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Recent declines of black abalone *Haliotis cracherodii* on the mainland coast of central California

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ABSTRACT: The black abalone *Haliotis cracherodii* was once abundant in many intertidal habitats in southern California, USA. Beginning in 1985, however, black abalone in southern California suffered mass mortalities attributed to a condition termed withering syndrome. The mass mortalities and withering syndrome were confined to southern California except for Diablo Cove, 70 km north of Point Conception, where mortalities were limited to the immediate vicinity of a warm-water discharge. Beginning in 1992, we monitored 5 locations along the mainland coast of central California to determine whether mass mortalities of black abalone would occur there. Abalone numbers decreased at the 3 southern sites but not at the 2 northern sites. The decline was greatest at the southernmost site, Government Point (near Point Conception), where there was a 97% reduction in numbers between 1992 and 1995. The 2 sites immediately upcoast of Government Point, Boathouse and Point Arguello, experienced a 39 to 46% decline, while the 2 northernmost sites (Stairs and Purisima) experienced a slight increase in abalone. All abalone size classes declined at Government Point, Boathouse and Point Arguello, indicating the decline was not caused by overharvesting. Symptoms of withering syndrome, assessed by pulling on individuals, were noted at Boathouse and Point Arguello. Withering syndrome was also detected in the final survey at Stairs, as was a slight decline in abalone abundance, suggesting that mass mortalities may be beginning there. Our observations demonstrate that widespread mass mortality associated with withering syndrome has reached central California and is progressing northward from Point Conception.

KEY WORDS: Abalone · Rocky intertidal · Population decline · Central California · Mass mortalities

INTRODUCTION

Black abalone was considered an undesirable species suitable only for bait for most of the present century (Cox 1962), until declines in the stocks of other, more desirable species of abalone combined with the great abundance of black abalone at islands off the coast of southern California, USA, led to the development of a valuable commercial export fishery in 1968. This fishery, like the majority of other abalone fisheries, saw a rapid rise, which peaked in 1973, and a decline in harvest tonnage (Parker et al. 1992). Black abalone were virtually eliminated along the mainland coast of southern California, apparently due to heavy fishing pressure, expanding coastal development and pollution (Young 1964, Haaker et al. 1986, Tegner 1989, Shepherd & Breen 1992, Miller & Lawrenz-Miller 1993).

Since the mid 1980s, the once-abundant black abalone has also practically disappeared from the northern Channel Islands off southern California. Harvest-

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ing is unlikely to have caused the observed decline in densities; although the commercial fishery was intensive, regulations forbade taking this species without the use of snorkeling or diving gear, creating a refuge for abalone in the upper intertidal. In response to the virtual collapse of the black abalone stock, the California Department of Fish and Game closed the commercial fishery for black abalone at Santa Barbara, Anacapa and Santa Cruz Islands in 1991 and extended the moratorium to both commercial and sport harvesting throughout California in fall 1993.

A mysterious terminal condition, termed withering syndrome, appears to be the cause of the catastrophic decline in black abalone at the Channel Islands. Withering syndrome symptoms include an atrophied foot muscle, discoloration of the epipodium, reduced activity and inability to adhere tightly to the substratum. In 1985, commercial fishermen saw moribund black abalone and many empty shells on the southern shore of Santa Cruz Island (Lafferty & Kuris 1993). Shortly thereafter, in 1986, biologists noted withering syndrome at Anacapa Island (Haaker et al. 1992). Subsequent surveys noted declines in abundances throughout the Channel Islands (Douros 1987, Tissot 1991, 1995, Haaker et al. 1992, Richards & Davis 1993, VanBlaricom et al. 1993). In most cases, the reduction in numbers was associated with clear signs of withering syndrome. Because co-occurring species did not change significantly (Richards & Davis 1993), it appeared that declines were restricted to black abalone. Declines were not attributable to harvesting because all size classes decreased in abundance (Parker et al. 1992). Although explanations for the mass mortalities included environmental changes (Davis et al. 1992), such as warm-water El Niño-Southern Oscillation events (Tissot 1988, 1990, 1995), the pattern of geographic and temporal spread of withering syndrome best supported an infectious disease process independent of environmental factors (Lafferty & Kuris 1993). Warm temperature, although not associated with the initiation of withering syndrome, was associated with increased rates of mortality (Lafferty & Kuris 1993). Recently, Gardner et al. (1995) reported an association between withering syndrome and rickettsia-like prokaryotes that infect the digestive tract of apparently diseased abalone (VanBlaricom et al. 1993). Possible pathogen vectors such as ectoparasitic pycnogonids have been associated with moribund abalone (Richards & Davis 1993). The late spread to (and slower die off at) San Miguel Island, the most northern of the Channel Islands, suggested that cooler temperatures or oceanographic currents might prevent the spread of withering syndrome north of Point Conception (Richards & Davis 1993). In 1988, however, researchers at Pacific Gas and Electric Diablo Canyon Power Plant (approximately 70 km north of Point Conception) reported moribund black abalone with symptoms similar to those at the Channel Islands. These die-offs appeared to be restricted to the immediate vicinity of the power plant's thermal discharge within Diablo Cove, where water temperatures were elevated 10°C above ambient waters, and quickly led to population reductions of greater than 90% at some sites (Steinbeck et al. 1992). Withering syndrome was not evident in the cooler waters outside of the cove.

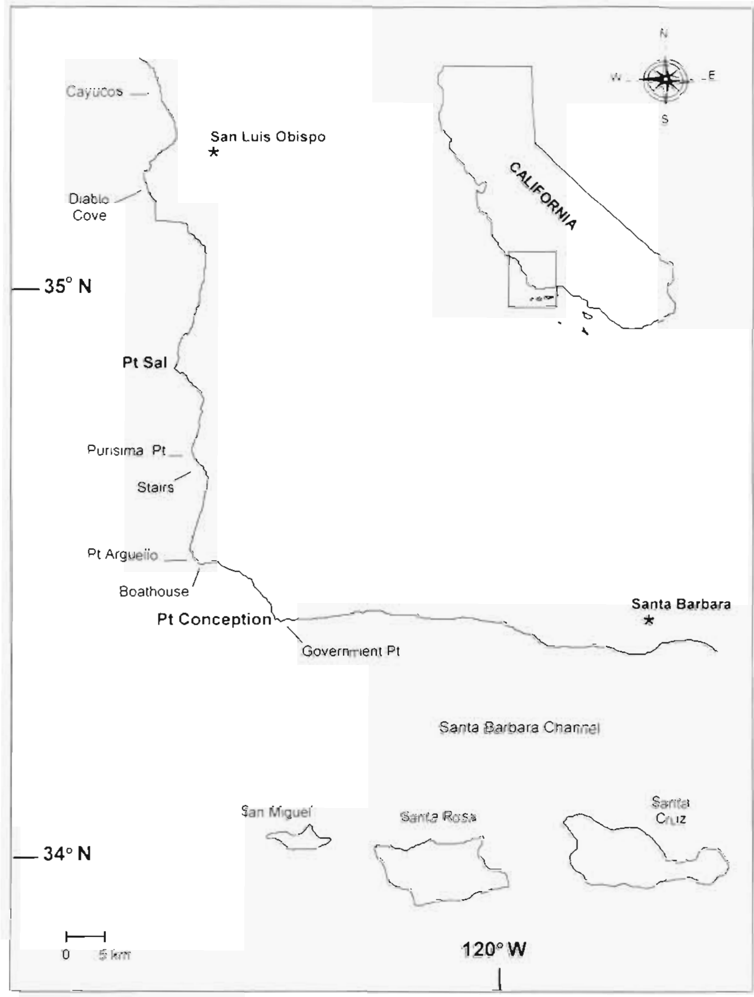

Fig. 1. Black abalone monitoring sites along the central California coast

To determine if withering syndrome and the mass mortalities would become widespread along the mainland coast, we monitored black abalone in central California (Fig. 1). In 1988, the California Department of Fish and Game established a permanent site near Point Arguello specifically to monitor black abalone populations. Four additional sites were established in Santa Barbara County, California, in late 1991 to detect changes in the abundances of key species, including black abalone (Ambrose et al. 1995). After almost 4 yr of monitoring, our data indicate that substantial declines in abalone density occurred at the 3 southernmost sites in a temporal pattern consistent with a northerly spread of withering syndrome.

METHODS

We monitored black abalone at 5 sites in northern Santa Barbara County (Fig. 1). We chose our sites where abalone were numerous and the intertidal area was accessible and suitable for establishing permanent plots. All sites were subjected to some sport (but not commercial) harvesting, but accessibility to fishermen varied from site to site. The southernmost site, Government Point (34° 26.62' N, 122° 27.32' W), was on private land. All other sites were within Vandenberg Air Force Base. At Boathouse (34° 33.17' N, 122° 36.37' W), our plots were only a short walk from the parking area, and fishermen often used the intertidal on weekends and holidays. Point Arguello (34° 33.19' N, 122° 37.27' W) was most protected from harvesting, as it was within a harbor seal haul-out closure area and was strictly off-limits to all but researchers. Stairs (34° 43.88' N, 122° 36.86' W) was near a civilian fishing beach. Purisima Point (34° 45.19' N, 120° 38.14' W), a fishing area, was a 20 min hike from the nearest road and had been an abalone closure zone since 1988.

At each site, we established 3 permanent sampling plots where abalone were numerous. However, the lowest plot at Government Point (51 m^2) could not be sampled during some surveys, so data from this plot were excluded from analyses. Total areas sampled were 123 m^2 at Government Point, 59 m^2 at Boathouse, 80 m^2 at Point Arguello, 30 m^2 at Stairs and 60 m^2 at Purisima Point. The sizes and shapes of plots varied among sites according to abalone density or aggregation and local topography. For example, abalone at Stairs occurred in long, narrow cracks that were widely dispersed, so the plots were similarly arranged. In contrast, abalone at Government Point were most abundant in one area of deep tide pools, so the plots there were more rectangular and were contiguous.

We sampled most sites in winter (January to March) and fall (September to November) of each year from 1992 to 1995 by searching for abalone within permanently marked plots. We also sampled in spring (April to May) in 1995. Sampling did not begin at Purisima Point until fall 1993. Each time we sampled, we carefully searched plots and measured (to the nearest 5 mm) shell lengths of all abalone found without removing the abalone from the substratum. We temporarily marked each abalone after measurement with a yellow crayon to avoid measuring it again. Sometimes it was necessary to estimate the lengths of abalone that were lodged deeply in cracks or were otherwise inaccessible. Because smaller abalone (<50 mm) often occurred behind larger individuals, this size class was potentially undersampled. Flashlights were necessary at some sites to search crack and crevice habitat. Starting in 1992 at Point Arguello and in 1993 at the rest of the sites, a haphazard selection of abalone were subjected to a pull-test to check for withering syndrome. The pull-test consisted of gently tapping the animal and then grasping the shell by hand and tugging. We replaced individuals pulled free. Healthy animals are extremely difficult to dislodge while weakened abalone readily detach from the rock (VanBlaricom et al. 1993). We also used this test in July 1995 to search for withering syndrome in areas between our permanent sites. Starting in 1992, empty shells were collected at Point Arguello and scored as fresh (if the interior of the shell was clean and shiny) or old. Size frequency data for live individuals at Point Arguello were pooled into an 'all sizes' category.

RESULTS

Abalone numbers declined at the 3 southern sites but not at the 2 northern sites (Fig. 2). Regression analysis of abalone number versus time revealed significant negative slopes for the 3 southern sites, whereas the 2 northern sites have significant positive slopes (Table 1).

The declines occurred in all size classes. The regressions for Boathouse and Government Point remain significant with sport harvestable (>127 mm) animals removed from the analysis (Table 1B). These trends are also evident when only animals larger than 50 mm are included (Table 1C), indicating that possible undersampling of small individuals does not affect the association. When only abalone smaller than 50 mm are included, the trend was still evident (Table 1D), although $p \approx 0.06$ (2-tailed).

Abalone declined earliest at Government Point, their numbers dropping from 87 in winter 1992 to 47 in fall 1992. We were unable to sample at this site in winter

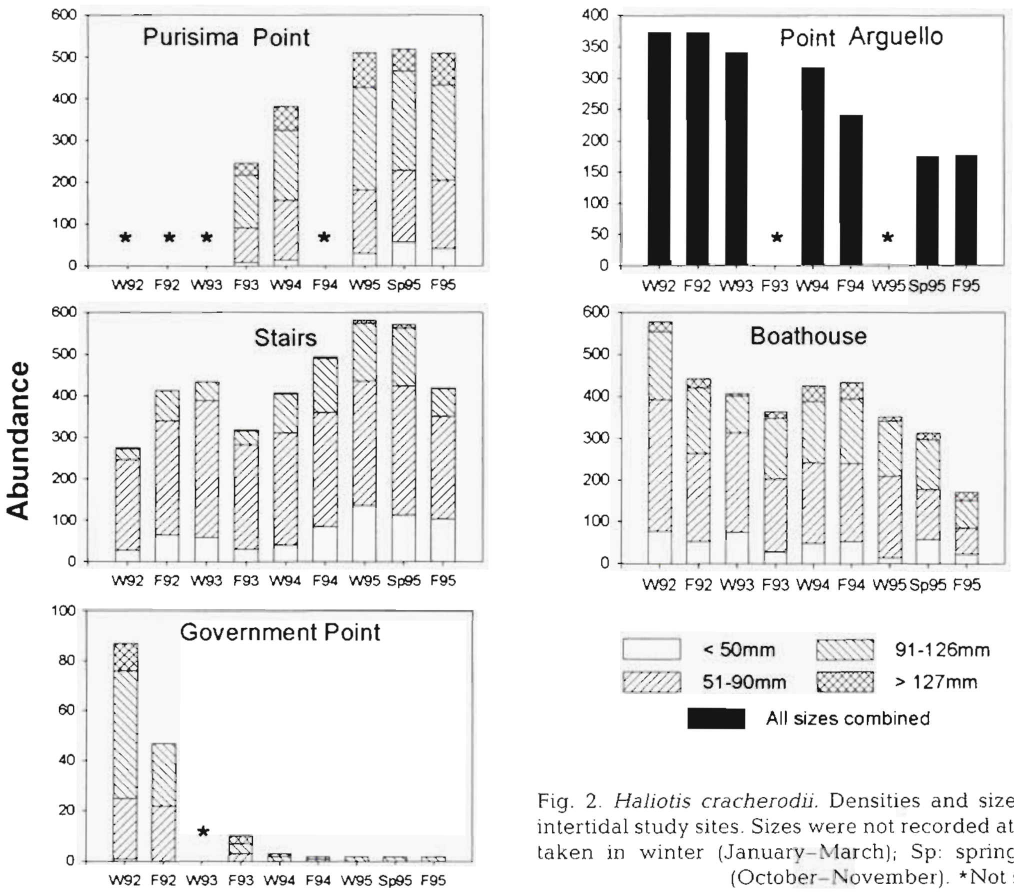

Fig. 2. *Haliotis cracherodii*. Densities and sizes of abalone sampled at 5 intertidal study sites. Sizes were not recorded at Point Arguello. W: samples taken in winter (January-March); Sp: spring (April-May); and F: fall (October-November). *Not sampled

1993 because of heavy surf. We found only 7 abalone in the vicinity by July 1995, 2 of which were within plot boundaries; all appeared healthy. Withering syndrome was not observed at this site, except for 1 weakened animal in January 1992.

Abalone abundance dropped at Boathouse in fall 1992, but then remained fairly constant until winter 1995. Field observations from fall 1993 revealed a few fresh empty shells, but all abalone subjected to a pull test appeared healthy. One deceased, withered animal was found in winter 1994. By February 1995, numbers had decreased but no withering syndrome-afflicted abalone were evident. However, California Department of Fish and Game wardens reported dead and dying abalone at this site in April 1995. In May, we found many fresh shells and pull-tests revealed that 3% of the population were weakened. During additional surveys in July, 7% of abalone tested showed clear signs of withering syndrome.

At Point Arguello, withering syndrome occurred in low frequencies from 1989 to 1993. However, abalone abundance in the plots did not decline until winter 1994, when the total number of abalone with withering syndrome and the fraction of shells that were fresh rather than old both increased (Fig. 3).

Abalone, especially smaller individuals (Table 1), increased at Stairs. Empty shells were rarely observed there. However, pull-tests in July 1995 revealed that 2.6% of abalone tested were withered, and lower densities were apparent in October 1995.

Black abalone numbers increased in 1993 and 1994 at the Purisima Point site, with no declines or other signs of withering syndrome. There were more legal-sized animals here than at the other sites, and we found few empty shells.

There was a significant positive association between the change in density and the latitude of each site (Table 2, Fig. 4). Two other large, motile invertebrates, the owl limpet *Lottia gigantea* and seastar *Pisaster ochraceus*, were monitored at 3 of the sites and did not show similar changes in density with latitude (Table 2).

DISCUSSION

Our observations demonstrate that widespread mass mortality of black abalone is no longer confined to southern California. The black abalone declines moved northward from Point Conception. The progression from Government Point to Boathouse/Point

Table 1 *Haliotis cracherodii*. Regression statistics for analysis of abalone number versus time. The model used was number = intercept + slope(time). Point Arguello was not included in the analyses of different sizes because the size of abalone in censused plots was not kept separate from those outside of the plots. *t*: *t*-statistic

Site	Intercept	Slope	*t*	r^2	p (2-tail)
A. All abalone sizes					
Purisima Point	54.3	11.69	4.659	0.88	0.019
Stairs	318.1	4.88	2.600	0.49	0.035
Point Arguello	401.0	-4.84	-6.053	0.88	0.002
Boathouse	534.9	-6.19	-3.892	0.68	0.006
Government Point	66.1	-1.85	-4.830	0.80	0.003
B. Abalone less than legal size (127 mm)					
Purisima Point	48.6	10.04	4.494	0.87	0.021
Stairs	317.5	4.77	2.574	0.49	0.037
Boathouse	515.9	-6.25	-4.304	0.73	0.004
Government Point	60.1	-1.71	-5.104	0.81	0.002
C. Abalone greater than 50 mm					
Purisima Point	80.7	9.94	4.079	0.85	0.027
Stairs	292.6	2.86	1.982	0.36	0.088
Boathouse	463.6	-5.21	-3.428	0.63	0.011
Government Point	65.6	-1.84	-4.861	0.80	0.003
D. Abalone less than 50 mm					
Purisima Point	80.7	1.75	2.910	0.74	0.062
Stairs	292.6	2.02	3.193	0.59	0.015
Boathouse	463.6	-0.98	-2.227	0.42	0.061
Government Point	65.6	-0.02	-2.238	0.46	0.067

Table 2. *Haliotis cracherodii, Lottia gigantea, Pisaster ochraceus*. Change in species density (%) between initial and final (winter 1995) samples for all sites. –: species not sampled at that site

Site	Abalone	Owl limpets	Seastars
Government Point	-0.97	+0.22	+1.91
Boathouse	-0.70	+0.20	-0.39
Point Arguello	-0.46	–	–
Stairs	+0.52	+0.43	-0.53
Purisima Point	+1.07	–	–

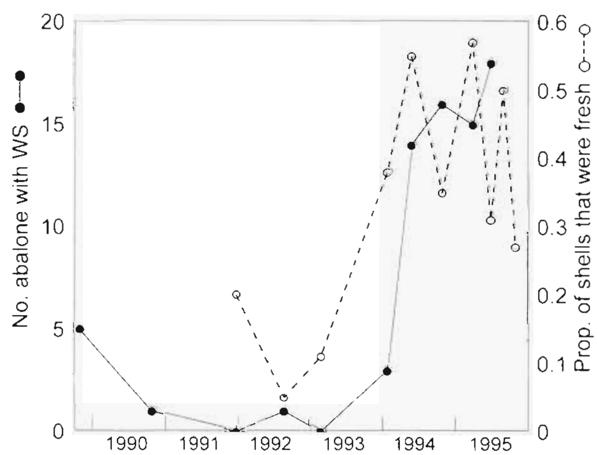

Fig. 3. *Haliotis cracherodii*. Occurrence of withering syndrome and fresh abalone shells at Point Arguello. Counts of abalone with withering syndrome were conducted within permanent plots and occasionally the surrounding area; since area searched was similar but not identical during each census, data should be viewed as a general indication of trends. Shells were censused from the general area in and around the permanent plots

Arguello, a distance of about 25 km, took about 2 yr. The progression from Boathouse/Point Arguello to Stairs, a distance of about 23 km, took about 1 yr. This progression is consistent with the advancement expected by an infectious agent (Lafferty & Kuris 1993).

In April 1995, withering syndrome was detected in 14 of 29 abalone collected just west of the Cayucos Pier, an area 100 km to the north of our monitored sites (P. L. Haaker unpubl.). In November 1995, several withered abalone and numerous fresh shells were observed 4 km north at Cayucos Point (authors' pers. obs.). These observations suggest that the continued spread may not be limited to a gradual progression up the coastline. (Note that withering syndrome was recorded in Diablo Cove in 1988, but was limited to the area near the Diablo Canyon Power Plant's thermal discharge.) Highly motile vectors of withering syndrome or localized current patterns might explain this discontinuous progression, but at this point these mechanisms remain speculative. Long-term monitoring at Año Nuevo (Tissot 1991), in San Mateo County,

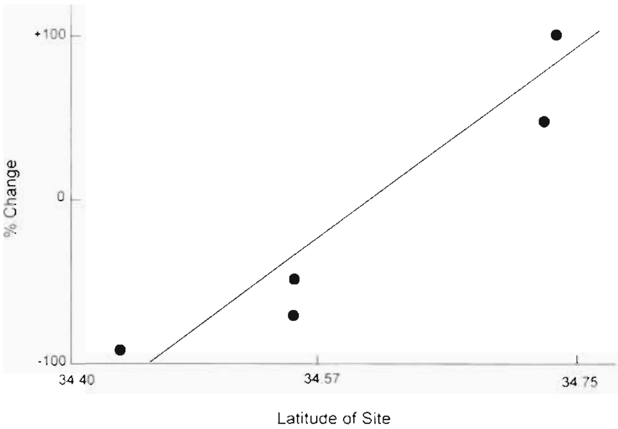

Fig. 4. *Haliotis cracherodii.* Change in abalone density as a function of latitude. Latitude (minutes and seconds) was converted to base 10 for the analysis. The regression equation [% change = 656 × (latitude) – 22.719] is significant ($p = 0.01$) with $r^2 = 0.92$

California, will allow the detection of the spread of withering syndrome into the northern range of the species Unfortunately, we know little of the southward spread of withering syndrome beyond San Clemente Island and San Diego into Baja California, Mexico. Recent conversations with fishermen from Bahia Tortugas, Baja California Sur, Mexico, suggest that withering syndrome might have been present there around 1992. Black abalone apparently suffered unexplained mass mortalities at that time, and now only small numbers remain. Withered pink and green abalone have been observed by fishermen there as well.

The decline of black abalone in central California was generally associated with withering syndrome. At Stairs, abalone abundance began declining a few months after withered abalone were found. At Boathouse, there was an initial decline in fall 1992, after which abundances stabilized until winter 1995. The cause of the initial decline is not known, but it seems unlikely to have been due to withering syndrome because we found no direct evidence of this condition until 1 withered animal was found in winter 1994. On the other hand, the winter 1995 decline was clearly associated with withering syndrome, which was prevalent at Boathouse by March 1995. There is some question about the cause of the abalone decline at Government Point, since it was not accompanied by overt signs of withering syndrome. However, Government Point is very exposed, with exceptionally strong swell and surge (Littler 1978); an absence of empty shells suggests they are poorly retained at the site. Animals weakened by withering syndrome might not persist for long at this site. For example, the large swells in winter 1993 that prevented us from sampling could also have removed any afflicted abalone. Because abundance declined across all size categories, sport harvesting does not explain the changes we observed. Poaching seems unlikely due to the difficulty of gaining access to the site either by land or by boat. Sea otter predation remains a possibility, although exposed intertidal areas provide a partial refuge from otter predation (Ebert 1968, VanBlaricom & Estes 1988). Seastars and owl limpets, the other large motile invertebrates monitored at Government Point, did not decline, so the decline in abalone was probably not due to a general disturbance such as sand burial, thermal stress or storms. The nature and timing of the decline, along with unambiguous evidence of withering syndrome at more northerly sites, suggest that withering syndrome was responsible for the loss of abalone at Government Point. Because the decline was evident as soon as we began monitoring, it is possible the population at this site began declining before 1992.

Judging from past die-offs in the Channel Islands (Tissot 1995), we expect that densities at our sites will continue to drop. Recent declines at Boathouse and Point Arguello were only 40 to 45%, whereas declines in the Channel Islands typically continued until more than 95% of the population had disappeared (Richards & Davis 1993). Abalone populations at our 2 northern sites have not yet declined markedly; however, individuals may be infected months before symptoms appear (Haaker et al. 1992). Moreover, substantial recruitment at Stairs during 1994 and winter 1995 (Fig. 2, Table 1D) enhanced densities and may have obscured effects of withering syndrome to some extent. Recruitment lessened the severity of declines at San Miguel Island for several years before the population finally collapsed (Richards & Davis 1993). The sharp decline in the October 1995 sampling period and the results of the July 1995 pull tests suggest the beginning of a collapse at Stairs, although additional sampling is needed to confirm this.

At Government Point, as at the Channel Islands, less than 5% of the original population survived withering syndrome. Recovery of this population may be slow. Little is known about reproduction and early life history of black abalone, but in other abalone species recruitment may be patchy (Prince et al. 1987, McShane & Smith 1991). Successful spawning may not occur at such low population densities because fertilization may only be successful when male and female abalone are within a few meters of each other (Breen & Adkins 1980, Prince et al. 1988). Annual recruitment of juvenile black abalone at the Channel Islands declined steeply when adult populations dropped below half of initial densities (Richards & Davis 1993). However, juvenile black abalone have recently been observed at some island sites previously devastated by withering syndrome (Tissot 1995, J. Altstatt & D. Richards unpubl.).

The significance of the black abalone decline may extend beyond this one species. Divers have reported shrunken red and pink abalone, and a 1995 survey of San Miguel Island by California Department of Fish and Game biologists found that 1 to 4% of red abalone had visual signs of withering syndrome (Friedman 1995). Thus, existing abalone fisheries and mariculture operations may be threatened by the continued geographic spread of withering syndrome. The ecological ramifications of the decline of black abalone are not yet known, but the decline of a dominant space holder might be expected to alter the structure of the surrounding intertidal community. For example, increases in the densities of colonial sand castle worms *Phragmatopoma californica* and vermetid snails *Serpulorbis squamigerus* appear to result from the removal of black abalone (Douros 1985, Lafferty & Kuris 1993, Miller & Lawrenz-Miller 1993, Richards & Davis 1993). We are currently investigating these effects as withering syndrome spreads northward.

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