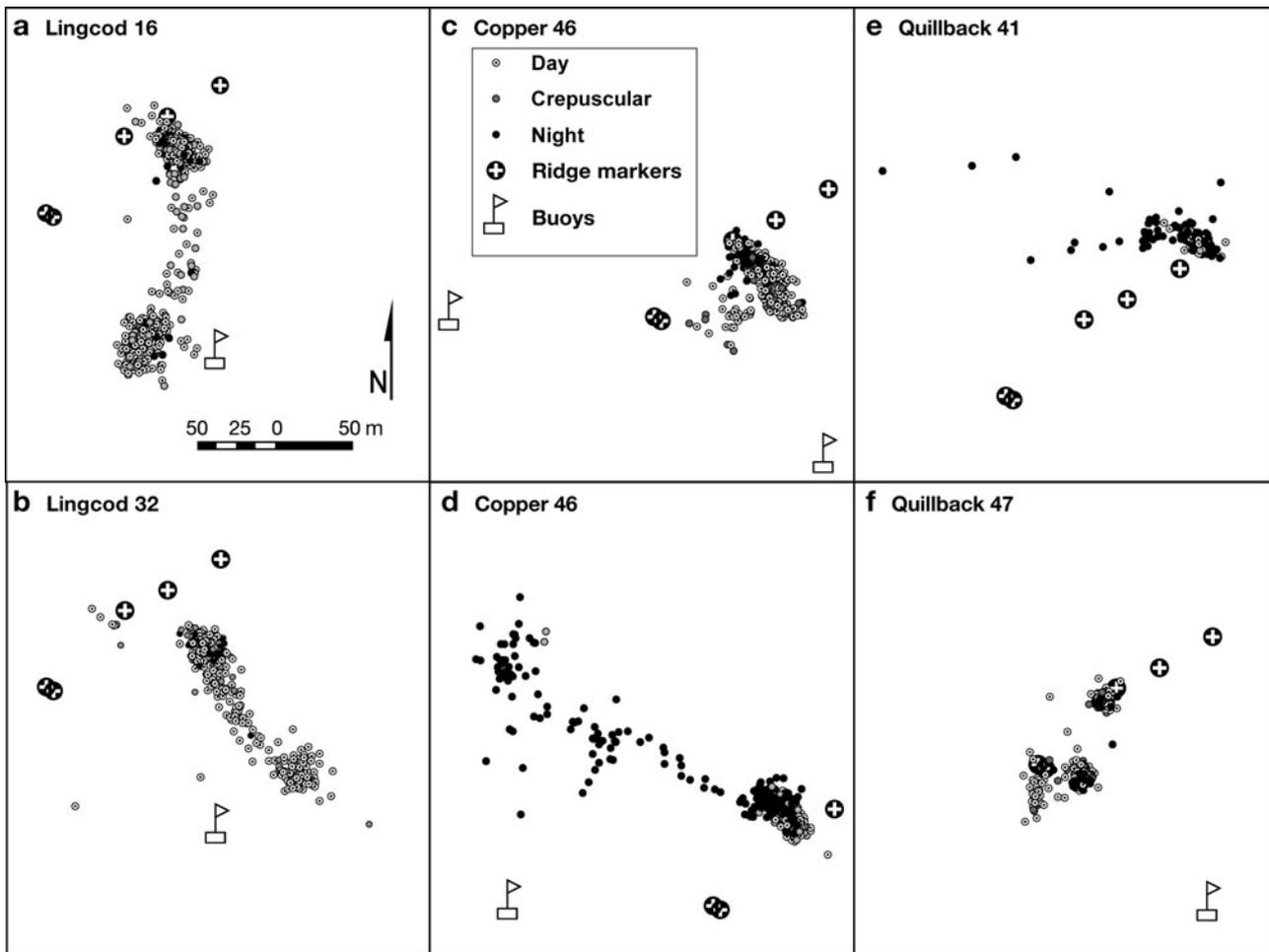


Fig. 5. *Ophiodon elongatus*, *Sebastes caurinus* and *S. maliger*. Examples of diel movement patterns by (a,b) lingcod, (c,d) copper rockfish, and (e,f) quillback rockfish. Symbols represent individual relocations. Ridge markers are included as a reference since not all VRAP buoys are shown

ularly tide-dependent occurring on both flood and ebb tides. The longer distance excursions tended to occur on nocturnal flood tides around the spring tide (Fig. 6d). Copper 46 showed the opposite pattern (Fig. 5c). It occupied an area near the ridge during both night and day, but moved to areas farther from the ridge only during the day (and crepuscular hours to some extent) and at both flood and ebb tides (Fig. 6c,d). Interestingly, this fish frequently made several excursions a day, returning to the ridge area during slack tide. Thus, while copper rockfish did not show multiple core areas, they still showed diel movement patterns similar to the lingcod and quillback. Their space use during these movements was much more diffuse, however.

The quillbacks showed behavior similar to the copper with 2 fish having nocturnal activity spaces and 1 having a diurnal one (Fig. 5e,f). For example, quillback 41 moved away from the ridge at night to another adja-

cent area only about 50 m away (although this does not show up as a separate core area). At other times it also ranged as much as 200 m from this area. Like copper 49 these long excursions tended to occur on flood tides during the spring tide portion of the tidal cycle (Fig. 6e,f). Also like copper 49, quillback 41 generally occupied an area along the bottom or west side of the ridge in the deeper bowl area. Quillback 48 behaved similarly to quillback 41. Quillback 47 appeared to exhibit the opposite behavior. It occupied 2 core areas during all times of day but moved to another area to the southwest primarily only during daylight hours and on ebb tides during the spring tide portion of the tidal cycle. These fish were approximately the same size (29 and 30 cm TL respectively). For the nocturnal individuals of both rockfish species, these movement patterns did not appear to be influenced by lunar phase in relation to the spring tide.

Over longer time periods, movement behavior also varied among individuals. For example, over the course of the 8 wk summer season, lingcod 17 completely shifted its activity space within its summer home range over 100 m from just east of the ridge to west of the depression to the northwest (Fig. 7a). Lingcod 745 disappeared for several weeks before returning to its original location (Fig. 7b). We cannot determine whether this individual was absent from the study area or concealed in such a way as to prevent its tag from being detected. However, given the length of time during which it was not recorded, the former seem more likely. Quillback 47, which showed diurnal movements earlier in the summer, ceased to make diel movements later in the summer (Fig. 7c). When comparing patterns of movement and areas of occupation in the summer to the winter, several fish (like copper 49 and lingcod 16) ceased to make the diurnal or nocturnal excursions they had made previously (Fig. 8a,b). Some fish, like lingcod 35 shifted their home ranges between summer and winter. In the case of lingcod 35, it shifted its home range approximately 50 m from the west/lower side of the ridge to the east/upper section (Fig. 8c). Two copper rockfish also moved their home ranges between winter and summer.

DISCUSSION

Tagging and tracking methodology

Overall our estimates of home range for lingcod, copper rockfish and quillback rockfish are consistent with previous work showing fairly small home ranges for these fishes, at least at shorter time scales. Our ability to continuously document details of fish behavior revealed enormous variability in the how fish use space and how use of space varies as a function of environmental variables. Given the similar estimates of home range size provided by the VRAP system and other acoustic tracking methodologies (e.g. Matthews 1990c), both appear adequate for the basic estimation of home range size. The continuous monitoring of fish position that the VRAP technology provides, opens up a range of options for the study of behavior much of

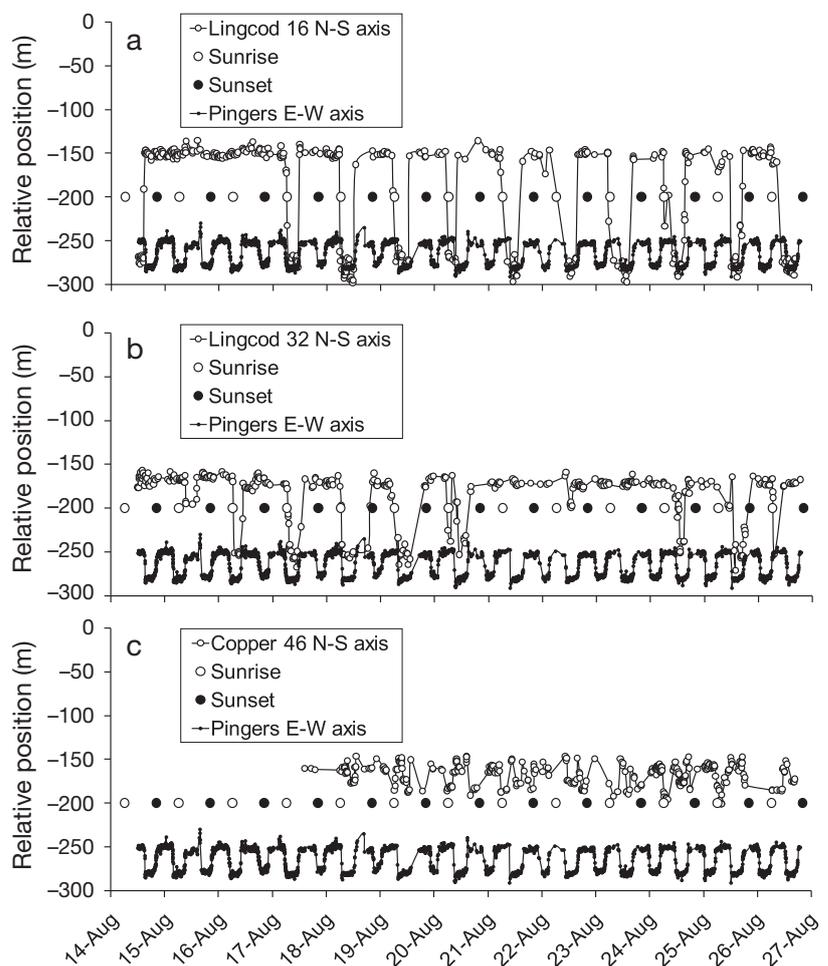


Fig. 6. *Ophiodon elongatus*, *Sebastes caurinus* and *S. maliger*. Examples of fish movement versus time showing (a,b) lingcod, (c,d) copper, and (e,f) quillback movements in relation to diel and tidal cycles from 14 to 26 Aug 2006. Values on the y-axis are relative and represent movement in meters, not actual position within the array. The movement of the fish is shown on either the east–west or north–south axis within the buoy array, depending on the fish's axis of greatest movement from one activity space to another. Fish movement was corrected for buoy movement as described in 'Materials and methods — Tagging and tracking methodology'. Time of sunrise (open circle) and sunset (closed circle) is shown as well. The apparent east–west movement of the permanent pingers indicates the tidal cycle. Smaller values on the y-axis for the permanent pinger movement indicate flood tide while larger values indicate ebb tide

which may be important both for the design of marine reserves and for addressing behavioral questions such as optimal foraging, predator avoidance, and habitat preference.

Home range size

Previous movement studies of lingcod have generally focused on longer time periods and larger spatial scales or did not specifically estimate home range size.

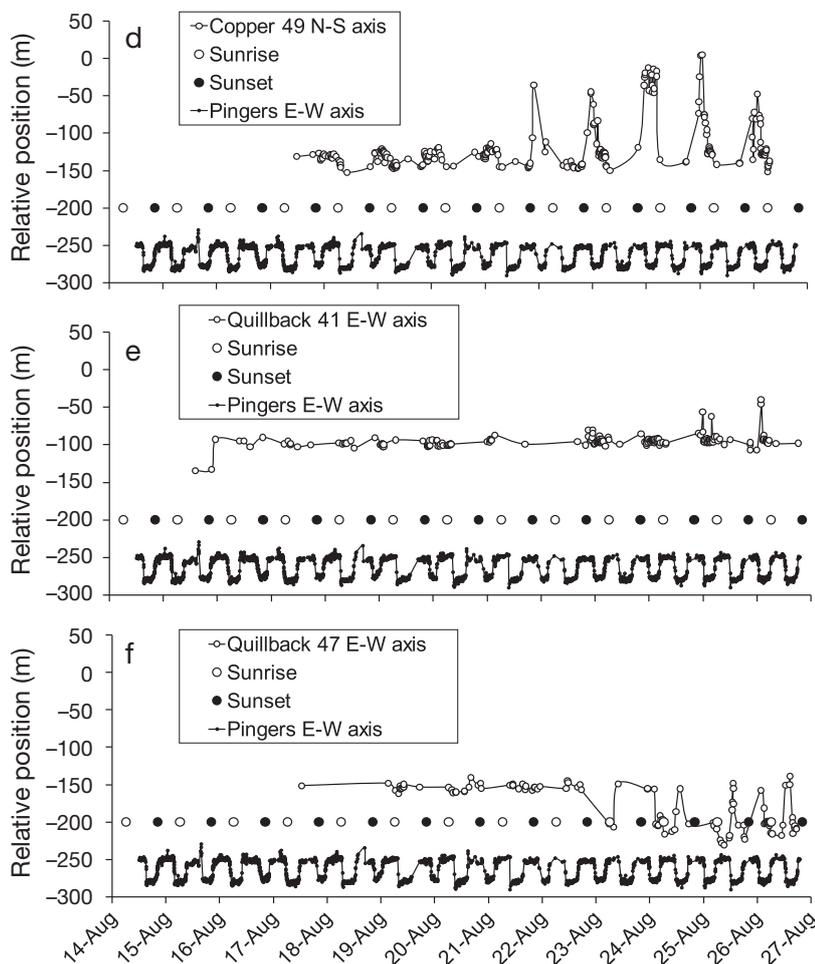


Fig. 6 (continued)

For example mark-recapture studies have shown that over the course of several years most lingcod will remain within approximately 8 km of their original tagging site, although some will move 50 km or more (Matthews et al. 1986, Jagiello 1990, Smith et al. 1990), and there may be an overall positive dispersal rate (Smith et al. 1990). Acoustic studies have found that lingcod may leave a particular reef occasionally, but will generally return within 14 d (Starr et al. 2004). Those that are experimentally displaced short distances (several km) generally return to their site of capture (Matthews 1992).

For lingcod, there appear to be at least 2 spatial scales on which movement occurs. At a smaller scale, fish have home ranges between 2000 to 3000 m² on average and may make diel movements within these home ranges (present study). Lingcod disappear from these fairly confined home ranges for periods of several weeks (Starr et al. 2004), and they may disperse to new locations (Jagiello 1990, Starr et al. 2004). Thus

their total space use may be quite large over the long term, and the design of a network of MPAs should take into account both the size of individual reserves as well as the distance between them if lingcod management or conservation is one of the primary aims.

For copper and quillback rockfish, our estimates of mean home range size are of the same order of magnitude as those found by Matthews (1990c) for low relief reefs in Puget Sound (ca. 4000 m²). Apart from the uplifted ridge through the center of our site, the study area is generally low relief. On high relief reefs, Matthews (1990c) found much smaller home ranges (<10 m²). If one looks more closely at our data, however, there appear to be 2 groups of fish in terms of home range size. Some rockfishes (both copper and quillback) in our study had small home ranges (612 to 783 m² for the summer data). The other rockfishes had home ranges at least 3 times as large (2394 to 5751 m²), with only 1 fish having an intermediate sized home range (1215 m²). Those individuals with large home ranges tended to make diel movements, while the fish with small home ranges tended to remain in the vicinity of the ridge. Thus some of the rockfish use this particular site more like a low relief site while others remain closer to

the ridge using the site more like a high relief one. Strikingly, these 2 behaviors in the summer converged in the winter with the mean of all winter home ranges taking an intermediate value (1787 m²). This suggests if there are 2 types of movement behaviors in the summer that are ecological in nature (i.e. alternate foraging strategies, social hierarchies, gender differences), these ecological processes are not at work in winter. Matthews (1990c) did not notice differences in home range or movement with diel phase or current strength, but only monitored 2 fish (1 quillback and 1 copper). Like Matthews (1990c), we did not see a difference in mean home range size at night versus during the day for the rockfishes, although lingcod had larger diurnal home ranges than nocturnal ones in the summer. However for the rockfish, the negative result at the population level occurred because some individuals had larger home ranges during the day while others did at night. Thus variability in behavior among individuals was important.

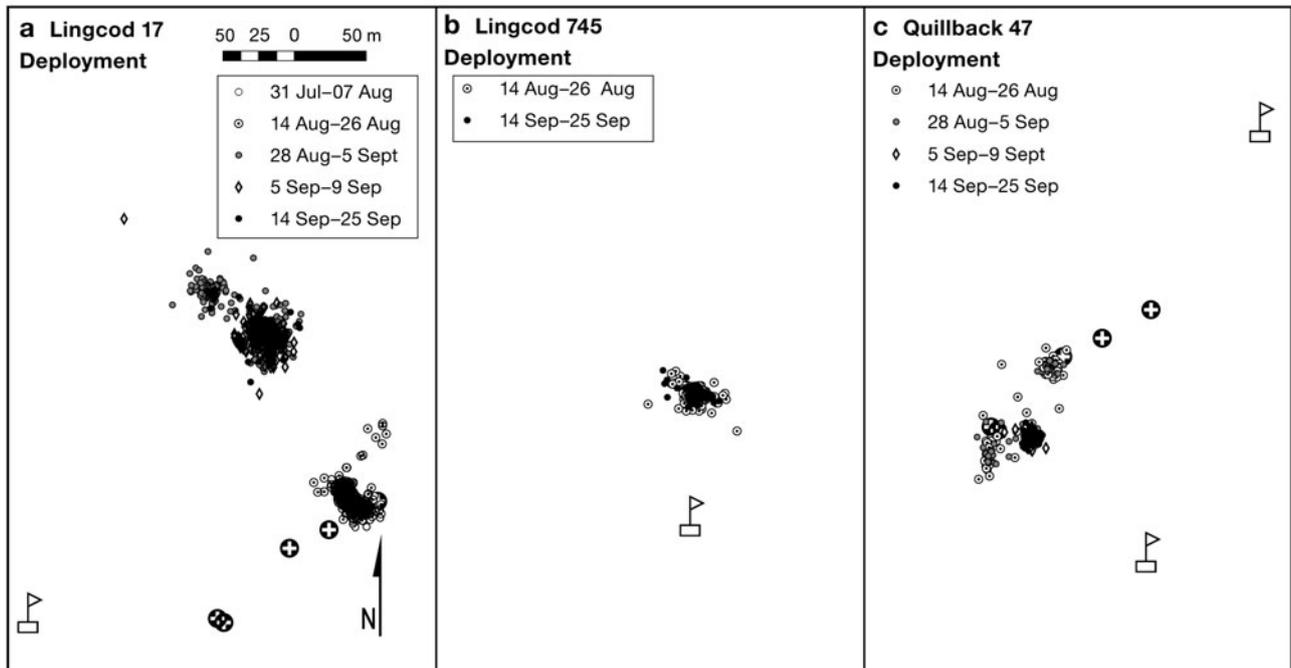


Fig. 7. *Ophiodon elongatus*, *Sebastes caurinus* and *S. maliger*. Examples of home range use within the summer 8 wk sampling period. For dates of the deployments, see panels. (a) Lingcod 17 shifted its home range. (b) Lingcod 745 was absent from its home range for several weeks. (c) Quillback 47 stopped ranging over the summer. Same scale in all panels, symbols as in Fig. 5

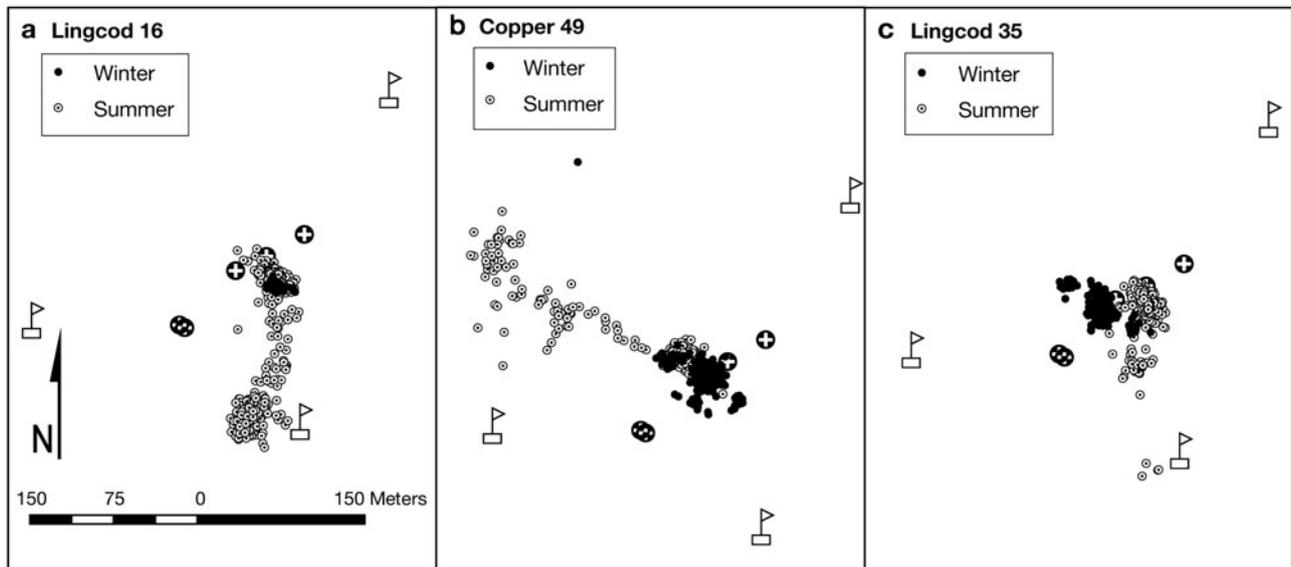


Fig. 8. *Ophiodon elongatus*, *Sebastes caurinus* and *S. maliger*. Examples of changes in home range space use between summer and winter sampling periods. (a,b) Individuals that ceased ranging from their core areas; (c) an individual that shifted its home range between summer and winter. Same scale in all panels, symbols as in Fig. 5

Movement behavior

The wide range of movement behavior and home range size within each of the 3 species is perhaps the most interesting aspect of the study. Much of the space use appears to have a diel pattern with a tidal component. Approximately half of the lingcod occupied a cer-

tain portion of their home range exclusively during the day, primarily on the flood tide, although 1 fish made similar movements on the ebb. As a result lingcod had larger diurnal home ranges than nocturnal ones during the summer when these diel movements occurred. Copper and quillback rockfish showed 3 basic patterns. Some fish remained fairly sedentary; some fish

moved to certain portions of their home range at night on the flood tide; others used certain portions of their home range only during the day ebb tide.

It seems likely that the diel movements are primarily related to feeding, not shelter seeking or reproductive behaviors. The ridge area represents the principle topological structure in the area, and would be the obvious point to seek refuge from predators or strong currents while inactive. Fish that moved tended to move away from the ridge into areas used exclusively at night or during the day (with some crepuscular crossover). In many cases the space use away from the reef was quite diffuse suggesting a more wandering type of behavior related to foraging or mate searching (although this seems unlikely for the time of year) not sheltering in place.

We do not have data on the distribution of food resources around our study site, so we cannot give a concrete explanation as to why the fishes would leave the ridge area to feed. In Puget Sound, lingcod eat large amounts of sand lances (Ammodytidae) and herring (Clupeidae) as well as rockfish (Scorpaenidae) depending upon the size of the lingcod (Beaudreau & Essington 2007). Individuals that made the longer movements of 150 to 200 m may have done so to better access pelagic food resources. Copper and quillback rockfish tend to feed near the bottom and their diets include shrimps, gammarid amphipods, and fishes to some extent. Benthic food resources may be more plentiful distant from the ridge due to lower overall grazing pressure, and higher food availability may offset higher predation risk due to lack of shelter. Off the coast of Alaska and British Columbia, these rockfish also consume sand lances and herring, and quillback may make foraging excursions into the water column (Love et al. 2002), so these rockfish may also be accessing pelagic food resources.

Other authors have noted movements related to sheltering in salema *Salpa salpa* (Jadot et al. 2006), blue rockfish *S. mystinus* (Jorgensen et al. 2006) and sheephead *Semicossyphus pulcher* (Topping et al. 2005), and reproduction in the sparid *Pagrus auratus* (Parsons et al. 2003). For species like blue rockfish (Jorgensen et al. 2006) and sheephead (Topping et al. 2005) all individuals showed the same diel patterns of movement and home range use unlike the rockfish here which showed a range of behaviors.

Individual behavior and MPA design

Quantifying the typical home range size of a fish has obvious applications to the design of MPAs. Likewise, understanding the individual variation in space use and movement behavior has implications regard-

ing spillover and edge effects (Zeller & Russ 1998, Kramer & Chapman 1999, Cole et al. 2000). For example, understanding what proportion of individuals move seasonally can help to estimate fishing mortality and the effectiveness of the reserves (Willis & Millar 2005). Within seasons, lingcod used fairly small home ranges for periods of several months. However, some individuals appear to make excursions from these localized areas for periods of up to a month after which they may disperse to new locations or return to their original home range (this study, Jagielo 1990, Starr et al. 2004). How common this type of behavior is has relevance for determining how much spillover (or just general movement out of reserves) may occur. Those fish that make the type of diel/tidal movements seen in our study are also potentially more susceptible to crossing reserve boundaries. When and how frequently they do so, may determine what the consequences are. For example, many of the lingcod in this study moved away from the ridge area on the morning flood tide, which would likely make them more susceptible to fishing than individuals that make nocturnal movements presuming that fishing pressure is generally lower at night.

CONCLUSIONS

Ecologically-based management of marine systems requires generalizations about nature, and this process of simplifying the complex natural world depends critically on a keen sense of natural history (Dayton 2003). Indeed, the essential challenge in translating basic ecological observations into management is weeding out less relevant information, while ensuring that management takes into account those critical processes that produce ecological structure. Although it might be tempting to base management (e.g. MPAs) on average home ranges of species, such an approach is insensitive to the variability of behavior expressed within and among different species of groundfish. Management of species such as those we investigated here rest not only on understanding average behavior, but also on understanding the processes generating variability in behavior (Gaines & Denny 1993). The high frequency behavioral observations reported here provide the level of observation necessary to develop meaningful hypotheses that can be tested experimentally. It is only with this second level of understanding that will allow us to make reasonable predictions as to how species will respond to environmental perturbations, such as climate change or habitat-loss, or to specific management strategies, such as the implementation of marine reserves or other spatial or temporal strategies for management and conservation. While the arena of

resource management often requires us to simplify complex systems, our results illustrate that such simplification will be difficult, and will depend ultimately on detailed behavioral data. As Dayton (2003) noted, along the path to science-based resource management, when it comes to natural history, there can be no shortcuts.

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