

MEASURING ABALONE (*HALIOTIS SPP.*) RECRUITMENT IN CALIFORNIA TO EXAMINE RECRUITMENT OVERFISHING AND RECOVERY CRITERIA

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ABSTRACT Abalone populations in southern California have declined dramatically since the 1950s when they supported a multi-species, commercial, and recreational fishery producing more than 3,000 t per year. Today the commercial fishery is closed statewide and the recreational fishery is closed south of San Francisco. In contrast, red abalone, *Haliotis rufescens* (Swainson, 1822), populations in northern California continue to sustain a 1,100 t per year free-diving recreational fishery. We used standardized Abalone Recruitment Modules (ARMs) made of half cinder blocks (area = 2.6 m²) to compare the recruitment of juvenile abalone in northern California, where stocks are abundant, with southern California where stocks have declined. We compared the abundance of abalone inside ARMs ($n = 12$) in Van Damme State Park (VDSP), northern California with abalone inside ARMs ($n = 82$) in the Channel Islands National Park from 2001 to 2003. Abalone densities on the reefs surrounding the ARMs at VDSP, averaged 8300/ha compared with abalone densities of 30/ha on reefs in three of the northern Channel Islands. Red, flat abalone, *H. walallensis* and pinto abalone, *H. kamtschatkana kamtschatkana* were found in the northern ARMs, whereas in the south red, pink, *H. corrugata*, threaded, *H. kamtschatkana assimilis*, and the endangered white abalone, *H. sorenseni*, were rare in the southern ARMs. Abalone were 30 times more abundant inside the ARMs in the north (5.30/ARM) compared with the south (0.18/ARM). Similar numbers of abalone were found in all 3 years in the ARMs in northern (69, 69, and 53 abalone) and southern California (14, 11, and 20 abalone). The majority of abalone in both the north and the south were less than 100 mm in shell length. Ironically, the rare flat abalone was more abundant in the north, than pink abalone were in the south, a species which once supported a major fishery. Clearly, abalone stocks in southern California are so low that recruitment is failing, despite their potential high fecundity and the fishery closure. These results demonstrate that ARMs can be used to monitor recruitment in the northern fishery, as well as establish quantitative recovery criteria to assess abalone restoration efforts that are desperately needed in the south.

KEY WORDS: juvenile abalone, abalone recruitment modules, monitoring, recruitment failure, abalone restoration

INTRODUCTION

Abalone populations in California once supported major fisheries, landing in excess of 3000 metric tons (t) per year (Cox 1962). Population declines, however forced the closure of both the recreational fishery south of San Francisco and the commercial fishery statewide in 1996. Populations in the south suffered serial depletion of five species within the *Haliotis* spp complex (Dugan & Davis 1993, Karpov et al. 2000). The white abalone, *H. sorenseni*, is now on the endangered species list and the primary cause of their decline has been attributed to overfishing (Hobday et al. 2001). In contrast, red abalone, *H. rufescens*, populations are still abundant in northern California where there is an active free-diving recreational fishery. Landings in the recreational fishery have been stable, averaging 1165 t in the mid 1980s (Tegner et al. 1992) with little change in 2000 (1238 t) (CDFG unpubl. data). Today, there is a need to quantify juvenile abalone recruitment in California to better manage fished populations in the north and to assess the status of depleted stocks in the south since the fishery closure. Specifically, temporal patterns of juvenile abundance can be used to assess the strength of future year classes entering the fishery as well as set restoration targets for populations following natural recovery or restoration efforts.

Recruitment of abalone, however, is difficult to quantify. Studies of larval dispersal and recruitment are rare (but see Sasaki & Shepherd 1995), with only a handful of studies examining the density and distribution of newly settled abalone (Prince et al. 1987, McShane & Smith 1991, Sasaki & Shepherd 2001). An

examination of densities of newly settled abalone (recruiting to the benthos) has been advocated for to quantify stock-recruitment relationships and density dependent survival, but these studies are impeded by the difficulties of sampling (McShane & Smith 1988). Most recruitment studies focus on the abundance of juvenile or young of the year abalone, sometime after settlement, when they are visible to divers (Sainsbury 1982, Shepherd & Turner 1985, Prince et al. 1988). Juveniles may be better predictors of the numbers of abalone surviving to become adults as compared with larval and newly settled abalone. Juveniles however, are also difficult to census (Yamaguchi 1975) sometimes requiring habitat destruction especially on complex rocky reefs.

Artificial structures made of cinder blocks have been used as standardized sampling units (Davis 1985) for juvenile abalone in southern California (Davis 1995). However, few juveniles have been found within these modules suggesting either recruitment failure, as is consistent with reef surveys showing little recruitment and few adults, or the modules are poorly suited to assess juvenile abalone in the wild. Recruitment overfishing may be difficult if not impossible to quantify (Harrison 1986, McShane 1992) because a sharp decrease in recruitment in species such as abalone with high individual fecundities may not occur (Harrison 1986).

Here we compare the numbers of juvenile abalone inside standardized recruitment modules made of cinder blocks deployed in northern California where densities of abalone are high, with southern California where densities are low. We examine the species composition, quantity, and size of juvenile abalone occurring inside abalone recruitment modules in 2001 and 2003. We quantify abalone populations on the natural rocky reefs surrounding the recruitment modules in both the north and south and compare them

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with the abalone inside the modules. We highlight the usefulness of collecting a time series of juvenile abalone recruitment information in California to aid in fishery management and evaluate the impacts of restoration programs. We examine the current status of abalone recruitment in southern California by comparing modern densities in the southern modules with the north and the south 10 years ago. We discuss the evidence for recruitment failure in southern California and the need for establishing measurable restoration goals.

MATERIALS AND METHODS

Northern California

Standardized abalone recruitment modules (ARMs) were deployed at Van Damme State Park (VDSP) (lat. 39°16'08"N, long. 123°47'58"W), northern California in August 2000 (Fig. 1). ARMs

were originally designed by E. Ebert and were made of concrete cinder blocks cut lengthwise, stacking the blocks five high and enclosing them in a wire frame (Davis 1995). Here, the design was modified to enhance resistance to intense wave action by using welded rebar cages, widening the block cube to lower the profile, stacking the blocks three high (rectangle measuring 813 mm × 610 mm × 305 mm high). The surface area of the blocks in each of the modified northern ARMs was 4.8 m², of which 2.6 m² was sheltered area created by the sides, top, and bottom of each "letter m."

VDSP is a popular and productive recreational abalone diving site dominated by rocky reef with seasonally abundant *Nereocystis* kelp canopy, a subcanopy of *Pterogophora* and numerous subtidal red algae including *Cryptopleura*, *Gigartina*, and *Iridaea*. Upright and encrusting coralline algae are also abundant. An estimated 25,500 (±5,430) red abalone were taken from VDSP in 2002 (CDFG unpubl. data).

Twelve ARMs were deployed between 9 and 12 m in three

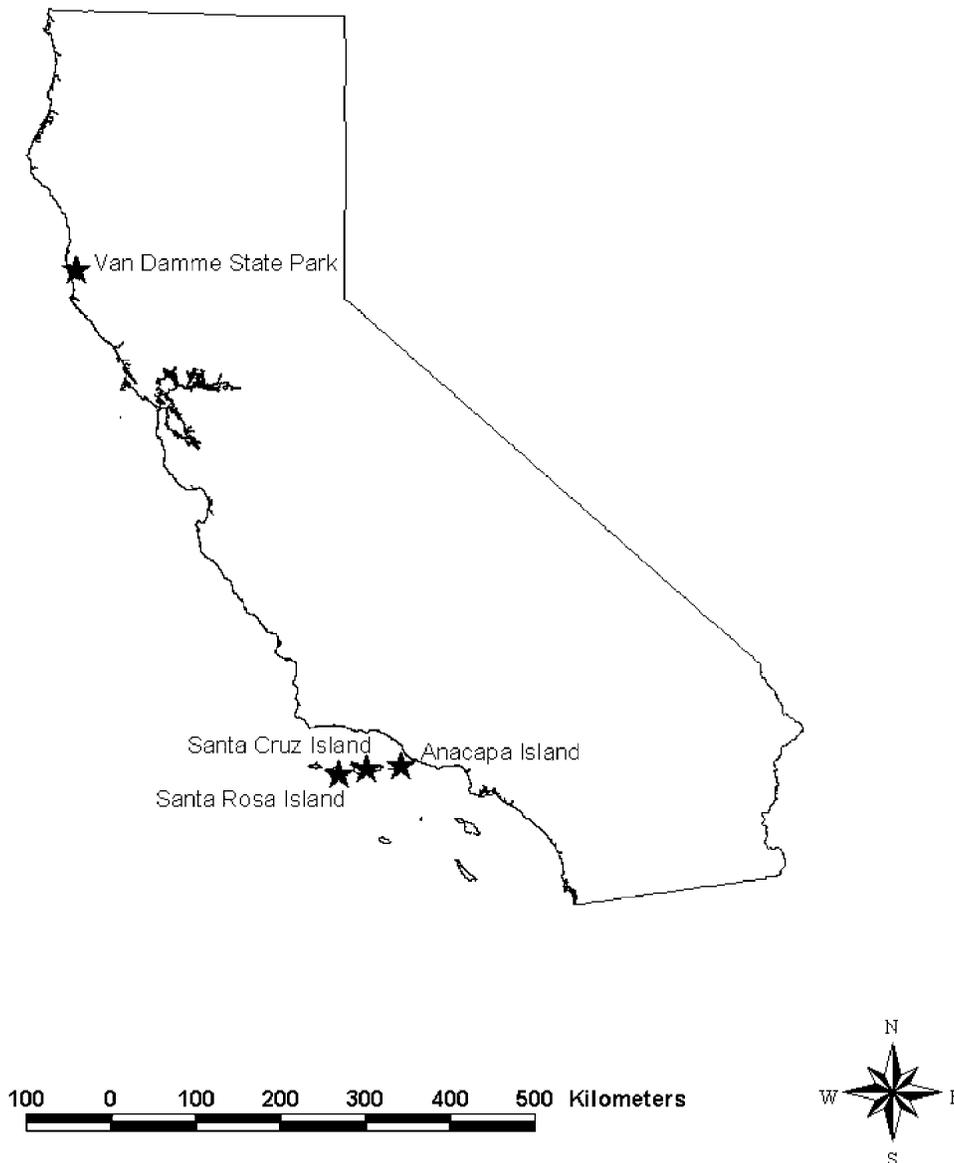


Figure 1. A map of California showing sites in both northern and southern California where ARMs were deployed and abalone recruitment was monitored.

groups of four. The modules were placed 3–6 m apart within the cluster of four. The northern cluster was approximately 140 m from the central cluster. The southern cluster was 710 m from the central cluster. Each ARM was bolted into the rocky substrate using 6-inch stainless lag bolts in each of the four corners and in the center of the module. Holes for the 5 bolts were drilled using a Chicago pneumatic drill with a 0.25 inch bit.

The ARMs were surveyed annually in August. ARMs were in place 1 y before the surveys began in August 2001, 2002, and 2003. One dive team surveyed each ARM, opening the lid and carefully removing each block counting and measuring all of the invertebrates and fishes inside the ARMs. Organisms outside or on the cage were not sampled. Organisms too numerous to count were gently swept into fine mesh bags (2 mm) to be counted and measured at the surface. Organisms cemented to the brick were measured and quantified underwater. Each block was set to the side while the next block was removed and the animals quantified. When the survey was completed, divers reassembled the ARM and replaced the lid securing it with wide cable ties. Each ARM took two divers approximately 40 min to survey.

Abalone density on the adjacent natural reef was quantified annually in August from 2000 using transects at depths between 8 and 16 m. Each transect (1m × 5m) was searched invasively for abalone in 2000 (*n* = 29), 2001 (*n* = 13) and 2002 (*n* = 32). Invasive searching targeted small cryptic abalone and included looking in rock crevices, turning large rocks and small cobble, in coralline algae, and under sea urchins.

Southern California

ARMs have been deployed and surveyed by the National Parks Service’s, Kelp Forest Monitoring Program in the northern Channel Islands since 1989 (Davis et al. 1997). These ARMs were cube shaped and slightly taller and narrower than the ARMs deployed in northern California (see details of the modifications required for the northern modules above). Each cage is made of plastic coated wire mesh (51 mm × 102 mm). The southern modules measured 600 mm × 600 mm × 500 mm high. Twenty half-cinder blocks were arranged four in a layer and stacked 5 layers high leaving the center core of the cube open. Each habitat provided 5.0 m² of which 3.0 m² was sheltered habitat created by the inside arches of the letter “m” which is comparable to the area of the northern California modules. The major differences between the southern and the northern module design was that the northern design had a lower profile, 18 half blocks and was bolted into the substrate whereas the southern modules were taller and more cube shaped, with 20 half blocks, an open core and were not bolted in place.

In 2001, 82 ARMs were sampled from three sites on Anacapa Island, five sites on Santa Cruz Island and two sites on Santa Rosa Island using the methods described earlier (Fig. 1). Each site comprised between 6 and 15 ARMs. Sites with 15 ARMs had three clusters of 5 ARMs each; at sites with only 6 or 7 all ARMs were grouped together in a single cluster. The majority of these sites were on the southern leeward side of the islands. In 2002, 84 ARMs were sampled and in 2003 at the same sites and islands 82 ARMs were sampled.

The density of adult red, pink, and green abalones were enumerated along transects on the natural reef. Adult abalone abundances were determined at each of the three islands with the ARMs. Depths of the transects at the three islands ranged from 5–16 m at Anacapa, 8–18 m at Santa Rosa and 4–18 m at Santa

Cruz Island. Deep-water species such as white and threaded abalone would not be found at these depths nor would shallow green abalone. A fixed reference line 100 m in length was bolted to substrate. Transects were placed perpendicular to this fixed reference line at random intervals. Transects covered an area 3 m × 20 m (60 m²). Twelve transects were completed at each site. Three sites were monitored at each of Anacapa Island (total area searched 2,160 m²) and Santa Rosa Island (2,160 m²) whereas 5 sites were monitored at Santa Cruz Island (total 3,600 m²).

The number of ARMs or replicates needed to detect “true” differences in the mean number of abalone in the north compared with the south was estimated using the test for sample size and the iterative method (Sokal & Rohlf 1981).

RESULTS

Abalone in the ARMs

Many more abalone were found inside the ARMs in northern compared with southern California in all 3 y (2001–2003) (Tables 1, 2). The number of abalone found inside the ARMs was consistent over the 3-y period (Tables 1 and 2). In the north 5.3 abalone were found per ARM. This was 30 times more abalone than observed in the south where the average was 0.18/ARM. In the north, three species of abalone were found inside the modules red flat and pinto abalone, whereas in the south, three species and one subspecies of abalone were found including two deep-water abalone (white and threaded abalone), albeit in very low numbers. In southern California, red, pink, white, and threaded abalone were found inside the ARMs in 2001–2003. In previous years, green abalone, *H. fulgens*, have also been observed in the ARMs (5 total in 10 y).

There was an 80% chance of detecting at least a 10% difference in the means of juvenile abalone density in northern compared with southern California at the 0.05 significance level with a sample size of 9 or more ARMs in each region.

Abalone on the Natural Reef

Abalone density on the natural reef surrounding the ARMs differed substantially between northern and southern California (Table 3). In northern California, abalone were found at high densities, while in southern California densities were near zero. Abalone density in the north averaged nearly 8500 abalone/ha (SD 2,302/ha) between 2000 and 2002 (Table 3). Of the 679 abalone measured in the north, 669 were red abalone, 9 were flat abalone and 1 was a pinto abalone (Table 3). Furthermore, abalone were abundant both shallower and deeper than the surveys. The density

TABLE 1.
Number and species of juvenile and adult abalone found within ARMs in Van Damme State Park, northern California in Aug. 2001, 2002, and 2003. One pinto abalone 83 mm was found in 2003.

Year	# ARMs	<i>H. rufescens</i>		<i>H. walallensis</i>		Total
		<50 mm	>50 mm	<50 mm	>50 mm	
2001	12	36	17	4	12	69
2002	12	25	25	3	16	69
2003	12	17	15	3	17	52
Total	36	78	57	10	45	190

TABLE 2.
Number and species of abalone inside ARMs southern California in 2001 to 2003.

Island	#ARMs	<i>H. rufescens</i>	<i>H. corrugata</i>	<i>H. sorrenseni</i>	<i>H. k. assimilis</i>
2001					
Anacapa Is.	20	0	2	0	0
Santa Cruz Is.	47	4	1	1	4
Santa Rosa Is.	15	2	0	0	0
Subtotal	82	6	3	1	4
2002					
Anacapa Is.	20	0	1	0	0
Santa Cruz Is.	48	1	0	0	5
Santa Rosa Is.	16	4	0	0	0
Subtotal	84	5	1	0	5
2003					
Anacapa Is.	20	0	1	0	0
Santa Cruz Is.	46	1	0	0	8
Santa Rosa Is.	16	10	0	0	0
Subtotal	82	11	1	0	8
	248	22	5	1	17

of flat abalone was higher in the ARMs (4.8 abalone m⁻²) than on the surrounding natural reef (0.012 abalone m⁻²) in the north.

Few abalone were observed during the surveys at the three Channel Islands. No abalone were observed at Santa Cruz Island on any of the surveys. In the south, white and threaded abalone were found inside the ARMs but were absent from the shallow surveys of surrounding reef, at the depths surveyed (Tables 2 and 3). At Anacapa Island only 7 pink abalone were observed over the 3-y period during which 6,480 m² were searched. At Santa Rosa

Island abalone densities were slightly higher with 20 red abalone observed (31/ha) in the same area searched (Table 3). In the south, the numbers of adult abalones were consistently low, with abalone found at a small fraction (3/11) of the total number of sites.

Size Frequency Distributions

Small (<50 mm) and large abalone were found inside the ARMs in both northern and southern California. In the north, a

TABLE 3.

Average density of abalone, *Haliotis* spp. found in the vicinity of ARMs in northern and southern California from 2000 to 2002. Density in northern California was determined along 2 m × 5 m (10 m²). Density in southern California was determined along 3 m × 2 m (60 m²). Abalone in northern California included red, flat and pinto abalone with red and pink abalone in southern California.

Site	Year	Area m ²	Count	Density/m ²	Density/Ha.
North					
Van Damme State Park	2000	290	320	1.10	11,034
	2001	130	71	0.55	5,462
	2002	320	288	0.90	9,000
Average		247	226	0.85	8,499
South					
Anacapa Island*	2000	2,160	2	0.001	9.26
	2001	2,160	3	0.001	13.88
	2002	2,160	2	0.001	9.26
Average			2.67	0.001	10.80
Santa Cruz Island	2000	3,600	0		
	2001	3,600	0		
	2002	3,600	0		
Average			0		
Santa Rosa Island**	2000	2,160	15	0.007	69.44
	2001	2,160	2	0.001	9.26
	2002	2,160	3	0.001	13.88
Average			6.67		30.86

Note: *All abalone found at Anacapa Island were pink abalone, *H. corrugata*.

**All abalone found at Santa Rosa Island were red abalone, *H. rufescens*.

peak in young of the year abalone (<30 mm) was observed in 2001, but this peak was less pronounced in 2002 when more midsize juvenile abalone (50 mm) were observed in the size frequency distribution (Fig. 2). In the south, all the abalone observed in the ARMs were small except one adult (Fig. 2).

Qualitatively, the shape of the size frequency distribution at the small end (left side) was relatively similar in 2002 inside the ARMs compared with on the natural reef. This was not the case in 2001 when more juveniles in the 20-mm size class appeared in the modules than in surveys of the natural reef (Fig. 3). Overall, many more adult abalone (>100 mm) were observed on the transects over the natural reef compared with the ARMs suggesting the ARMs are not suitable for sampling adults. In southern California, too few adult red ($n = 20$) and pink abalone ($n = 7$) were observed on the natural reef to warrant comparing their size distribution with the sizes of the juveniles inside the ARMs.

DISCUSSION

The dynamics of abalone recruitment and the nature of the stock-recruitment relationship remains poorly understood, yet has important implications for management and restoration. In this study, we found recruitment failure (0.18/ARM) in southern California where adult densities are two orders of magnitude below the proposed minimum viable population size (2,000/ha) (Shepherd & Brown 1993). Furthermore, we found that abalone recruitment in southern California has declined 20-fold over the past decade, despite the fishery closure. In 1990 ($n = 161$) and 1991 ($n = 154$) densities inside 45 ARMs at Santa Rosa and Santa Cruz Islands in the Channel Islands National Park (Davis 1995) were higher than

today (3.6/ARM). If conditions remain unchanged in the south, we may no longer be able to detect recruitment using <100 ARMs. This suggests that adult densities may have declined to the point where we are now observing recruitment overfishing.

In contrast, to the south higher numbers of juvenile abalone (5.30/ARM) were found in northern California from 2001 to 2003 where adult red abalone densities were 8,000/ha on the natural reefs. Similar numbers of juveniles in the north were found in the ARMs as compared with the natural reef (Fig. 3), however too few abalone were observed to make this comparison in the south. Elsewhere higher densities have been found inside artificial habitats than on the natural reef (Hayashi & Yamakawa 1988, DeFreitas 2003). The endangered white abalone (Hobday et al. 2001), the pinto, and threaded abalone (Rogers-Bennett et al. 2002a) were all found in ARMs indicating they are suitable for monitoring even rare species. In the north, flat abalone were regularly observed inside ARMs even though they make up less than 14% of the population (Rogers-Bennett & Pearse 2001). Our results suggest ARMs are a useful tool for monitoring juvenile abundance in an active fishery as well as where populations have declined. The numbers of juveniles within ARMs from healthy stocks in the north (5.3/ARM) can be used as minimum targets for restoration criteria in California.

We examined the abundance of juvenile abalone, some months after settlement as previous studies have done (Sainsbury 1982, Shepherd & Turner 1985, Prince et al. 1987). To assess year class strength, a time series of these data could be collected encompassing a variety of oceanographic conditions including high-frequency environmental fluctuations such as El Niños, as well as low frequency environmental fluctuations such as regime shifts

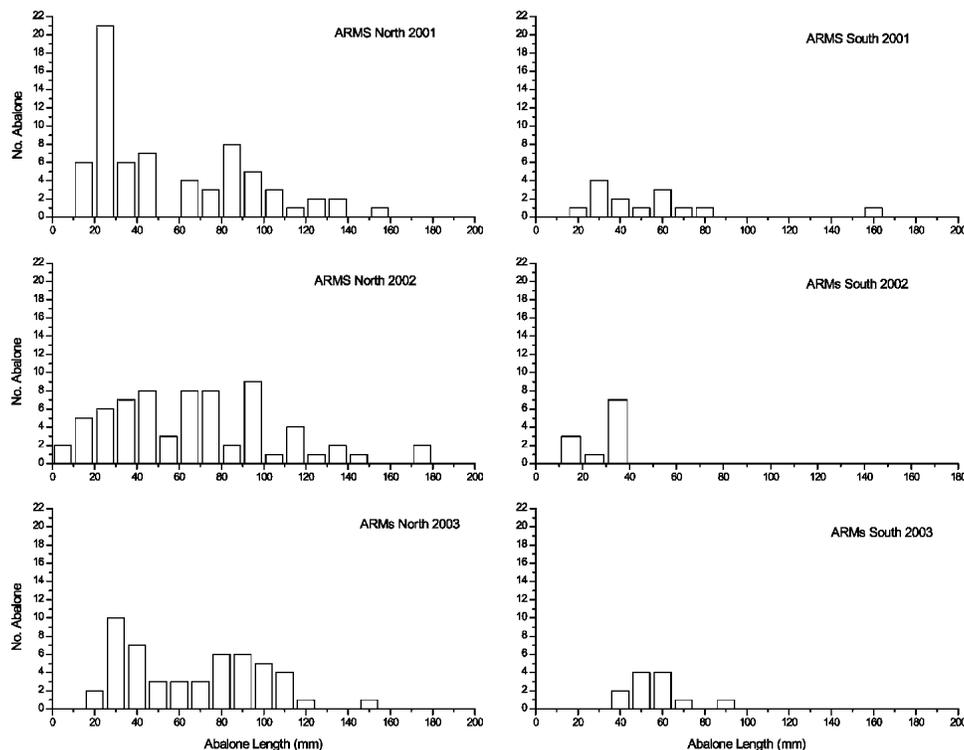


Figure 2. A comparison of the size frequency distributions of abalone *Haliotis* spp. found inside ARMs in southern and northern California in 2001, 2002, and 2003. The top two graphs are the abalone found in the ARMS in southern California and the bottom two graphs are the abalone found in the ARMs in northern California. The length of the abalone in mm is on the X axis and the number of abalone of that size is shown on the Y axis.

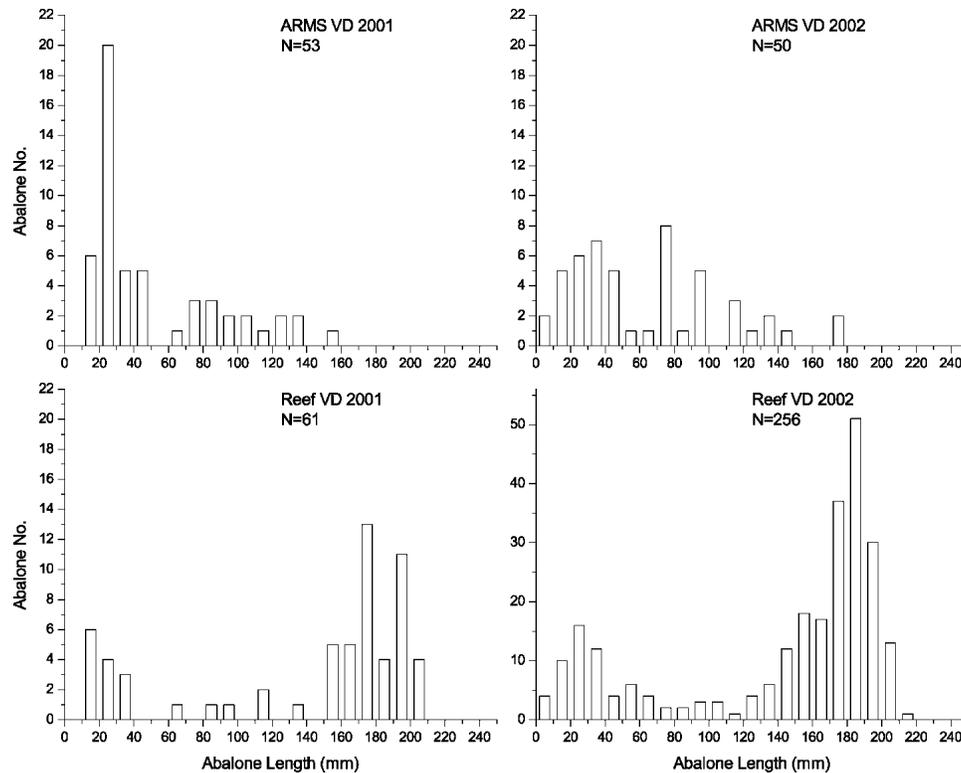


Figure 3. A comparison of the size frequency distribution of red abalone, *H. rufescens*, found inside ARMs and on the natural reef in Van Damme State Park, northern California in 2001 and 2002. No abalone measurements were made on the natural reef in 2003. The top two graphs are abalone found inside the ARMs and the bottom two graphs are abalone found on the natural reef.

(Mantua et al. 1997). Furthermore, recruitment levels could be assessed across a gradient of adult densities, in between the high and low densities that we have examined, to reveal the relationship between stock size and recruitment.

Establishing if there is a relationship between spawners and recruits at the local level is vital for protecting against localized recruitment overfishing. In southern Australia, where the longest time series of stock-recruitment measures exist for abalone (examining 2-y-old juveniles), no clear relationship was found in a reserve population (Shepherd 1990). Experimental adult removals however, demonstrated that there was a positive correlation between local adult density and the number of newly settled abalone (Prince et al. 1988). Either adult spawner density is linked with local recruitment, or larvae from local and distant sources preferentially settle and survive with high densities of adult abalone (Breen 1992). Abalone unlike other invertebrates, such as sea urchins, may have limited larval dispersal (Tegner & Butler 1985, Prince et al. 1987). This suggests restoration programs should not rely on natural larval dispersal to recover distant populations (Tegner 1993). A minimum density threshold (allee effect), has been suggested for abalone (Shepherd & Brown 1993) below which recruitment fails precipitating either local or global extinction (Roberts & Hawkins 1999). Our results in the south support this threshold concept. One mechanism proposed to explain this threshold is the significant drop in fertilization success at low densities despite high fecundities (Babcock & Keesing 1999). This is relevant not only for management of the recreational red abalone fishery in the north, but also for restoration of endangered and threatened species of abalone in southern California.

In conclusion, recent abalone population surveys (2002) in

southern California indicate that 98% of the remnant pink, green and white abalone populations are comprised of large old adults (CDFG unpubl. data). The absence of large juveniles and small adults from the size frequency distributions suggests that there has been little successful recruitment on these natural reefs in the past decade (except for red abalone at San Miguel Island) (Rogers-Bennett pers. obser.). Densities of pink abalone are low even inside reserves in southern California (Rogers-Bennett et al. 2002b). Today, the white abalone in southern California is at dangerously low population levels and the absence of small adults and juveniles suggest there has been 2 decades of recruitment failure (Hobday et al. 2001, Lafferty et al. 2004). Given the dire state of many abalone populations in southern California today abalone restoration programs cannot delay. We recommend that abalone restoration programs (1) incorporate strategies to assess juvenile recruitment (such as ARMS); (2) determine recruitment levels based on healthy stocks; and (3) use measurable quantitative recovery criteria (Gerber & Hatch 2002).

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LITERATURE CITED

- Babcock, R. & J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevis*: Laboratory and field studies. *Can. J. Fish. Aquat. Sci.* 56:1668–1678.
- Breen, P. A. 1992. A review of models used for stock assessment in abalone fisheries. In: S. A. Shepherd, M. J. Tegner & S. A. Guzmán del Prío, editors. *Abalone of the world, biology, fisheries, and culture*. Oxford: Fishing News Books. pp. 253–275.
- Cox, K. W. 1962. California abalones, family Haliotidae. *Calif. Dept. Fish. Game. Fish. Bull.* 118:1–133.
- Davis, G. E., D. J. Kushner, J. M. Mondragon, J. E. Mondragon, D. Lerma & D. V. Richards. 1997. Kelp Forest Monitoring Handbook vol. 1, Sampling Protocol. Channel Islands National Park. Ventura, California. pp. 96.
- Davis, G. E. 1995. Recruitment of juvenile abalone (*Haliotis* spp.) measured in artificial habitats. *Mar. Freshwat. Res.* 46:549–554.
- Davis, G. E. 1985. Artificial structures to mitigate marina construction impacts on spiny lobster, *Panulirus argus*. *Bull. Mar. Sci.* 37:151–156.
- DeFreitas, B. 2003. Estimating juvenile northern abalone (*Haliotis kamtschatkana*) abundance using artificial habitats. *J. Shellfish Res.* 22:819–823.
- Dugan, J. E. & G. E. Davis. 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* 50:2029–2042.
- Gerber, L. R. & L. T. Hatch. 2002. Are we recovering? An evaluation of recovery criteria under the U. S. *Endangered Species Act*. *Ecol. Appl.* 12:668–673.
- Harrison, A. J. 1986. Gastropod fisheries of the Pacific with particular reference to Australian abalone. In: G. S. Jamieson & N. Bourne. *North Pacific Workshop on stock assessment and management of invertebrates*. *Can. Spec. Publ. Fish. Aquat. Sci.* 92:14–22.
- Hayashi, I. & H. Yamakawa. 1988. Population fluctuations of three sympatric species of *Haliotis* (Mollusca: Gastropoda) in artificial habitats in Kominato, central Japan. *Aquaculture* 73:67–84.
- Hobday, A. J., M. J. Tegner & P. L. Haaker. 2001. Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Rev. Fish Biol. Fish.* 10:493–514.
- Karpov, K. A., P. L. Haaker, I. K. Taniguchi & L. Rogers-Bennett. 2000. Serial depletion and the collapse of the California abalone fishery. In: A. Campbell, editor. *Workshop on rebuilding abalone stocks in British Columbia*. Canadian Spec. Publ., Fish. and Aquat. Sci. pp. 11–24.
- Lafferty, K. D., M. D. Behrens, G. E. Davis, P. L. Haaker, D. J. Kushner, D. V. Richards, I. K. Taniguchi & M. J. Tegner. 2004. Habitat of endangered white abalone, *Haliotis sorenseni*. *Biol. Conserv.* 116:191–194.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace & R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78:1069–1079.
- McShane, P. E. 1992. Early life history of abalone: a review. In: S. A. Shepherd, M. J. Tegner & S. A. Guzmán del Prío, editors. *Abalone of the world, biology, fisheries, and culture*. Oxford: Fishing News Books. pp. 120–138.
- McShane, P. E. & M. G. Smith. 1988. Measuring recruitment of abalone *Haliotis rubra* Leach (Gastropoda:Haliotidae)—comparison of a novel method with two other methods. *Aust. J. Mar. Freshwat. Res.* 39:331–336.
- McShane, P. E. & M. G. Smith. 1991. Recruitment variation in sympatric populations of *Haliotis rubra* (Mollusca: Gastropoda) in southeast Australian waters. *Mar. Ecol. Prog. Ser.* 73:203–210.
- Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1987. Experimental evidence for limited dispersal of haliotid larvae (*Haliotis*; Mollusca: Gastropoda). *Aust. J. Mar. Freshwat. Res.* 36:701–706.
- Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1988. Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 122:91–104.
- Roberts, C. M. & J. P. Hawkins. 1999. Extinction risk in the sea. *TREE*. 14:241–246.
- Rogers-Bennett, L., P. L. Haaker, T. O. Huff & P. K. Dayton. 2002a. Estimating baseline abundances of abalone in California for restoration. *CalCOFI Rep.* 43:97–111.
- Rogers-Bennett, L., P. L. Haaker, K. A. Karpov & D. J. Kushner. 2002b. Using spatially explicit data to evaluate marine protected areas for abalone in southern California. *Conserv. Biol.* 16:1308–1317.
- Rogers-Bennett, L. & J. S. Pearse. 2001. Indirect benefits of marine protected areas for juvenile abalone. *Conserv. Biol.* 15:642–647.
- Sainsbury, K. J. 1982. Population dynamics and fishery management of paua, *Haliotis iris*. I. Population structure, growth, reproduction and mortality. *N. Z. J. Mar. Freshwat. Res.* 16:147–161.
- Sasaki, R. & S. A. Shepherd. 2001. Ecology and post-settlement survival of the Ezo abalone *Haliotis discus hannai*, on Miyagi coasts of Japan. *J. Shellfish Res.* 20:619–626.
- Sasaki, R. & S. A. Shepherd. 1995. Larval dispersal and recruitment of *Haliotis discus hannai* and *Tegula* spp. on Miyagi coasts of Japan. *Mar. Freshwat. Res.* 46:519–529.
- Shepherd, S. A. & J. A. Turner. 1985. Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference and abundance and predators of juveniles. *J. Exp. Mar. Biol. Ecol.* 93:285–289.
- Shepherd, S. A. & L. D. Brown. 1993. What is an abalone stock: implications of the role of refugia in conservation. *Can. J. Fish. Aquat. Sci.* 50:2001–2009.
- Shepherd, S. A. 1990. Studies on southern Australian abalone (genus *Haliotis*). Long-term recruitment and mortality dynamics of an unfished population. *Aust. J. Mar. Freshwat. Res.* 41:475–492.
- Sokal, R. R. & F. J. Rohlf. 1981. *Biometry*. San Francisco: Freeman. 859 pp.
- Tegner, M. J., J. D. DeMartini & K. A. Karpov. 1992. The red abalone fishery: a case study in complexity. In: S. A. Shepherd, M. J. Tegner & S. A. Guzmán del Prío, editors. *Abalone of the world, biology, fisheries, and culture*. Oxford: Fishing News Books. pp. 370–383.
- Tegner, M. J. & R. A. Butler. 1985. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the southern California Bight: implications for recovery of depleted populations. *Mar. Ecol. Prog. Ser.* 26:73–84.
- Tegner, M. J. 1993. Southern California abalones: can stocks be rebuilt using marine harvest refugia? *Can. J. Fish. Aquat. Sci.* 50:2010–2018.
- Yamaguchi, G. 1975. Estimating growth parameters from growth rate data: Problems with marine sedentary invertebrates. *Oecologia* 20:321–332.