Title

Movement and home range of pink abalone Haliotis corrugata: implications for restoration and population recovery

Authors

Coates, JH
Hovel, KA
Butler, JL
et al.

Publication Date

2013-07-12

DOI

10.3354/meps10365

Vol. 486: 189–201, 2013
doi: 10.3354/meps10365

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 12

Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery

Julia H. Coates[1,*], Kevin A. Hovel[1], John L. Butler[2], A. Peter Klimley[3], Steven G. Morgan[3]

[1]Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, California 92182-4614, USA
[2]National Marine Fisheries Service, Southwest Fisheries Science Center, 3333 North Torrey Pines Court, La Jolla, California 92037-1023, USA
[3]Graduate Group in Ecology, University of California, Davis, 1005 Wickson Hall, One Shields Avenue, Davis, California 95616, USA

ABSTRACT: Densities of abalone in southern California have been dramatically reduced by overfishing and disease, leading to the collapse of some populations, and low fertilization rates may be hindering population recovery. This is a pattern typical of abalone species globally. However, movement may produce clustered distributions that promote fertilization success in broadcast spawners, such as abalone, even at low regional densities. We translocated wild, adult pink abalone *Haliotis corrugata* to an existing pink abalone patch to create a high-density aggregation, and then used acoustic telemetry to characterize abalone movement and monitor aggregation maintenance for a period of 14 mo in the Point Loma kelp forest near San Diego, California. Abalone showed a minimal flight response to handling that did not differ between the resident or translocated groups. Most individuals exhibited small home ranges (median area 183 m^2) and homing behavior consisting of regular back-and-forth movement to a single point. Nomadic movement was also observed in several individuals. Though site fidelity may help maintain aggregations, abalone density decreased, and nearest neighbor distances increased at our site to near-initial levels after 18 mo via a combination of mortality, large movements of a few individuals, and small, incremental movements of most individuals. No coordinated movements that would suggest spawning behavior were observed. Translocation of wild abalone to produce aggregations may not result in high rates of fertilization success that promote population recovery. However, the homing behavior observed may provide more opportunities for mating than expectations based on static measures of density and aggregation state.

KEY WORDS: Movement · Restoration · Homing · Broadcast spawning · Allee effect · Translocation

INTRODUCTION

Fertilization success is a key factor in dictating population dynamics of marine species, particularly for broadcast spawning marine invertebrates (Levitan & Sewell 1998). A variety of factors influence fertilization success, including current speed, turbulence, substratum complexity, population density and aggregation state, and species-specific fertilization kinetics (Denny & Shibata 1989, Levitan et al. 1992, Levitan & Young 1995, Babcock & Keesing 1999, Yund 2000). Population density and aggregation state are the factors of chief concern when considering populations of harvested invertebrates that may be subject to increasing

---

*Email: juliahcoates@gmail.com

separation from potential mates. Sessile and sedentary invertebrates are particularly susceptible to fishery collapse due to a reproductive Allee effect (Gascoigne & Lipcius 2004). Furthermore, abalone recruitment rates have been positively correlated with population aggregation state (Dowling et al. 2004).

Many population models involving fertilization success in broadcast spawners assume that organisms are sessile. However, for sedentary organisms, such as abalone and sea urchins, movement has the potential to mitigate reproductive Allee effects, making prediction of fertilization success rates more complex than for truly sessile species. Moreover, abalone movement rates are highly variable within and among species, and for a given species, extended periods of little movement may be punctuated by long-distance excursions (Tutschulte 1976, Ault & Demartini 1987, Tarr 1995, Dixon et al. 1998, Officer et al. 2001). Thus, to determine the role of abalone movement in fertilization success and in overcoming Allee effects, more information is needed about species- and habitat-specific movement patterns and aggregation potential. Movement of adult abalone has implications not only for mate finding ability but also for population mixing, containment within marine reserves, the potential success of population restoration programs involving abalone transplantation, and establishing benchmark densities used for management.

Attempts to restore abalone populations sometimes involve releasing juvenile abalone in suitable coastal locations. However, juveniles are susceptible to predation, may exhibit high propensities for dispersal, and those reared in captivity may not exhibit some behaviors that promote growth and survival (Schiel & Welden 1987, Tegner & Butler 1985, Tegner 2000, James et al. 2007, Roberts et al. 2007, Hamasaki & Kitada 2008). Creating aggregations by transplanting wild adult abalone may be an attractive alternative to releasing juveniles due to relatively low cost and high reproductive output and survival of large adults. Red abalone *Haliotis rufescens* in California maintain distributions that are more clustered than appropriate crevice habitat (Micheli et al. 2008). Australian *H. laevigata* increase aggregation state prior to spawning (Shepherd 1986b), and *H. rubra* reaggregate following removal of individuals via fishing (Officer et al. 2001). These studies suggest that adults are attracted to each other and that artificial aggregations might be maintained. Aggregation state following manipulation for restoration might even increase beyond that during placement as individuals are brought into one another's area of sensory perception.

In this study, we employed acoustic methods to track the movement of pink abalone *Haliotis corrugata* in a high density artificial aggregation within a southern California kelp forest. Pink abalone is a former fisheries species in southern California estimated to be at 0.01% of its peak abundance in the 1950s (Rogers-Bennett 2002). Little recovery has been observed in population density since the cessation of pink abalone fishing in 1997. This suggests low productivity at low densities and that recovery may require active restoration efforts. We investigated the movements of pink abalone in the context of responses to manipulation for restoration, and in the context of long-term natural behaviors that might reveal interactions among conspecifics and indicate mechanisms behind observed spatial distributions. Specifically, we tested whether (1) translocated abalone used to form an aggregation moved more than abalone that were native to the site; (2) an aggregation created by displacing abalone would be maintained over a period of 18 mo; and (3) individuals display coordinated movements that might correspond to spawning behavior.

MATERIALS AND METHODS

Tagging and translocation

Our study was conducted in the Point Loma kelp forest near San Diego, California, USA (Fig. 1). A site for artificial aggregation was located in typical pink abalone habitat consisting of giant kelp *Macrocystis pyrifora*, understory kelps, and boulders on bedrock of claystone with shallow ledges undercutting the bottom. The boundary was designated as a circle with a 9 m radius, creating a 254 m^2 area (Fig. 1). This area contained 23 adult pink abalone already residing in the site, representing a density of 0.09 abalone m^{-2}. To characterize the broader regional density and aggregation state of pink abalone around the site, we conducted 20 belt transect surveys (4 × 30 m) and 21 nearest neighbor distance surveys at randomly generated coordinates within a 9-hectare area centered on the site. Mean density on transects was 0.041 ± 0.033 abalone m^{-2} (mean ± SD) and mean and median nearest neighbor distance was 3.5 ± 4.1 m and 1.9 m respectively, for 19 out of 21 surveys on which abalone could be found.

We created an artificial pink abalone aggregation at our site in early fall, when water temperatures and abalone ripeness are near their highest levels along

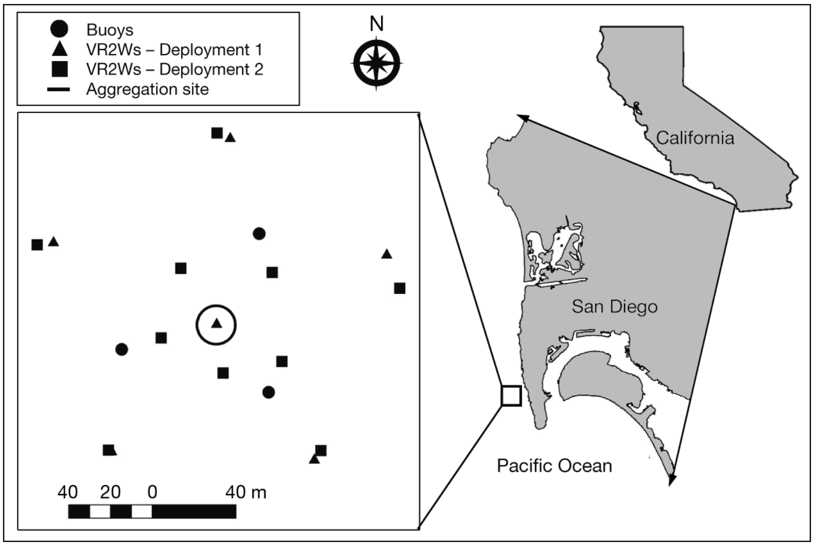

Fig. 1. Study location in the Pt. Loma kelp forest, California, USA, and inset showing aggregation site and positioning of Vemco VRAP buoys and VR2W receivers

the southern California and Baja California coastline (Guzman-del Proo et al. 2000, Button 2008). On 23 September 2009, the 23 native abalone in the site were removed from the substrate using an abalone iron and tagged as described below. Abalone were measured for shell length, sexed by visual inspection of the gonad, and tissue was removed *in situ* before being returned to their initial position within 5 min. If the sex was questionable, the body wall and gonad were pierced with a syringe and a small amount of gonad material drawn out and later inspected with a compound microscope. Tags consisted of both ultrasonic transmitters (Vemco model V9, 9 × 20 mm, Amirix) and stainless steel washers with unique printed numbers. Tags were wrapped in stainless steel wire, which was then looped through the 2 last respiratory pores of the abalone. On the day following resident abalone tagging, we tagged, measured, and sexed an additional 23 adult pink abalone from an area approximately 2.2 km to the north within the kelp forest. On the same day, we placed these individuals haphazardly throughout the site in groups of 2 to 6, thereby creating a final density within the site of $0.18\ \mathrm{m}^2$, close to the theoretical minimum spawning density ($0.2\ \mathrm{m}^{-2}$) required to sustain a viable population (California Department of Fish and Game 2002). We performed SCUBA surveys of the aggregation site and immediate surroundings throughout the study to check for dead animals. Shortly after the initial tagging, we tagged 3 additional abalone on or near the boundary of the site to replace individuals that had died.

Telemetry

We deployed 2 tracking systems (Vemco VRAP and Vemco VPS,) to track pink abalone movement at the aggregation site for a total of 14 mo. Both systems were used to record abalone spatial position from 23 September to 19 November 2009 (Deployment 1), and only the Vemco VPS system was used to record abalone spatial position from 26 May to 2 December 2010 (Deployment 2). Tracking was not possible from January through April 2010 due to rough ocean conditions. The VRAP system provides spatial position data in real time and was useful for ground-truthing during Deployment 1, but was not practical for long-term deployment due to the need for frequent maintenance, particularly in open water conditions. The VPS system provides information that is not collected in real time, but does not require frequent maintenance, making it more appropriate for long-term monitoring. Concurrent tracking using both systems during Deployment 1 allowed a comparison of performance of the 2 systems.

To deploy the VRAP system, we anchored 3 acoustic receiver buoys in an approximately equilateral triangle with 80 m sides centered on the aggregation area (Fig. 1). Buoys were anchored with bungee cords that were under constant strain to minimize tidal movement. We then placed an acoustic transmitter, used to estimate system resolution, at the center of the aggregation area about 1 m off the bottom. Abalone position information streamed from acoustic receiver buoys to a base station on land in a line of sight to the buoys. Abalone that appeared to be moving long distances or appeared not to move at all were noted and their coordinates were used to locate the abalone using SCUBA to ground truth system information and confirm animals as live or dead.

The VPS system uses an array of omnidirectional Vemco VR2W acoustic receivers moored 1.5 m off the bottom to detect transmitter signals, and triangulation of transmitter positions is achieved in post-processing by Vemco using proprietary software. The array design during Deployment 1 used 6 receivers, 1 at the aggregation site center and 5 placed 100 m apart in a circle around the site, and 6 synctags, 1 at the site center and 5 placed 50 m apart in a circle around the site (Fig. 1). Synctags are the same transmitters used for animal tags but are fixed in place and are used to synchronize the internal clocks of each receiver. Calibration of these clocks is based on the arrival time of transmissions from synctags a known distance away, for multiple receivers detecting the same transmission. For Deployment 2, we added 5 receivers to the inside of the circle, concentrating potential to detect transmitters in a smaller area, and reduced the number of synctags to 4. This change in array design during Deployment 2 was done as an effort to increase abalone position frequencies.

Data processing

Both telemetry systems provided an estimate of accuracy with each animal tag and synctag position, and these were used to filter the datasets prior to use (Supplement 1 available at www.int-res.com/articles/suppl/m486p189_suppl.pdf). Briefly, we generated estimates of positioning error for all tags by examining the relationship between the distance from the triangulated synctag position to the true position measured in the field. Various threshold levels of allowable error were used to filter the data for a set of the most frequently positioned animals to examine how choice of error threshold altered apparent space use. We then chose a threshold value of positioning error that balanced loss of spatial information and increased confidence in individual positions. VPS triangulated positions for synctags that were preserved below the threshold had a median distance from the known position of 2.7 m and 0.6 m during Deployments 1 and 2, respectively (90th percentiles of 6.6 m and 2.1 m). VRAP triangulated positions for synctags that were below the chosen threshold had a median distance from the known position of 3.4 m.

We combined data collected from the VRAP and VPS systems during Deployment 1 to perform analyses on the most complete dataset possible (Supplement 2). We then used GIS to plot positions for each animal and removed obvious erroneous positions (i.e. outlying positions that would require unreasonable movement speeds) before home range and movement analyses.

Home range calculations

Home ranges were calculated using the extension Home Range Tools (HRT) version 1.1 in ArcGIS 9.2. We calculated 50, 90, and 95 % kernel utilization distribution (KUDs), and used a 90 % KUD (90 KUD) as our measure of home range area for most analyses. The 90 KUD is the area where an abalone has a 90 % chance of being found at a given moment. Raster cell size was set to the minimum of 1 m to match the fine spatial scale of the data.

Behavioral analyses

To characterize the general extent of pink abalone movement, we calculated (1) 90 KUD home ranges, and (2) mean step length both for abalone and for synctags. To determine if abalone were moving more than the apparent movement of stationary synctags, we compared the sizes of 90 KUDs using both full datasets and datasets made to have equal numbers of positions. Mean step length between abalone and synctags was compared using 2-tailed *t*-tests (Supplement 3). Data were checked for normality visually and for homogeneity of variances using Bartlett's test, and were transformed when necessary to meet the assumptions of these and all subsequent tests (Underwood 1997). We also calculated (3) total displacement of abalone between first and last positions, and (4) displacement from first position to the center of the developed home range for all individuals that were positioned for ≥2 wk, regardless of when positions were collected during the study. Additionally, to determine whether translocating abalone caused a flight response, we calculated (1) displacement and (2) home ranges for abalone over the first 20 d of the experiment and compared these variables between translocated and resident abalone with separate 2-tailed *t*-tests. This period was chosen due to evidence of a shift in behavior after 20 d and only abalone that were positioned during most of the first 20 d following aggregation and having >20 positions were used in this analysis.

Aggregation maintenance

To determine whether our artificial aggregation was maintained over time, we partitioned Deployment 1 into 9 consecutive time blocks and then calculated the area that encompassed the positions of all abalone during those blocks. The first 3 blocks, which immediately followed translocation, were 2 d in length to distinguish any immediate flight response. All subsequent time blocks were 7 d in length, except for one that was lengthened to 14 d due to the scarcity of position detections. For each time block, we noted the average position of each abalone as well as the median nearest neighbor distance. When an abalone that should have been present because it was known to be alive and in the study area was not detected, it was assumed to be in the same average position as in the previous time block. This assumption conservatively biases the analysis towards a lack of movement. We plotted abalone average positions for each time block in GIS and used Hawth's Tools to produce a minimum convex polygon (group MCP) that connects the outermost positions of animals in the group. This series of group MCP areas was used to track the spatial expansion of tagged individuals. Hawth's Tools were also used to produce the distances from each abalone to its closest neighbor.

Long-term patterns

To examine long-term variability in movement among individuals, we calculated monthly 90 KUD for 8 abalone that were consistently positioned for at least 3 mo. We excluded the first 20 d of Deployment 1 from these analyses to avoid a potential flight response. Monthly 90 KUDs were graphically examined for coordinated expansion or contraction of home ranges among individuals. This would suggest coordinated behaviors associated with spawning or environmental variability. We also examined homing behavior for 5 individuals regularly detected for at least 2.5 mo. Homing behavior (i.e. the consistent return to one or a few positions) may be due to forays away from and back to a particular location such as a den or home scar, or by more random back-and-forth movements within a restricted space such as a preferred foraging ground. To quantify homing behavior, for each of the 4 abalone, we calculated the bearing between subsequent positions and the bearing between each position and the center of the abalone's home range. We chose a single point at the estimated center of the 50 KUD as home range center for each abalone. The distribution of differences between these 2 bearings should be centered on zero if the animal is showing high fidelity to a home site.

RESULTS

System performance

During Deployment 1, while both systems were in place, the VRAP system outperformed the VPS system by detecting more animals with greater frequency (Table 1). However, the VPS had the potential for very good detection frequency. During Deployment 2, the VPS receiver density was increased and concentrated in a smaller area around the aggregation, increasing potential for higher detection frequencies while maintaining the same areal coverage. The new array did produce excellent detection frequencies, but only for a small number of abalone (Table 1). We identified 33 tagged abalone remaining in or near the study area in SCUBA surveys during Deployment 2; however, many of these were never detected. Some abalone present in Deployment 2 may have occupied rocky crevices that prevented transmission detection (J. H. Coates pers. obs.), while others were frequently detected due to their position and increase in receiver density. It is also possible that there was a seasonal decrease in movement that resulted in the lack of detection of many abalone during Deployment 2 and this may not be evident in an analysis of those that were detected. We recommend that future studies use as many receivers as possible in high concentration when tracking abalone.

Analysis of behavior

Basic characteristics

Pink abalone generally exhibited small home ranges, traveled small distances around a home range center (Fig. 2B), and had low displacement (linear distance) from initial to final position and from initial position to the center of an eventual home range (Table 2). This is evident in a histogram (Fig. 3) of the frequency of distances moved from the first position to last and from first to center of the home range. The peak frequency of excursions from the initial placement was in the 10 m distance class; the greatest number of movements relative to the center of the home range was in the 5 m distance class (Fig. 3).

Table 1. *Haliotis corrugata*. Number of pink abalone detected by the VRAP and VPS systems deployed in the Pt. Loma kelp forest, California, USA, and detection frequencies (number of detections per abalone per day) during Deployment 1 and Deployment 2

Deployment	System	Abalone detected	No. of positions abalone^{-1} d^{-1} Median	First quartile	Third quartile	Range
1	VRAP	47	42	7	144	2–386
1	VPS	42	6	2	24.2	1–170
2	VPS	16	155	11.2	237.7	2–5108

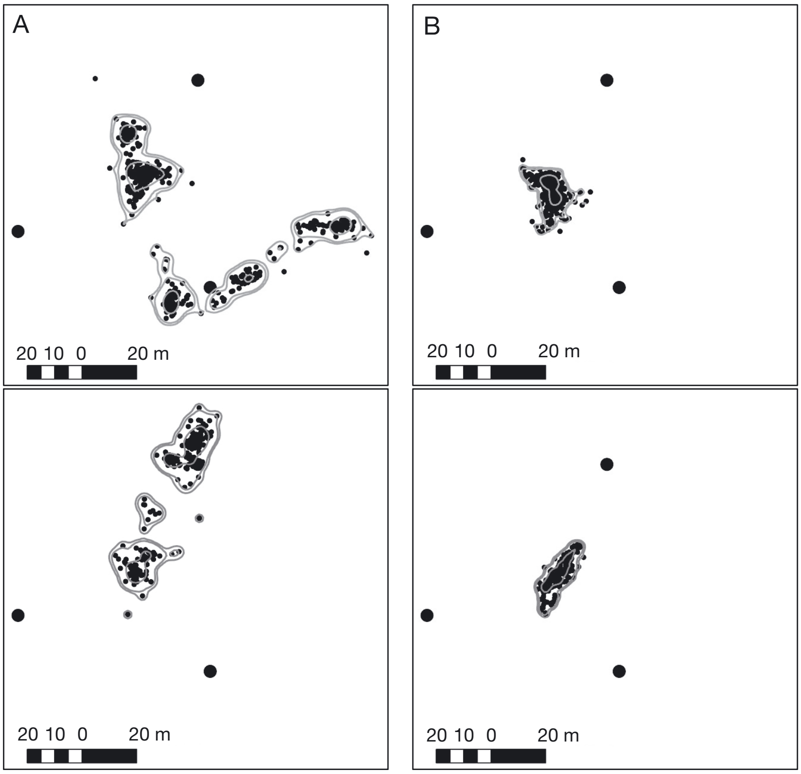

Fig. 2. *Haliotis corrugata*. Positions of (A) 2 abalone displaying typical nomadic behavior, and (B) 2 abalone showing typical homing behavior and restricted space use. Gray lines represent home range areas as 50, 90, and 95% kernel utilization distribution (KUD)

Table 2. *Haliotis corrugata*. Median, first and third quartiles, and range for displacement of pink abalone from the first to last position and from first position to home range center, and comparison of median home range area for animal tags and synctags

	Displacement (m)		Home range area (m^2)	
	First to last	First to home site	Abalone	Synctag
Median	7.8	4.2	182.7	35.8
1st quartile	5.5	3.0	126.0	22.5
3rd quartile	17.3	10.1	227.2	50.4
Range	2.3–77.9	1.4–81.0	83.6–1006.4	21.4–51.7

Hence, most abalone traveled small distances around a home range. While the majority of abalone home ranges were small, they were all larger than the home ranges calculated for synctags. The 'apparent' movement of synctags, due to error in positioning, results in apparent home ranges that can be compared to the abalone to determine whether their movements are real. The median abalone home range was 5-fold larger than the median synctag home range, indicating movement by all tagged abalone (Table 2). Step lengths were significantly longer for abalone than for synctags (Supplement 3). There was no significant difference in mean 90 KUD between male and female abalone (Table 3). We found no evidence of a difference in flight response between resident and translocated abalone; both 90 KUD and displacement after aggregation were very similar between the 2 groups (Table 3). Sex could be determined for 34 abalone and of those, 19 were female and 15 were male. Given the resolution of the tracking data, we were unable to determine how spatial position of these individuals of known sex varied relative to each other with time.

Aggregation maintenance

The group MCP grew for approximately the first 20 d of the study and then plateaued (Fig. 4); however, growth in group MCP areas was predominantly due to extensive movements by only 7 out of the 49 tagged animals, and most abalone remained within 2 m of their neighbors and inside or near the aggregation site boundary. Though abalone did not aggregate by moving closer together after being placed in close proximity, the median nearest neighbor distance increased by less than a meter throughout Deployment 1. Only 1 abalone left the listening range, and thus the plateau in group MCP was not primarily a product of loss of abalone with a tendency to move.

Long-term patterns

We found little evidence of coordinated movements among abalone that might constitute collective response to environmental conditions or spawning behavior. Monthly 90 KUDs varied within and among individuals but also was inconsistent among individuals (Fig. 5). There was no apparent difference between males and females.

Abalone displayed fidelity to a home site within their home ranges. This can be observed in plots of the frequency of abalone movement bearings relative to the center of their home range. Fig. 6 displays

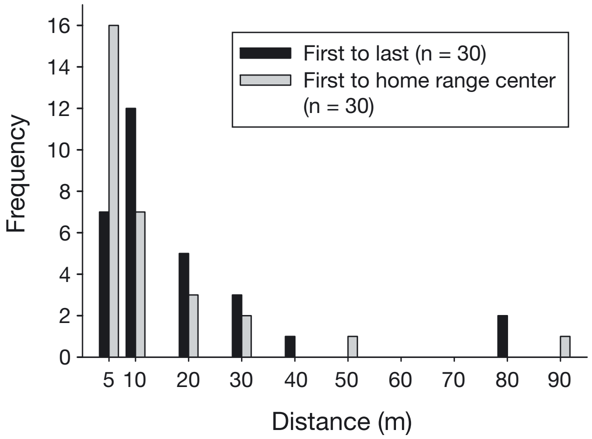

Fig. 3. *Haliotis corrugata*. Frequency of distances moved from first to last position (black) and first position to the center of the developed home range (gray) for pink abalone with ≥2 wk of positions regardless of the time period of positioning during the study

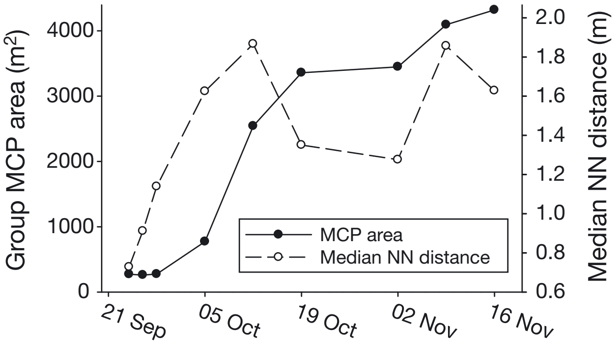

Fig. 4. *Haliotis corrugata*. Growth in the area encompassing tagged pink abalone (group minimum convex polygon, MCP) during Deployment 1 (solid line), and concurrent growth in median nearest neighbor (NN) distance (dotted line)

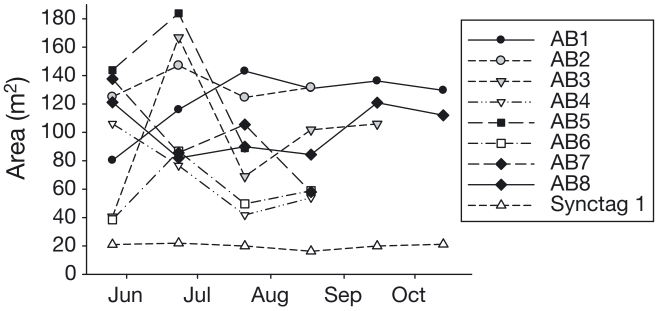

Fig. 5. *Haliotis corrugata*. Home range sizes during 4 wk time periods for a subset of pink abalone positioned for 3 or more consecutive periods. Numbers represent different individuals (males = black symbols, females = gray symbols, neither or unknown = open symbols). 'Synctag 1' represents the central synctag (see 'Materials and methods: Telemetry')

plots for 3 of the 5 individuals analyzed and the remaining 2 individuals are displayed in Supplement 3. These relative bearings were produced by noting the compass direction an abalone moved at each step and the corresponding compass direction the abalone would have needed to move to go in the direction of home range center. These compass directions were then converted to radians and the difference between them represents a 'relative' bearing. A value of zero indicates the abalone moved in exactly the direction required to take it from its current position to its home range center. Peaks in relative bearing around zero seen in Fig. 6 show that abalone movements were most frequently directed towards the center of their home ranges. This suggests strong homing behavior to a single point in space that is closely identified with the home range center. Fig. 6 also shows the individual home range that corresponds to each relative bearing frequency distribution and these indicate the range of distances the abalone moved away from and back to the home range center. In comparison, apparent movement of the central synctag was centered on the central anchor point but showed a broader and less focused distribution of directions, indicating that abalone homing behavior was not an artifact of positioning error.

Table 3. *Haliotis corrugata*. *t*-tests comparing home range areas of male and female pink abalone for the entire study period, and home range area and displacement of resident and translocated abalone during the first 20 d following aggregation

Group	n	Med.	1st quart.	3rd quart.	df	*t*	p
Home range							
Male	10	192.1	137.6	496.8	15	0.65	0.51
Female	12	167.3	145.8	347.7			
Resident	10	163.4	141.6	205.4	24	0.09	0.93
Translocated	16	144.6	119.1	206.6			
Displacement							
Resident	13	7.0	4.5	15.5	28	0.65	0.51
Translocated	17	8.6	6.3	27.3			

Over the course of our study, 17 out of the 49 tagged pink abalone (35%) were lost to a combination of mortality and emigration. We confirmed 9 mortalities of tagged abalone by finding empty tagged shells. Four of these mortalities occurred shortly after the experiment began and are likely the result of injury during handling or perhaps increased vulnerability to

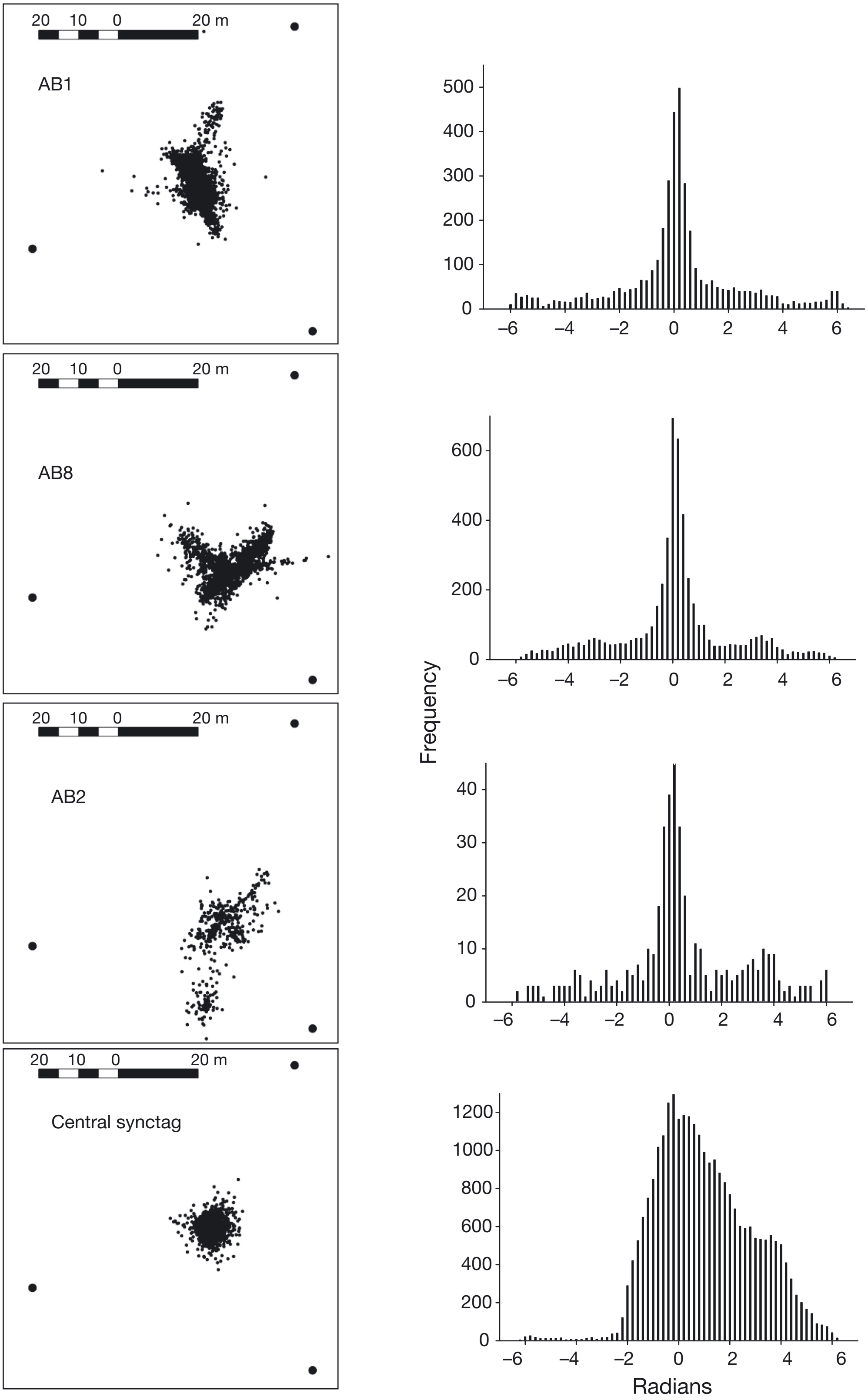

Fig. 6. *Haliotis corrugata*. Positions of 3 pink abalone that were detected over long time periods and the central synctag with associated plots of bearings relative to the home range center

predators, whereas the other 5 were likely natural mortality. An additional 8 abalone were never relocated (via tracking or on surveys) and could represent mortalities or emigration from the study site. A final survey on 31 March 2011 identified 21 live tagged abalone remaining within the site boundary (9 m radius circle) and 7 untagged abalone that had immigrated to the site resulting in a density of 0.11 abalone m^{-2}. We then surveyed out to a 15 m radius and found an additional 5 live tagged abalone and 5 more untagged abalone, resulting in a density of 0.05 m^{-2} for the entire 15 m radius circle. Density within the original aggregation site before and after manipulation was 0.09 m^{-2} and 0.18 m^{-2}, respectively. Thus, over the long term, the density at aggregation was not maintained and remained only slightly higher than the unmanipulated state.

DISCUSSION

In this study, we used acoustic telemetry to quantify and characterize the movements of pink abalone in an artificial aggregation in a southern California kelp forest. Tagged pink abalone typically remained at or near the site of translocation and only slightly reduced their aggregation density over the course of 2 mo following translocation of individuals to a new site. While they were tracked, most abalone restricted their use of space to a small home range and those that could be tracked for long periods made regular movements away from and back to a home site. Though these behaviors bode well for maintenance of abalone aggregations, site density was reduced by 42% after 18 mo due to emigration and mortality, resulting in a density only slightly greater than the unmanipulated state. Homing behavior could increase the opportunities of individuals to interact with conspecifics; however, we observed no coordinated movement among individuals that suggested spawning behavior. We conclude that pink abalone movements are more dynamic than previously realized and have the potential to modify expectations of fertilization success. However, aggregation of wild abalone as a restoration strategy has mixed potential for success.

Abalone movement

Many pink abalone in our study had small home ranges and high site fidelity over the course of several months. Similarly, in Australia few marked *Haliotis rubra* were recaptured more than 10 m from their starting position after 4 mo (Dixon et al. 1998), and 47% of marked and recaptured *H. midae* in South Africa remained within a small site after 3 yr, with 81.5% of individuals in exactly the same position (Tarr 1995). In contrast, marked *H. rufescens* on the northern California coast moved 1 to 6 m per day and up to 150 m least linear distance per month, and did not return to previous sites (Ault & Demartini 1987). Abalone movement rates are higher in shallower, more hydrodynamically active environments (Shepherd 1986a, Ault & Demartini 1987, Dixon et al. 1998). Thus, some of the observed differences among species may be attributed to habitat as well as to experimental technique. It is important to note that mark-recapture techniques used in the previous studies may underestimate movement rates if abalone continually move to and from a home site, which we were able to observe with continuous tracking in our study.

Abalone must be able to sense and move to conspecifics to maintain an aggregated distribution in the face of loss due to harvest, natural mortality, and emigration. Aggregated distributions, even within low regional densities, have been observed in California pink and red abalone (Button 2008, Micheli et al. 2008), as they were by our surveys. Aggregated distributions would have likely resulted from a balance between site fidelity and exploration of new territory on the part of all or a subset of individuals, and our long-term movement records shed light on some of these processes. First, there appears to be a clear divide between 2 behavioral modes (Fig. 2). Most of the abalone restricted their use of space, resulting in small median home range size and total displacement (either from initial to final positions or from initial positions to a home range center). In contrast, a small number of abalone displayed more exploratory, nomadic behavior for which defining a home range area is less appropriate. The dual behavioral modes we observed are analogous to 'partial migration', wherein some individuals display migratory patterns while others remain residents (Chapman et al. 2011). Some of the ecological drivers (e.g. variation in body condition and relative need for food or mate resources) that are attributed to partial migration plasticity may explain varied abalone behaviors. It is not clear how frequently individual abalone may switch between these behavioral modes.

Second, analysis of the bearings of movement within the home range for a subset of abalone with high positioning frequency indicated that pink abalone in our study moved away from and back to a consistent point within the landscape. We commonly observed abalone returning to their home range center after moving on the order of 10 to 20 m away, sometimes within a single day. One abalone in particular (AB2) occupied an entirely new area for several days, but also eventually returned to its previous home range. Homing to a point location has been observed in some abalone species but only from a distance of ≤1 m from the home (Nakamura & Soh 1997, Nakamura & Archdale 2001), though abalone in these studies were housed in laboratory aquaria that may have severely restricted their movement. Pink abalone observed during our study often had an identifiable home 'scar' or clean area of rock beneath them that was devoid of other macrofauna. Scars also have been observed in several other cases (Ault & Demartini 1987, Tutschulte & Connell 1988, Tarr 1995) and may have contributed to assumptions that individuals never leave these sites. Homing may be more common in abalone than suggested by many field surveys, which often are not conducted on an appropriate temporal scale to detect homing.

Homing behavior has been observed in a variety of vertebrate and invertebrate taxa in terrestrial and marine habitats (Borger et al. 2008) and often is a product of strong fidelity to sites that offer superior opportunities for feeding (Thums et al. 2011), breeding (Espeland et al. 2007), predator avoidance (Mitamura et al. 2009), or territorially defending limited resources (Kadota et al. 2011). Home ranges may also arise due to tradeoffs between travel cost and acquisition of resources (Buchmann et al. 2011). For instance, abalone are likely to face tradeoffs between acquisition of food or mates and increased susceptibility to predators. An abalone that moves may be better able to locate food when drift algae is limited, or may experience higher fertilization success by moving closer to conspecifics. However, traveling may increase susceptibility to predators because abalone (1) must leave their home scar and seek refuge within crevices that may not match their body size; (2) may travel over substrata that may weaken their ability to adhere to the substrate; and (3) may increase their visibility to searching predators.

We found no common pattern in home range size variation among abalone tracked for 7 mo. Therefore, no evidence existed for coordinated changes in movement patterns over time that might indicate group reaction to spawning cues. The size frequency distribution of juvenile pink abalone in the Point Loma kelp forest in summer 2010 (data not shown) suggest that the adult population spawned in summer 2009 and winter 2009–2010. Therefore, mate seeking movements were most likely during Deployment 2. Spatially explicit models of broadcast spawner fertilization dynamics have shown that increases in aggregation state improves fertilization success at low (Lundquist & Botsford 2004, Zhang 2008) as well as intermediate (Levitan & Young 1995) population densities, but it is unclear if aggregation behavior is related to reproductive timing.

Mate seeking behavior might be dependent upon an appropriate density of individuals, above or below the theoretical minimum viable population (MVP) density identified by the California Abalone Recovery and Management Plan. This density (0.2 m^{-2}) is based on studies of recruitment failure in south Australian abalone (Shepherd & Brown 1993) and the densities of red abalone in southern California before population declines (Tegner et al. 1989, Karpov et al. 1998). Thus, the MVP is not specific to pink abalone and species-specific refinements are needed. Though observations of abalone behavior that are directly related to spawning are limited, the distribution of the Australian abalone *Haliotis laevigata* changes from random to aggregated just before the spawning season (Shepherd 1986b). In a rare field study noting abalone sex, Seamone & Boulding (2011) found that Canadian northern abalone *H. kamtschatkana* were significantly aggregated without regard to sex. However, nearest neighbor distances of opposite sexes were only closer than expected under a random distribution at the lowest density site (0.12 adults m^{-2}). While this and other studies confirm that abalone aggregate irrespective of sex at a range of densities, they also may indicate a sex-dependent behavioral response to low density that would improve fertilization.

While our initial aggregation density was not maintained, the observed homing behavior has the potential to bring individuals close to one another. Abalone fertilization rates drop dramatically over the first 5 m between mates (Babcock & Keesing 1999). Therefore, abalone traveling 10 to 20 m within their home ranges can overcome distance challenges to fertilization. Pink abalone spawn asynchronously relative to other southern California abalone species (Tutschulte & Connell 1981). Therefore, if they do exhibit mate seeking behavior rather than aggregation irrespective of sex or spawning readiness, a lack of coordinated movement might be expected.

Implications for restoration

Manipulating abalone populations to restore populations or increase fishery yield has been attempted predominantly through planting juvenile stages and releasing larvae, expensive techniques that have met with mixed success in short-term survival (e.g. Schiel & Welden 1987, Tegner & Butler 1985, Tegner 2000, James et al. 2007, Roberts et al. 2007, Hamasaki & Kitada 2008). Long-term survival of hatchery released larvae and juveniles was recently assessed by Read et al. (2012), who found that up to 26% of emergent adults were from hatcheries. While this is encouraging, the overall density was still considered to be low. Therefore, larger scale hatchery enhancement efforts with genetic diversity management may be required. Shepherd et al. (2000) attempted a stock enhancement for abalone in Australia via larval release and monitoring of subsequent settlement and survival. The technique was not recommended due to density dependence and unpredictability in larval survival and settlement success.

Despite the homing behavior and small home ranges that we observed, our results suggest little benefit to aggregation of wild adults over other restoration techniques. While many individuals maintained small home ranges with strong fidelity to a single point and short displacement from initial position for several months (some for over a year), movement and mortality eventually resulted in density returning close to the pre-manipulation state. In contrast to our results, Tutschulte (1976) increased adult pink abalone density at Santa Catalina Island, California by nearly 3-fold and after 1 yr density was approximately 2 times greater than before manipulation. If density maintenance like that observed by Tutschulte (1976) is more common than ours, artificial aggregation of adults might still be a useful restoration technique due to the additional advantage of being able to move abalone to safer or more productive areas.

The first criterion that should be satisfied for aggregation to be a useful technique is a lack of flight response following manipulation. Though there was some indication that handling and tagging abalone induced a mild flight response in some individuals, we consider this criterion largely met in our study. Mean home range size for all abalone in the aggregation was slightly larger and more variable during the first 20 d post-aggregation compared to the following 38 d. The area encompassing all tagged abalone, as well as the median nearest neighbor distance, grew over the first 20 d post-aggregation and then stabilized. This, however, was predominantly due to the movements of a few abalone. Notably, we found no difference in movement between resident and translocated abalone, suggesting that the additional handling necessary to transport abalone to a new site did not result in a greater disturbance response than for resident abalone.

In the long-term, the value of creating abalone aggregations for restoration depends not only on losses due to movement, but also to mortality. Abalone losses in our study were comparable to another study conducted in the Pt. Loma kelp forest in which yearly survival of pink abalone was found to be 0.77% (±0.05% SE) during a 3 yr study (Button & Rogers-Bennett 2011). Given the reductions in density that occurred at our site over the course of the study, manipulation of a much larger group of individuals into greater densities would be needed to combat expected losses due to mortality and emigration. Manipulation of abalone carries the potential for injury and death and it is not yet clear that the potential reproductive benefits of aggregation outweigh this cost. A cautionary approach might be to consider our results as evidence for the potential efficacy of marine reserves for stabilizing or enhancing abalone populations. This is because our results indicate that groups of abalone already existing in suitable habitat for foraging and protection from predators likely have small home ranges. These abalone will achieve larger body sizes and enhanced larval output, and with small home ranges, may rarely emigrate to outside fished areas. Restoration actions or reserves could have a good chance at success if sites are chosen carefully and the number of abalone involved is sufficient to counteract expected losses.

Acknowledgements. We thank Dr. C. Catton for sharing her expertise and support in the field. Dr. L. Rogers-Bennett provided support in development of the tagging method. Volunteer SCUBA support was provided by R. Jenkinson, C. Lennert, S. Mao, and A. Warneke. Thanks to the Biotelemetry Laboratory at UC Davis for lending VRAP equipment and training. This study was funded by the NOAA Species of Concern Program and the Joint Doctoral Program in Ecology at San Diego State University and University of California Davis. This is contribution number 30 from the San Diego State University Coastal & Marine Institute.

LITERATURE CITED

Ault JS, Demartini JD (1987) Movement and dispersion of red abalone, *Haliotis rufescens*, in northern California. State of California, The Resources Agency, Department of Fish and Game, Sacramento, CA, p 196–213

Babcock R, Keesing J (1999) Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. Can J Fish Aquat Sci 56:1668–1678

➤ Borger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol Lett 11:637–650

➤ Buchmann CM, Schurr FM, Nathan R, Jeltsch F (2011) An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. Oikos 120:106–118

Button C (2008) The influence of density-dependent aggregation characteristics on the population biology of benthic broadcast-spawning gastropods: pink abalone (*Haliotis corrugata*), red abalone (*Haliotis rufescens*), and wavy turban snails (*Megastraea undosa*). PhD dissertation, University of California, San Diego, CA

Button CA, Rogers-Bennett L (2011) Vital rates of pink abalone *Haliotis corrugata* estimated from mark-recapture data to inform recovery. Mar Ecol Prog Ser 431:151–161

California Department of Fish and Game (2002) Draft abalone recovery and management plan. California Department of Fish and Game, Marine Region, Sacramento, CA

Chapman BB, Bronmark C, Nilsson JA, Hansson LA (2011) The ecology and evolution of partial migration. Oikos 120:1764–1775

Denny MW, Shibata MF (1989) Consequences of surf-zone turbulence for settlement and external fertilization. Am Nat 134:859–889

Dixon CD, Gorfine HK, Officer RA, Sporcic M (1998) Dispersal of tagged blacklip abalone, *Haliotis rubra*: implications for stock assessment. J Shellfish Res 17:881–887

Dowling NA, Hall SJ, McGarvey R (2004) Assessing population sustainability and response to fishing in terms of aggregation structure for greenlip abalone (*Haliotis laevigata*) fishery management. Can J Fish Aquat Sci 61: 247–259

Espeland SH, Gundersen AF, Olsen EM, Knutsen H, Gjosaeter J, Stenseth NC (2007) Home range and elevated egg densities within an inshore spawning ground of coastal cod. ICES J Mar Sci 64:920–928

Gascoigne J, Lipcius RN (2004) Allee effects in marine systems. Mar Ecol Prog Ser 269:49–59

Guzman-del Proo SA, Salinas F, Zaytsev O, Belmar-Perez J, Carrillo-Laguna J (2000) Potential dispersion of reproductive products and larval stages of abalone (*Haliotis* spp.) as a function of the hydrodynamics of Bahia Tortugas, Mexico. J Shellfish Res 19:869–881

Hamasaki K, Kitada S (2008) The enhancement of abalone stocks: lessons from Japanese case studies. Fish Fish 9: 243–260

James DS, Day RW, Shepherd SA (2007) Experimental abalone ranching on artificial reef in Port Phillip Bay, Victoria. J Shellfish Res 26:687–695

Kadota T, Osato J, Hashimoto H, Sakai Y (2011) Harem structure and female territoriality in the dwarf hawkfish *Cirrhitichthys falco* (Cirrhitidae). Environ Biol Fishes 92: 79–88

Karpov KA, Haaker PL, Albin D, Taniguchi IK, Kushner D (1998) The red abalone, *Haliotis rufescens*, in California: importance of depth refuge to abalone management. J Shellfish Res 17:863–870

Levitan DR, Sewell MA (1998) Fertilization success in free-spawning marine invertebrates: review of the evidence and fisheries implications. Publ Spec Can Sci Halieut Aquat 125:159–164

Levitan DR, Young CM (1995) Reproductive success in large populations: empirical measures and theoretical predictions of fertilization in the sea biscuit *Clypeaster rosaceus.* J Exp Mar Biol Ecol 190:221–241

Levitan DR, Sewell MA, Chia FS (1992) How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecology 73: 248–254

Lundquist CJ, Botsford LW (2004) Model projections of the fishery implications of the Allee effect in broadcast spawners. Ecol Appl 14:929–941

Micheli F, Shelton AO, Bushinsky SM, Chiu AL and others (2008) Persistence of depleted abalones in marine reserves of central California. Biol Conserv 141: 1078–1090

Mitamura H, Uchida K, Miyamoto Y, Arai N and others (2009) Preliminary study on homing, site fidelity, and diel movement of black rockfish *Sebastes inermis* measured by acoustic telemetry. Fish Sci 75:1133–1140

Nakamura K, Archdale MV (2001) Activity patterns of abalone under experimental conditions. Aquacult Res 32:169–179

Nakamura K, Soh T (1997) Mechanical memory hypothesized in the homing abalone *Haliotis diversicolor supertexta* under experimental conditions. Fish Sci 63: 854–861

Officer RA, Dixon CD, Gorfine HK (2001) Movement and re-aggregation of the blacklip abalone, *Haliotis rubra* Leach, after fishing. J Shellfish Res 20:771–779

Read KD, Lemay MA, Acheson S, Boulding EG (2012) Using molecular pedigree reconstruction to evaluate the long-term survival of outplanted hatchery-reared larval and juvenile northern abalone (*Haliotis kamtschatkana*). Conserv Genet 13:801–810

Roberts RD, Keys EF, Prendeville G, Pilditch CA (2007) Viability of abalone (*Haliotis iris*) stock enhancement by release of hatchery-reared seed in Marlborough, New Zealand. J Shellfish Res 26:697–703

Rogers-Bennett L (2002) Estimating baseline abundances of abalone in California for restoration. CCOFI Rep 43: 97–111

Schiel DR, Welden BC (1987) Responses to predators of cultured and wild red abalone *Haliotis rufescens* in laboratory experiments. Aquaculture 60:173–188

Seamone CB, Boulding EG (2011) Aggregation of the northern abalone *Haliotis kamtschatkana* with respect to sex and spawning condition. J Shellfish Res 30:881–888

Shepherd SA (1986a) Movement of the southern Australian abalone *Haliotis laevigata* in relation to crevice abundance. Aust J Ecol 11:295–302

Shepherd SA (1986b) Studies on southern Australian abalone genus *Haliotis* VII. Aggregative behavior of *Haliotis Laevigata* in relation to spawning. Mar Biol 90:231–236

Shepherd SA, Brown LD (1993) What is an abalone stock: implications for the role of refugia in conservation. Can J Fish Aquat Sci 50:2001–2009

Shepherd SA, Preece PA, White RWG (2000) Tired nature's sweet restorer? Ecology of abalone (*Haliotis* spp.) stock enhancement in Australia. Publ Spec Can Sci Halieut Aquat 130:84–97

Tarr RJQ (1995) Growth and movement of the South African abalone *Haliotis midae*: a reassessment. Mar Freshw Res 46:583–590

Tegner MJ (2000) Abalone (*Haliotis* spp.) enhancement in California: what we've learned and where we go from here. Publ Spec Can Sci Halieut Aquat 130:61–71

Tegner MJ, Butler RA (1985) The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. Calif Fish Game 71: 150–163

Tegner MJ, Breen PA, Lennert CE (1989) Population biology of red abalones, *Haliotis rufescens*, in southern California and management of the red and pink, *Haliotis corrugata*, abalone fisheries. Fish Bull 87:313−339

Thums M, Bradshaw CJA, Hindell MA (2011) In situ measures of foraging success and prey encounter reveal marine habitat-dependent search strategies. Ecology 92: 1258−1270

Tutschulte T (1976) The comparative ecology of three sympatric abalones. PhD dissertation. University of California, San Diego, CA

Tutschulte T, Connell JH (1981) Reproductive biology of 3 species of abalones *Haliotis* in southern California USA. Veliger 23:195−206

Tutschulte TC, Connell JH (1988) Feeding behavior and algal food of three species of abalones (*Haliotis*) in southern California. Mar Ecol Prog Ser 49:57−64

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Yund PO (2000) How severe is sperm limitation in natural populations of marine free-spawners? Trends Ecol Evol 15:10−13

Zhang Z (2008) A simulation study of abalone fertilization. J Shellfish Res 27:857−864

Editorial responsibility: Richard Osman,
Edgewater, Maryland, USA

Submitted: September 13, 2012; Accepted: April 8, 2013
Proofs received from author(s): July 7, 2013