Status Review Report for Black Abalone
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Status Review Report for Black Abalone (*Haliotis cracherodii* Leach, 1814)

[AUTHORS: Butler, DeVogelaere, Gustafson, Mobley,
Neuman, Richards, Rumsey, Taylor, VanBlaricom]

NMFS Southwest Region
501 West Ocean Boulevard, Suite 4200
Long Beach, CA 90802

[DATE: Month, Year]

U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Executive Summary

The black abalone (*Haliotis cracherodii* Leach, 1814) is a relatively large prosobranch gastropod mollusk ranging from approximately Pt. Arena in northern California, USA, to Bahia Tortugas and Isla Guadalupe, Mexico. Populations of black abalone on offshore Islands, especially those of southern California, were particularly large prior to the middle 1980s. Black abalone occur in rocky intertidal and shallow subtidal habitats on exposed outer coasts, where they occur primarily in crevice microhabitats and feed preferentially on large drifting fragments of marine algae such as kelps. Black abalone reach a maximum size of about 20 cm (maximum diameter of the elliptical shell) but more typically reach sizes in the range of 10-14 cm. Maximum longevity is thought to be 20-30 years. Black abalone have separate sexes and are broadcast spawners. Lecithotrophic larvae are thought to be planktonic for 4-10 days before settlement and metamorphosis. Dispersal capability of larvae is limited, and genetic data indicate population structure on a spatial scale consistent with known dispersal characteristics. Black abalone shells are abundant in midden deposits left by Native American cultures in a number of locations, but especially in the Channel Islands of southern California, suggesting that black abalone served as a significant source of human nutrition among indigenous peoples along the coasts of California and Baja California in times past. Black abalone were popular targets for recreational harvest through much of the twentieth century, and have been harvested commercially since the 1950s. During a brief period in the early 1970s black abalone were the predominant commercially harvested abalone species in California as measured by tonnage landed. Black abalone have been harvested intermittently by commercial fishing cooperatives along the coast of the Baja California Peninsula, primarily in the region between the U.S.-Mexico border and the border between the States of Baja California and Baja California Sur. Since 1990, commercial harvests of black abalone in Mexico have declined by more than 98%.

A lethal disease, withering syndrome, was first detected in black abalone at Santa Cruz Island, California, in 1985. The disease is caused by a *Rickettsia*-like prokaryotic pathogen of unknown origin that invades digestive epithelial cells and disrupts absorption of digested materials from the gut lumen into the tissues. Progressive symptoms include pedal atrophy, diminished responsiveness to tactile stimuli, discoloration of the epipodium, and a loss of ability to maintain adhesion to rocky substratum. The etiological agent of withering syndrome has been formally described and is presently known as '*Candidatus* Xenohaliotis californiensis'. Withering syndrome spread progressively through the California Islands from 1986 to the middle 1990s, and spread to mainland populations in both California and Mexico beginning in 1988 at a site near Diablo Canyon, California. Withering syndrome has caused mass mortalities of 95% or greater in black abalone at virtually every location that has been investigated. At present (January 2008), all known black abalone populations south of Monterey County, California, have experienced major losses, thought largely to be due to withering syndrome. Available evidence indicates that mass mortalities associated with the disease continue to expand northward along the California coast. Information from Mexico indicates widespread occurrence of withering syndrome and mass mortalities of black abalone over the past two decades.

Rate of black abalone mortality associated with withering syndrome is known to be enhanced by periods of ocean warming, such as those associated with recent El Niño – Southern Oscillation oceanographic events in the Pacific Ocean. This pattern suggests that progression of ocean warming, associated with large-scale climate change, may facilitate further and more prolonged vulnerability of black abalone to effects of withering syndrome.

Other factors may have contributed to losses in black abalone populations in recent decades. Consumption by natural predators may be important to survival rate for all ages and sizes of black abalone. Excessive harvests, especially in California by commercial interests and recreational fishers, probably contributed to losses as well. Close proximity and ready access of mainland populations of black abalone to human activity and population centers probably have facilitated high rates of illegal harvest for many decades in California and Mexico. Black abalone are probably vulnerable to certain types of pollution such as major oil spills in coastal marine waters, but few such occurrences have been documented to date.

All forms of legal harvest of black abalone were suspended by the State of California in 1993, in response to documentation of population damage caused by withering syndrome. In 1997 the State of California placed all abalone harvests south of the Golden Gate under indefinite moratorium. At present the only surviving fishery for abalone in California is the recreational harvest of red abalone (*Haliotis rufescens* Swainson, 1822) in northern California. On 23 June 1999 the black abalone was added to the list of Candidate Species by the National Marine Fisheries Service (NMFS; 64 FR 33466), in the context of consideration for federal protected status pursuant to the Endangered Species Act of 1973 (ESA; 16 U.S.C. 1531 et seq.) as amended. The black abalone was transferred to the NMFS List of Species of Concern on 15 April 2004 (69 FR 19975). The species was added to the Red List of Threatened Species by the World Conservation Union (IUCN) in 2003, and was classified as “critically endangered”. NMFS initiated an informal status review for black abalone on 15 July 2003, and conducted biological scoping workshops on 29-30 January 2004 and 31 July-1 August 2006. A formal status review was announced by NMFS on 17 October 2006 (71 FR 61021). On 27 December 2006 NMFS received a petition from the Center for Biological Diversity (CBD) requesting that black abalone be added to the List of Threatened and Endangered Species as defined by the ESA, and that critical habitat for the species be designated concurrent with a decision on listing. As required by section 4(b)(3)(A) of the ESA, NMFS published a finding on 13 April 2007 (72 FR 18616) indicating that the CBD petition presented substantial scientific information, and that the petitioned action might be warranted.

In June 2007 NMFS convened the Black Abalone Status Review Team (SRT) with the charge to develop a Black Abalone Status Review Report (Status Review) as mandated by the ESA. The purposes of the Status Review are to evaluate available information and data on the following topics as they relate to ESA listing: (1) long-term trends in abundance throughout the species range; (2) potential factors for the species’ decline throughout its range (e.g., over-harvesting, natural predation, disease, habitat loss, etc.); (3) historic and current range, distribution and habitat use of the species; (4) status of populations in Baja California, Mexico; (5) historic and current estimates of population size and available habitat; (6) knowledge of various life history parameters (size/age at maturity, fecundity, length of larval stage, larval dispersal dynamics, etc.); and (7) projections of population growth or decline and risk of extinction.

The work of the SRT has been facilitated by the large number of longitudinal fishery-independent studies that have been made in black abalone populations. Many are of substantial duration, with four exceeding two decades. A strikingly consistent pattern in the extensive data, detected across a number of locations, is the reduction of black abalone densities to low numbers in apparent response to the effects of withering syndrome. Recent analyses of interactions of population trends and local size frequency distributions indicate that, in virtually all such cases, densities have been reduced to a point where successful fertilization may not be possible. This pattern is a consequence of the breeding system in black abalone, requiring that animals of different gender spawn in temporal synchrony while in close proximity in order to achieve successful fertilization and larval production. Because of the extreme turbulence typical of rocky intertidal habitats on exposed outer coast locations, isolated individual black abalone have no chance of successful fertilization, even if in optimal health and reproductive status, because gametes are immediately dispersed before encounter with gametes of the opposite sex is possible.

The SRT has concluded that reduction in local densities below thresholds necessary for successful fertilization during spawning has been a widespread and pervasive consequence of population reductions by withering syndrome and other factors. Based on available information and the collective experience and expertise of the SRT, it is concluded that the likelihood that black abalone can spontaneously develop attributes that would reverse effects of reduced densities is extremely low. The SRT also has concluded that a reduction or cessation of the northward spread of withering syndrome effects, to those populations of black abalone not yet affected by the disease, is highly unlikely. Although illegal harvest, natural predation, and possibly other factors may be contributing to the present status of black abalone, it is the view of the SRT that risks associated with withering syndrome are the primary cause for concern about the survival of black abalone as a species.

The SRT agrees unanimously that without identification, development, and implementation of effective measures to counter the population-level effects of withering syndrome, black abalone are likely to become effectively extinct within 30 years. The actual loss of all black abalone may linger for a longer period of undetermined duration because long-lived individuals may persist after local populations are no longer able to reproduce because of reduced local densities. However, persistence of a few individuals at very low density will not forestall extinction of the species. The Team therefore believes that black abalone is in danger of extinction throughout all of its range . Continued maximum levels of protection from other sources of anthropogenic mortality will be essential to maintain any hope of recovery of black abalone while population-scale disease counter-measures are considered, developed, and implemented.

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NMFS gratefully acknowledges the commitment and efforts of the following SRT members and thanks them for generously contributing their time and expertise to the development of the Black Abalone Status Review Report:

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Chris Mobley NOAA/NOS Channel Islands National Marine Sanctuary	Melissa Neuman NOAA/NMFS Southwest Regional Office	Dan Richards DOI/NPS Channel Islands National Park
Scott Rumsey NOAA/NMFS Northwest Regional Office	Barbara Taylor NOAA/NMFS Southwest Fisheries Science Center	Glenn VanBlaricom, Chair USGS Washington Cooperative Fish and Wildlife Research Unit

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1.0 Introduction

Black abalone (*Haliotis cracherodii* Leach, 1814) was added to the Candidate Species list of the National Marine Fisheries Service (NMFS) on 23 June 1999 (64 FR 33466), transferred to the NMFS Species of Concern list on 15 April 2004 (69 FR 19975), and has since been considered for addition to the List of Endangered and Threatened Species as created by the Endangered Species Act of 1973 as amended (ESA; 16 U.S.C. 1531 *et seq*.). The species is currently listed on the World Conservation Union (IUCN) Red List of Threatened Species (Smith *et al.*, 2003; the World Conservation Union was previously known as the International Union for the Conservation of Nature and Natural Resources, whose acronym "IUCN" remains in use). NMFS initiated an informal ESA status review of black abalone on 15 July 2003, and conducted biological scoping workshops on 29-30 January 2004 and 31 July-1 August 2006. NMFS formally announced initiation of a black abalone status review on 17 October 2006 (71 FR 61021), and solicited information from the public regarding life history and current status of the species, historic and current distribution and abundance patterns, potential factors for the species' decline (e.g., overharvesting, natural predation, disease, habitat loss, etc.); and ongoing conservation measures being taken to protect the species.

On 27 December 2006, NMFS received a petition from the Center for Biological Diversity (CBD) of Tucson, Arizona, requesting that NMFS list black abalone as either an endangered or threatened species under the ESA and designate critical habitat for the species concurrently with the listing determination. As required by Section 4(b)(3)(A) of the ESA, NMFS published a finding on 13 April 2007 (72 FR 18616) stating that the CBD petition presented substantial scientific information and that the petitioned action might be warranted.

1.1 Scope and Intent of Present Document

In June 2007, NMFS convened the Black Abalone Status Review Team (SRT), comprised of experts in the fields of abalone biology and ecology, community ecology, conservation biology, population dynamics and modeling, and marine policy and management, to develop a Black Abalone Status Review Report (Status Review) as mandated by the ESA. The purposes of the Status Review are to evaluate available information and data on the following topics as they relate to ESA listing: (1) long-term trends in abundance throughout the species range; (2) potential factors for the species' decline throughout its range (e.g., overharvesting, natural predation, disease, habitat loss, etc.); (3) historic and current range, distribution, and habitat use of the species; (4) status of populations in Baja California, Mexico; (5) historic and current estimates of population size and available habitat; (6) knowledge of various life history parameters (size/age at maturity, fecundity, length of larval stage, larval dispersal dynamics, etc.); and (7) projections of population growth or decline and risk of extinction.

The Status Review will aid NMFS in determining if the species warrants listing under the ESA. A listing decision is made by NMFS after considering the Status Review and its conclusions as well as current conservation efforts.

1.2 Key Questions in ESA Evaluations

1.2.1 The “Species” Question

In determining whether a listing under the ESA is warranted, two key questions must be addressed: 1) is the entity in question a "species" as defined by the ESA; and 2) if so, is the "species" in danger of extinction or likely to become an endangered species in the foreseeable future throughout all or a significant portion of its range?

For the purpose of the ESA, a species is defined as “any species or subspecies of wildlife or plants, or any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature.” Black abalone is a marine invertebrate and is not a subspecies, therefore it may not be subdivided into a listable unit beyond the taxonomic species level. In a case such as this, the status of the species throughout its entire range must be considered when evaluating extinction risk.

1.2.2 Extinction Risk

Section 3 of the ESA defines the term "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." The term "threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." NMFS considers a variety of information when evaluating the level of risk faced by a species. Important considerations include: 1) absolute numbers and their spatial and temporal distribution; 2) current abundance in relation to historical abundance and carrying capacity of the habitat; 3) any spatial and temporal trends in abundance; 4) natural and human-influenced factors that cause variability in survival and abundance; 5) possible threats to genetic integrity (e.g., artificial rearing); and 6) recent events (e.g., a drought or a change in management) that have predictable short-term consequences for abundance of the species. Additional risk factors, such as disease prevalence or changes in life history traits, may also be considered in evaluating risk to populations. The determination of whether a species is “in danger of extinction” or “likely to become an endangered species within the foreseeable future” should be made on the basis of “the best scientific and commercial information” available regarding its current status.

1.3 Summary of Information Presented by the Petitioners

NMFS received a CBD petition on 27 December 2006 requesting that NMFS list black abalone as either an endangered or threatened species under the ESA and designate critical habitat for the species concurrently with the listing determination. Section 4(b)(3)(A) of the ESA requires that NMFS make a finding as to whether a petition to list, delist, or reclassify a species presents substantial scientific or commercial information to indicate that the petitioned action may be warranted. The joint NMFS/U.S. Fish and Wildlife Service ESA implementing regulations (50 CFR 424.14) define “substantial information" as the amount of information that would lead a reasonable person to believe that the measure proposed in the petition may be warranted. In determining whether substantial information exists for a petition to list a species, NMFS considers several factors, including information submitted with and referenced in the petition and all other information readily available in NMFS files. To the maximum extent practicable, this finding is to be made within 90 days of the receipt of the petition, and the finding is to be published promptly in the Federal Register.

NMFS published a 90-day finding on 13 April 2007 (72 FR 18616). The 90-day finding summarized the best available information on the status of black abalone to date. The principal cause of black abalone population decline in southern and central California is attributed to over-harvesting (Karpov *et al.*, 2000), the onset of a lethal disease known as withering syndrome in southern California in the 1980s (Lafferty and Kuris, 1993), and the disease's northward progression. Black abalone populations have declined by over 99 percent (Brian Tissot, unpublished data) in southern California (except for certain specific locations on San Nicolas and Santa Cruz Islands). Recruitment rates are very low in many locations throughout their range. In areas where remnant healthy populations are producing recruits, these recruits are retained locally and are not recolonizing historically populated areas only tens of kilometers away (Miller and Lawrenz-Miller, 1993; Raimondi *et al.*, 2002; Miner *et al.*, 2006). Given documented declines in abundance throughout a significant portion of the range of the species and the potential negative effects of ongoing and future threats posed primarily by the northward spread of withering syndrome, as described in the petition and in the information in NMFS files, NMFS determined that the petition presented substantial information and that listing black abalone under the ESA might be warranted.

1.4 Summary of New Information Sources-Not Included in the Petition

At least three sources of data were not included in the CBD petition because these data were collected after the petition was received on 27 December 2006.

1.4.1 San Nicolas Island

The long-term population monitoring program for black abalone was continued at San Nicolas Island from January through March 2007 (VanBlaricom, 1993; VanBlaricom unpublished data). The 2007 data closely matched those collected 2001 through 2006, and no major changes in trend were detected on an Island-wide scale. Densities at all except for one (site 8) of the nine survey sites (as described in VanBlaricom, 1993) remained at approximately 1% of the typical density measured at each respective site prior to the first appearance of withering syndrome at the Island in 1992 (VanBlaricom *et al.*, 1993). Recruitment likewise was largely absent from all sites except site 8. Thus, recent data, collected since receipt of the CBD petition and publication of the 90-day finding, are consistent with those available prior to that time.

Site 8 has been of particular interest because declines associated with withering syndrome have not been as substantial as those observed at other sites. Densities reached a minimum in 2002 at about 3% of pre-disease levels. Densities doubled from 2002 to 2006. Data from 2007 indicate the first decline in black abalone densities (a reduction of 8% compared to 2006) at site 8 since 2002. Recruitment of emergent abalone to the adult population has been consistent at site 8 since 2002.

1.4.2 Northern Channel Islands

The long-term population monitoring program for black abalone was continued at the northern Channel Islands (National Park Service unpublished data) in 2007. The 2007 data closely matched those collected from 2001 through 2006, and no major changes in trends were detected. Densities at all sites with fixed plots remained at or near zero, less than 1% of pre-disease levels at each site.

Only one monitoring site (Willows Anchorage on Santa Cruz Island) has shown recruitment and an overall increase in abundance in recent years. Between 2004 and 2007, the number of abalone on the reef increased from 5 to 47 during timed searches (equivalent to a density of approximately 0.04 abalone per square meter). The mean size of black abalone at Willows Anchorage in 2007 was 62 mm. Thus, recent data, made available since receipt of the CBD petition and publication of the 90-day finding, are consistent with those available prior to that time.

1.4.3 Mainland-North of Pt. Conception, California

Recent surveys conducted by Peter Raimondi and colleagues (unpublished data) indicate that the progression of withering syndrome is continuing up the mainland coast of California, north of Pt. Conception, although currently disease progression is occurring more slowly than that witnessed in Southern California . The mainland can be divided into three regions, with respect to black abalone populations: (1) North- all sites north of Point Sierra Nevada; (2) Central- sites from Point Sierra Nevada in the north to Rancho Marino to the south; and (3) South- sites from Cayucos (north) to Government Point (Pt Conception) in the South (Figure 1). In North sites abundances have been steady since sampling initiated, recruitment is common and there is no evidence of the impacts of withering syndrome. Central sites are currently being affected by withering syndrome. Populations continue to decline, but not at a catastrophic rate. No recruitment is occurring. At southern sites, populations have crashed due to withering syndrome, there has been no recruitment and habitats once having abalone have been altered, making re-colonization increasingly less likely. Overall there has been no change over the last year.

2.0 Taxonomy and Species Description

Abalone, members of the gastropod genus *Haliotis*, are prosobranch marine gastropods that occur throughout most of the world (Cox, 1962). There are approximately 60 extant species (Geiger, 1999) found in temperate to tropical waters from the intertidal zone to depths of over 50 m. All are benthic, occurring on hard substrata, relatively sedentary, and generally herbivorous, feeding on attached or drifting algal material. There are seven extant species of abalone native to the west coast of North America (Geiger, 1999). The taxonomic classification of black abalone is as follows.

Phylum Mollusca
Class Gastropoda
Subclass Prosobranchia
Order Archaeogastropoda
Superfamily Pluerotomariacea
Family Haliotidae
Genus *Haliotis*
Species *cracherodii*

Leach (1814) gave the first formal description of this shallow-living (upper intertidal zone to subtidal depths of 6 m) abalone, recounting the shell as smooth, circular, and black to slate blue in color (Figure 2). There are five to nine open respiratory pores (tremata) that are flush with the shell's surface. Typically, the shell's interior is white (Haaker *et al.*, 1986), with a poorly defined or no muscle scar (Howorth, 1978). Adults attain a maximum shell length of approximately 20 cm (within this document, abalone size is indexed by linear measure of the maximum diameter of the elliptical shell). The muscular foot of the black abalone allows the animal to clamp tightly to rocky surfaces without being dislodged by wave action. Locomotion is accomplished by an undulating motion of the foot. A column of shell muscle attaches the body to the shell. The mantle and black epipodium, a sensory structure and extension of the foot which bears lobed tentacles of the same color (Cox, 1960), circle the foot and extend beyond the shell of a healthy black abalone. The internal organs are arranged around the foot and under the shell (Figure 3).

Bartsch (1940) recognizes two subspecies, *H. cracherodii cracherodii* Leach, 1814 and *H. cracherodii californiensis* Swainson, 1822, and places several other described taxa in synonymy with these two subspecies. These subspecies were differentiated on the basis of *H. c. cracherodii* "having the [shell] perforations [= tremata] much larger and more distantly placed, and consequently much less numerous" than *H. cracherodii californiensis*, which had "small and numerous perforations" (Bartsch 1940, p. 56-57). The subspecies *H. cracherodii californiensis* has been described at Guadalupe Island off of the Baja California, Mexico coast (Abbott 1974, Howorth 1978).

In a recent reassessment of the species in the Family Haliotidae, Geiger (1998) considers all the previously described subspecies of black abalone to be varieties that represent either ecomorphs or examples of shell deformations, which are synonymous with a single species, *Haliotis cracherodii*. Geiger (1998, p. 95-97) lists the taxa associated with *H. cracherodii*, followed by their currently recognized valid species name, as follows:

> *cracherodii* Leach, 1814: valid
> *californiensis* Swainson, 1822: var., syn. of *cracherodii* Leach, 1814
> *bonita* Orcutt, 1900: *cracherodii* var. *californiensis* Swainson, 1822
> *expansa* Talmadge, 1954: *cracherodii* Leach, 1814

holzneri Hemphill, 1907: var. of *cracherodii* Leach, 1814
imperforata Dall, 1919: homonym, *cracherodii* Leach, 1814
lusus Finlay, 1927: var. of *cracherodii* Leach, 1814
rosea Orcutt, 1900: *cracherodii* Leach, 1814
splendidula Williamson, 1893: *cracherodii* Leach, 1814

Geiger (1998) considers the number of shell perforations or respiratory openings (tremata) to be an invalid or erroneous diagnostic character for abalone at the species level, since the number of perforations changes with growth of the shell and also varies greatly between populations. In regards to subspecies of black abalone, Geiger (1998, p. 87-88) states that:

> Taxa erected solely because of differences in the number of open tremata have to be rejected, as in the case of … *H. cracherodii* Leach, 1814, with its subspecies *bonita* Orcutt, 1900, and *californiensis* Swainson, 1822. Specimens from some populations on Guadalupe Island off Baja California show the morphology of *H. cracherodii californiensis*. These specimens have more and smaller tremata, which are also more closely spaced than in specimens from the mainland. Specimens from populations having the *californiensis* morphology that have been cultured on the mainland of central California changed the size and spacing of the tremata to those of typical *H. cracherodii cracherodii* (B. Owen, pers. comm.); this indicates that these characters are under environmental control.

3.0 Natural History of Black Abalone

3.1 Population Structure, Distribution, Habitat, and Abundance

3.1.1 Historical and Current Distribution

There is some debate regarding the historical range of black abalone. Many, beginning with Oldroyd (1927, p. 230-231), have cited the historical range as extending from Coos Bay, Oregon, to Cabo San Lucas, Southern Baja California (Geiger, 2000). However, the northernmost documented record of black abalone (based on museum specimens) is from Crescent City (Del Norte County, California; Geiger, 2004; Figure 4). Prior to Oldroyd (1927)—who listed the range of black abalone as extending from Coos Bay, Oregon to Santa Rosalia, Lower California—we were unable to locate any literature reference to the occurrence of black abalone in Oregon. In his treatise on 'The Mollusks of Western North America' the early conchologist Philip Pearsall Carpenter compiled in tabular format all the then known distribution records of the Mollusca from Vancouver Island to San Diego (Carpenter 1872, p. 635-664). None of these early sources identified *H. cracherodii* as occurring north of San Francisco or the Farallon Islands (Carpenter 1872, p. 651). Pilsbry (1890, p. 79) in the 'Manual of Conchology' gives the range of *H. cracherodii* as "Farallones [sic] Is. to San Diego, Cal." In addition, Thompson (1920) in an article on the abalone species of northern California stated that:

> *Haliotis cracherodii*, the black abalone, reaches as far north as Point Arena, where an occasional specimen is found by local men. But one was obtained from that locality. They are also found at Duxbury Reef, and are reputed to be found now and then in the regions between Point Arena and San Francisco, but no actual evidence was obtained. In no locality in northern California do they reach any abundance, however, which would justify calling them anything but rarities until Duxbury Reef is reached…

McCauley and Marriage (1955) report upon a summer 1953 survey of the abalone resources of Oregon's coast by members of the shellfish staff of the Oregon Fish Commission. Physical surveys and interviews of local residents familiar with the intertidal fauna indicated that both the red abalone, *Haliotis rufescens* Swainson, 1822, and the flat abalone, *H. wallalensis* Stearns, 1899, occurred in small numbers in southern Oregon, but the black abalone "was not encountered during this survey" (McCauley and Marriage 1955, p. 12). These authors cite Bonnot (1948), who in turn cites Oldroyd (1927), for evidence that black abalone have "been found in the vicinity of Coos Bay," Oregon (McCauley and Marriage 1955, p. 12).

Most experts agree that the current range of black abalone extends from Point Arena (Mendocino County, California) to Northern Baja California. Black abalone are rare, however, north of San Francisco (Morris *et al.*, 1980) and south of Punta Eugenia (P. Raimondi, pers. comm.). Within this broad geographic range, black abalone generally inhabit coastal and offshore island intertidal habitats on exposed rocky shores where bedrock provides deep, protective crevice shelter (Leighton, 2005).

3.1.2 Population Structure and Genetics

A common feature of marine invertebrate populations with pelagic larvae is limited spatial variation in genetic structure, sometimes across large spatial scales (e.g., Lessios *et al.*, 1998). Such patterns pose substantial analytical and statistical challenges in efforts to identify population structure (e.g., Waples, 1998; Hellberg *et al.*, 2002). However, in species with limited dispersal capability of pelagic larvae, the probability of detecting population structure using genetic data is improved. Application of multiple approaches to genetic analyses also improves the ability to resolve population structure. Because black abalone are thought to have a limited pelagic larval duration and limited dispersal capability in space, it follows that a range of appropriate genetically based approaches to determination of population structure should provide evidence for the existence of, and contributing environmental factors to, population structure.

Three separate recent studies have evaluated population structure in black abalone, using genetic approaches. Hamm and Burton (2000), using various methods to assess relatedness among populations of black abalone (e.g. allozymes, alpha(1)-antitrypsin (AAT) microsatelltie analysis, and cytochrome c oxidase I (COI) from mitochondrial DNA), concluded that patterns of population-scale genetic diversity in samples of seven populations between Point Conception and Scott Creek (north of Monterey Bay) indicated minimal gene flow among populations and thus a low degree of interchange via larval dispersal. These analyses suggest that these black abalone populations are composed predominantly of individuals that were spawned locally. Populations of black abalone over a 300 km range in central California showed population differentiation at allozyme loci which was three times greater than for red abalone populations studied over the entire extent of California (Burton and Tegner, 2000). Chambers *et al*. (2006) examined the genetic structure of mainland and island black abalone populations using protein electrophoresis. Mainland and island locations were genetically differentiated based on allele frequency differences. Among the island populations, evidence for genetic differentiation still existed, but was weaker than that exhibited between mainland and island populations. These data are generally consistent with local recruitment augmented by relatively more gene flow among island populations than among island and mainland populations. Gruenthal (2007) used COI DNA sequences, nuclear microsatellites, and amplified fragment length polymorphisms (AFLP) to evaluate levels of connectivity in black abalone populations from the central California mainland coast, and from four of the southern California Islands. Significant divergence among populations was found in COI and in 142 AFLP loci. The pattern of divergence among loci suggested isolation by distance, consistent with a stepping-stone model of connectivity as defined by Kimura and Weiss (1964). Patterns of differentiation were positively associated with the ocean current field during the abalone spawning season. Overall connectivity was described as low and may be linked to posited limited dispersal distances in black abalone larvae. Gruenthal's (2007) data are generally consistent with those of the earlier studies by Hamm and Burton (2000) and Chambers *et al*. (2006).

3.1.3 Depth Range and Patterns

Of the seven species of abalone found in California (Geiger, 1999), black abalone is bathymetrically the most shallow species, occurring primarily in rocky intertidal habitats (Morris *et al.*, 1980). Black abalone range vertically from the high intertidal zone to 6 m depth, with most animals found in middle and lower intertidal. In highly exposed locations downwind of large offshore kelp beds, the majority of abalone may be found in the high intertidal where drift kelp fragments tend to be concentrated by breaking surf. This pattern may be a response to food availability, given that kelp tends to dominate the diet throughout the range of the species. This pattern is common on the north- and west-facing shores of San Nicolas Island (VanBlaricom, unpublished observations).

Leighton (1959) found evidence for ontogenetic shifts in depth distribution among juvenile abalone on the Palos Verdes Peninsula. Juvenile black abalone (10-30 mm) were found at mid-intertidal depths on undersides of rock providing clear beneath-rock open space while juveniles in the 5-10 mm size range were found at higher intertidal zones in narrow crevices and in depressions abraded into rock surfaces by the intertidal chiton, *Nutallina californica* (Reeve, 1847). Black abalone observed at greater depths (3-6 m) typically were mature adults.

3.1.4 Habitat

As discussed above, black abalone occur over a broad latitudinal range, although the range appears to have narrowed somewhat from historic times. This broad range, in addition to their small-scale distribution (high intertidal to 6 m depth), is associated with an evolved capability to withstand extreme variation in environmental conditions such as temperature, salinity, moisture, and wave action.

Black abalone occur on a variety of rock types, including igneous, metamorphic, and sedimentary rocks at a number of locations. Complex surfaces with cracks and crevices in upper and middle intertidal zones may be crucial recruitment habitat and appear to be important for adult survival as well (Leighton, 1959; Leighton and Boolootian, 1963; Douros, 1985, 1987; Miller and Lawrenz-Miller, 1993; VanBlaricom *et al.*, 1993; Haaker *et al.*, 1995). Complex configurations of rock surfaces likely afford protection from predators, direct impacts of breaking waves, wave-born projectiles, and excessive solar heating during daytime low tides.

3.1.5 Abundance

There are two types of data that can be examined to provide a better understanding of variation in black abalone abundance over time: fishery-dependent and fishery-independent data. Based on a detailed examination of these two data types, Tissot (2007) evaluated trends in black abalone abundance over the last 3 decades. Specific methodologies and results from this study are reviewed in section 5.4.1, but several points are relevant here.

3.1.5.1 Fishery-dependent Information

Human exploitation of abalone has been occurring in the southern California Islands since the late Pleistocene (~10,500 years ago (ya)) and in central California for about 5,000 years. To date it has not been possible to reconstruct species-specific harvest information based on abalone shells observed in middens (Erlandson *et al.*, 1996). An intertidal fishery focused on red, green (*Haliotis fulgens* Philippi, 1845), and black abalone began in the 1850s in California and in the 1880s in Baja California, Mexico (Bonnot, 1930; Lundy, 1997). The California fishery peaked at 1,860 metric tons in 1879 (Cox, 1962). By 1913, the intertidal fishery was closed because of concerns regarding overfishing (Bonnot, 1930). From 1913-1928, commercial and recreational dive fisheries developed, but black abalone were not documented prior to 1940. Prior to this time during the 18th and 19th centuries, two consumers of black abalone populations in Southern California had been removed. First, the Native American Chumash and Gabrielino/Tongva cultures of the southern California Islands were disrupted and ultimately destroyed by immigrants of largely European origin or by fur hunters of Russian, European, and American origins. The last remnants of indigenous human populations on the islands were relocated to the mainland by missionaries in the middle 19th century. Second, the aforementioned fur hunters were responsible for the annihilation of southern sea otter populations south of Point Conception by the time of the U.S. Civil War. As noted in section 3.5.3 of this Status Review, there is uncertainty regarding the ecological importance of sea otter predation on black abalone, but the potential for strong interactions is substantial given known effects of sea otter predation on red abalone.

California Department of Fish and Game (CDFG) landings data (1940-1993) indicate that black abalone were intensively exploited only after other more marketable species had been largely depleted (see also section 3.4.5 of this Status Review). Black abalone landings peaked in 1973 at 868 metric tons (mt). During the peak decade of black abalone fishing from 1972-1981, Rogers-Bennett *et al*. (2002) estimate that approximately 3.5 million individuals were taken in the commercial fishery and an additional 6,729 animals were taken in the recreational fishery. By 1993 both fisheries for black abalone were closed due to concerns regarding severe population declines (Haaker *et al*., 1992).

Rogers-Bennett *et al*. (2002) estimated baseline abundance (i.e., abundance prior to overfishing and mass mortalities due to withering syndrome) for black abalone using landings data from the peak of the commercial and recreational fisheries (1972-1981), assuming that the population was at least as large as the number taken in the fishery, that the fishery “sampled” all size classes, and that no new individuals were added to the population during the ten-year peak of the fishery. With these assumptions, the baseline minimum estimate of abundance for black abalone prior to overexploitation and withering syndrome was 3.54 million animals. This estimate provides a historic perspective on patterns in abundance, defines a relevant baseline abundance against which to compare modern day trends, and helps to assess the species’ current status and risks. However, the utility of the estimate is somewhat limited for defining recovery criteria, because the estimate was calculated using data from a period of time when black abalone reached extraordinary abundance levels, particularly in the islands off southern California, possibly in response to the elimination of subsistence harvests by indigenous peoples and predation by sea otters.

The abalone fishery in Mexico dates to approximately 1860, but modern commercial harvests did not develop until the 1940s. The fishery is pursued by 22 fishing cooperatives, distributed across four management zones on the Pacific coast of the Baja California peninsula (Figure 5). Five cooperatives are present in management zone 1, which is the northernmost of the zones and extends from the U.S.-Mexico border and de Islotes Coronado, to Punta Malarrimo, Baja California Sur, and includes Isla Cedros. Reported commercial fishery data for black abalone, 1990-2003, comes entirely from management zone 1. The harvest season in zone 1 is 1 July through 30 November. Black abalone are also reported to occur on Islas Guadalupe and San Jerónimo. The commercial catch of black abalone in Mexico declined from a high of 28 mt in 1990, to <0.5 mt in 2003, an overall decline of >98% (J. Palleiro, unpublished data, Sierra-Rodriguez *et al*. 2006). These data suggest similar fishery declines to those in California. The decline in Mexico is attributed primarily to large mortality events associated with withering syndrome.

3.1.5.2 Fishery-independent Information

The earliest fishery-independent black abalone abundance estimates are from 1975 at survey stations on the Palos Verdes Peninsula in Los Angeles County, California (Miller and Lawrenz-Miller, 1993). Black abalone densities ranged from 1.0 to 6.8 m^{-2}, but declined throughout the survey interval to less than 0.3 m^{-2} by 1987. Douros (1987) reported densities as great as 127 m^{-2} in certain surge channels at Santa Cruz Island in 1983-1984, but typical densities within a study site ranged from 30 to 90 m^{-2}. Other field studies during the 1980s on Santa Cruz Island surveyed fixed sample areas using a stratified sampling program wherein quadrats were placed randomly within zones. These surveys yielded black abalone densities of 0 to 50 m^{-2} (Haaker *et al.*, 1992). Tissot (1995), also studying black abalone populations on Santa Cruz Island, found averages of 43 to 58 m^{-2} for surf-exposed and protected subpopulations respectively in 1987. These densities declined over the next six years due to withering syndrome, dropping to less than 1 m^{-2} by 1993.

Several studies monitoring black abalone abundance at other Channel Islands found similar declines through the late 1980s and early 1990s. From 1985 to 1989, mean densities for black abalone populations on Anacapa, Santa Rosa, Santa Barbara, and San Miguel islands were obtained annually along permanent transects established by the Channel Islands National Park (Richards and Davis, 1993). Densities ranged from 20 to 50 m^{-2} on early visits, but fell to < 10 m^{-2} by 1989 for all islands except for San Miguel, as mass mortalities associated with withering syndrome occurred in the interim (see also section 3.4.5.2 of this Status Review).

Densities and other attributes of black abalone populations have been monitored at nine locations distributed around the periphery of San Nicolas Island since 1981 (map and methods in VanBlaricom 1993). Prior to 1992 mean abalone densities by site (based on mean survey areas of 230 m^2 per site) ranged from 4 to over 30 m^{-2}. The highest local density of black abalone recorded among the several studies of island populations in the 1980s was 296 individuals, primarily adults, in a single quadrat of 1 m^2 at San Nicolas Island on 23 November 1988 at site 7 (VanBlaricom, unpublished data). Major declines in abundance due to withering syndrome occurred at San Nicolas Island between 1992 and 1996 when densities dropped to < 1 m^{-2} at all sites except site 8.

In recent years, three fishery-independent surveys for black abalone have been conducted along the mainland coast and offshore islands of Baja California, Mexico. In 2002 a survey for black abalone was conducted at Bahia Tortugas, just south of Punta Eugenia and located at the north end of management zone 2 (Figure 5). Only four individuals were found, ranging in size from 121 to 152 mm (Sierra Rodriguez *et al.* 2006). A second survey was conducted in 2004. Black abalone were found at low densities where they occurred, with 98% of located animals measuring < 120 mm in size. No animals were found with symptoms of withering syndrome during the 2004 survey. Black abalone were found along the mainland coast of management zone 1, and on Isla

Guadalupe and Isla San Jerónimo. The only black abalone found in Baja California Sur were at Bahia Tortugas (Sierra-Rodriguez *et al*. 2006).

Peter Raimondi and colleagues (Raimondi, unpublished data) conducted surveys in regions of upwelling on rocky intertidal benches along the northern Baja California coast from Costa Azul to Punta Baja (Figure 5) in 2005. Twelve sites, suspected to have been affected by withering syndrome, were surveyed for suitable habitat (rocky crevices) in the mid to low intertidal and then timed searches were conducted for black abalone. Fresh shells and every live animal were measured to the nearest 5 mm (< 40 mm) or 10 mm (≥40 mm). Black abalone were not densely aggregated at any site surveyed in this study, however, a large proportion of the individuals found were small individuals (<50 mm). This evidence of recent recruitment in northern Baja California is promising given that there is no evidence of successful recruitment to mainland California sites affected by withering syndrome (south of Pt. Piedras Blancas, located just south of the boundary of Monterey and San Luis Obispo Counties; Figure 1). Raimondi offers two hypotheses to explain the discrepancy between the patterns of recruitment in the two regions: 1) healthy populations exist somewhere in Mexico (perhaps on offshore islands) and these are seeding northern areas; or 2) recruitment dynamics are different for withering syndrome-impacted sites in Mexico versus those in California. Fresh shells, in some cases with remnant flesh still attached, were found at three of the twelve sites suggesting that withering syndrome may still be impacting areas of Northern Baja California. Large numbers of older shells were identified at a few sites suggesting that black abalone were abundant in these areas in the past.

3.1.5.3 Summary

Both the fishery data and fishery-independent long-term monitoring data indicate significant declines of black abalone abundance beginning in southern California in the mid-1980s. The first evidence of this decline came from Palos Verdes in the late 1970s (Miller and Lawrenz-Miller, 1993) and early 1980s. By 1986, declining populations and associated observations of withering syndrome had spread to the northern Channel Islands, starting at Anacapa, progressing to Santa Rosa, Santa Cruz, and Santa Barbara islands and finally reaching San Miguel Island in 1989 (Tissot, 1991; Davis *et al.*, 1992; Tissot, 1995). By the early 1990s, declines were observed on San Nicolas Island (VanBlaricom *et al.*, 1993) and north of Point Conception on the mainland to Government Point, Santa Barbara County (Altstatt *et al.*, 1996). During the 1990s, declines in abundance were noted north of Government Point to Cayucos in San Luis Obispo County (Altstatt *et al.*, 1996; Raimondi *et al.*, 2002). Noted declines were also observed in central Baja California, Mexico, around Bahia Tortugas during El Niño events in the late 1980's and 1990s (Altstatt *et al.*, 1996; Tissot, 2007). Recent fishery-independent surveys along the Northern Baja California coast suggest that densities remain low and withering syndrome has affected, and may still be impacting, some mainland areas (Raimondi, unpublished data).

3.1.6 Movement

Little is known about movement patterns of larval or juvenile black abalone anywhere in their range (Miner *et al.*, 2006). Planktonic larval abalone movement is almost certainly determined primarily by patterns of water movement in nearshore habitats near spawning sites. Individual larvae may be able to influence movement to some degree by adjusting vertical position in the water column, but to our knowledge the ability of black abalone larvae to move in this way has not been documented. Movement behavior of post-metamorphic juvenile black abalone is likewise unknown. Leighton (1959) and Leighton and Boolootian (1963) indicate that black abalone larvae may settle and metamorphose in the upper intertidal, using crevices and depressions (including those formed by abrasive action of other intertidal mollusks) as habitat. Leighton and Boolootian (1963) suggest that young black abalone move lower in the intertidal as they begin to grow, occupying the undersides of large boulders that have free space below. To our knowledge there is no published information on direct observations of movement behavior of small (< 20 mm) juvenile black abalone in the field.

Adult black abalone generally appear to be immobile when viewed at low tide. Observations during high tide are difficult because of the breaking surf that typifies black abalone habitat. A few limited qualitative observations have been made at high tide during periods of relative calm. Leighton (2005) reported observing actively moving black abalone during night dives at the Mission Bay entrance jetty near San Diego. At San Nicolas Island, limited qualitative observations have been made of intertidal habitats during daytime high tides (VanBlaricom, unpublished observations). No observed abalone were moving, and all generally were located in the same microhabitats as typically observed during low tides. In a few cases it has been possible to stimulate movement of adult black abalone at low tide at San Nicolas Island, by persistent prodding (VanBlaricom, unpublished observations). In a few such cases, abalone have been observed to move in directed fashion at rates up to 2 m per minute over distances of 5-10 m. Thus, black abalone are capable of substantial movement over short time spans.

We are aware of four quantitative studies of movement of black abalone. Bergen (1971) tagged 72 black abalone at Santa Cruz Island. The size range of tagged abalone was 35 to 148 mm. Movements were monitored over a period of 60 days using photographic methods on successive visits. Abalone < 65 mm in size moved more frequently than those larger than 100 mm, and movement was more frequent during night hours as compared to daylight hours. The larger animals moved only infrequently over short distances. Blecha *et al.* (1992) studied movements of 416 tagged juvenile and adult black abalone from 1979 to 1984 at one study site near Diablo Canyon, on the central California mainland coast. Positions were determined on successive visits in relation to fixed reference points. Data were recorded on two time scales. Long-term information represented movements over periods of tens to hundreds of days. Short-term movements were those observed on successive visits to study sites over periods of 2-3 days. Blecha *et al.* (1992) found that smaller adult abalone (< 65 mm) moved more frequently than large animals on both time scales. Smaller abalone also moved at higher rates (83-387 cm per day) than larger animals (54-119 cm/day) on the short time scale. Rates of movement were not reported for the longer time scale. Blecha *et al*. (1992) reported observations of large individual abalone remaining in exactly the same location for periods up to 12 years. Blecha *et al.* (1992) also did an experimental evaluation of linkages of size, movement rate, and potential for recovery from localized disturbance. All abalone were removed from an isolated crevice in 1980, and the crevice was monitored for abalone recolonization for five subsequent years. Recolonizing animals ranged in size from 45 to 95 mm, suggesting that immigration by juvenile and smaller adult size classes was the primary mechanism for recovery. The pattern suggests that restoration of large adult animals in a disturbed location occurs by growth of smaller colonizing animals rather than direct immigration by larger animals.

VanBlaricom and Ashworth (In preparation) studied movements of 413 tagged adult black abalone at two locations (sites 1 and 7 as described in VanBlaricom, 1993) on San Nicolas Island from 1981 through 1990, with occasional qualitative observations continuing until 2001. Tagged animals were all larger than 70 mm in size, with most animals > 100 mm. At each visit to the survey sites, the location of each relocated tagged abalone was determined using polar coordinates (distance and compass heading) relative to a stainless steel eyebolt embedded in solid rock and secured with marine epoxy compound. All locations during the study were recorded during daytime low tides. Net movements between successive relocations were calculated trigonometrically. Movement rates were reported as cm/month. The modal movement rate interval at both sites was 0-5 cm per month. Some individuals were not observed to move during the quantitative portion of the study, including one that was seen repeatedly at exactly the same location over a period of 11 years. Movement rates exceeding 50 cm per month were quite rare. Maximum observed movement during the study was approximately 20 m. The distribution of movement rates was quite similar at both study sites. The data are minimum net movements per unit time, as observations could not be made continuously. Thus, significant components of movement behavior could have been overlooked, including those that might occur during times other than daytime low tides.

California Department of Fish and Game and National Park Service biologists tagged 278 black abalone at Middle Anacapa Island in 1985 (Richards, unpublished data). Abalone were tagged inside fixed irregular plots (1.1-2.3 m^2) and presence was noted on subsequent surveys. After 18 months, 48 were still within the same plot. An additional 19 were found nearby, often within two meters of their original plot, and none were found more than eight meters away. One abalone was found still in the same plot after 36 months.

3.2 Diet

Early dietary characterizations of black abalone indicated that benthic diatoms were the primary food category consumed (Bonnot, 1930; Croker, 1931; Phillips, 1937; Bonnot, 1948; Campbell, 1949). Later studies recognized that macrophytes are the predominant food for black abalone (Leighton, 1959; Cox, 1962; Leighton and Boolootian, 1963). Leighton and Boolootian (1963) indicated that kelps and a few species of red algae are common food of black abalone in the field, and that laboratory animals grew most rapidly when fed brown algae. Webber and Giese (1969), Bergen (1971), Hines and Pearse (1982), and Douros (1987) have all confirmed the importance of large kelps in the diet of black abalone. The primary food species are said to be *Macrocystis pyrifera* (Linnaeus, 1771) and *Egregia menziesii* (Turner, 1808) in southern California (i.e., south of Pt. Conception) habitats, and *Nereocystis leutkeana* (Gmelin, 1768) in central and northern California habitats.

Categories of plant material ingested by free-ranging animals almost certainly link to ontogenetic trends in microhabitat use. Larvae are lecithotrophic and apparently do not feed. From the time of post-larval metamorphosis to a size of about 20 mm, black abalone are highly cryptic, occurring primarily on the undersides of large boulders with free space below, or in deep narrow crevices in solid rocky substrata. In such locations the primary food sources are thought to be epilithic microbial and possibly diatom films (Leighton, 1959; Leighton and Boolootian, 1963; Bergen, 1971). At roughly 20 mm black abalone move to more open locations, albeit still relatively cryptic, gaining access to both attached macrophytes and to pieces of drift plants cast into the intertidal zone by waves and currents. As black abalone continue to grow, the most commonly observed feeding method is entrapment of drift plant fragments. Feeding by entrapment involves elevation of the anterior portion of the foot during high tides, when animals are swept by water surges associated with breaking waves. When drifting algal pieces are pushed against the abalone, the foot clamps down against the rock, pinning algal fragments under the foot, where they can easily be abraded by the radula and ingested (Leighton and Boolootian, 1963). Leighton and Boolootian (1963) also reported that black abalone may feed on attached living plants in their intertidal habitats. Although black abalone are primarily herbivorous, data from the southern California Islands indicate that abalone will, on occasion, entrap and attempt to ingest a range of novel items, including live pelagic red crabs, dead seabirds and salps, molted lobster carapaces, terrestrial iceplant, and fast food wrappers (VanBlaricom and Stewart, 1986; VanBlaricom, 2003). Such observations indicate that the entrapment response of black abalone, when feeding on drift material, may be non-selective and stimulated by tactile rather than chemical cues.

To our knowledge the only quantitative account of adult black abalone diet by plant species is that of VanBlaricom (2003). Entrapped plant materials were identified during black abalone population surveys at nine sites distributed around the shoreline of San Nicolas Island from 1983 through 2003, with 1,552 entrapped items observed. Kelps were by far the most commonly observed entrapped items, and the giant kelp, *Macrocystis pyrifera* (78% of total sample by frequency), was the predominant entrapped species. Other important food species observed were the kelps *Egregia menziesii* (10%) and *Eisenia arborea* Areschoug, 1876 (7%). Ten other plant species were observed at low frequencies (all < 1%). The data suggest that browsing on attached living intertidal plants may provide only a small portion of overall diet. Importance of kelp in black abalone diet was reported to vary with location in the sample at San Nicolas Island. At locations with large upwind offshore kelp forests, frequencies of *Macrocystis* in the sample of entrapped material were highest (to 89%). Locations that did not have large offshore kelp forests or were not downwind of the forests indicated lower frequencies of entrapped *Macrocystis* (as low as 33%), with correspondingly higher frequencies of other kelps.

3.3 Reproduction

Black abalone have separate sexes and are "broadcast" spawners (see also section 5.4.1.3 of this Status Review). Gametes from both parents are shed into the sea, and fertilization is entirely external. Resulting embryos and larvae are minute and defenseless, receive no parental care or protection of any kind, and are probably subject to a broad array of physical and biological sources of mortality. Species with a broadcast-spawning reproductive system are subject to strong selection for maximum fecundity of both sexes. Only through production of large numbers of gametes can broadcast spawners overcome high mortality of gametes and larvae and survive across generations. It is not uncommon for broadcast-spawning marine species, a group including many taxa of fish and invertebrates, to produce millions of eggs or sperm per individual per year. Broadcast spawners are also subject to other kinds of selection for certain traits associated with reproduction, including spatial and temporal synchrony in spawning and mechanisms that increase probabilities for union of spawned gametes.

3.3.1 Fecundity

Female black abalone become reproductively mature at a size of about 50 mm, and males at about 40 mm (Leighton, 1959; Ault, 1985). Fecundity is poorly known for female black abalone and, to our knowledge, has not been estimated for males. Ault (1985) has estimated that adult female black abalone may release $> 2 \times 10^6$ eggs per spawning episode. Black abalone are capable of a number of spawning episodes per spawning season. Parker *et al*. (1992) indicate that fecundity in female pink (*Haliotis corrugata* Wood, 1828) and green abalone ranges from 3.5 to 6.5×10^6 eggs per individual per year, and suggest that fecundity in black abalone is comparable. Leighton (2005) described results of studies by Gonzales and Ortiz (1986), including fecundity estimates of 0.8×10^6 eggs for a female of 106 mm in size and 1.2×10^7 eggs for a female of 140 mm. Gonzales and Ortiz (1986) are said by Leighton (2005) to report that fecundity declines in larger black abalone, suggesting senescence in older animals.

3.3.2 Spawning period and length

Three studies have been made of gonadal maturation patterns and spawning periods in black abalone. Boolootian *et al.* (1962) reported data on maturation cycles for black abalone in Monterey Bay, based on data collected in 1956 and 1957. A second study of maturation and spawning cycles in Monterey Bay was reported by Webber and Giese (1969). Data collectively indicate that black abalone gonads reach maximum volumes from April through September in Monterey Bay. Webber and Giese (1969) reported that mature gametes could be found in both sexes most of the year at Cypress Point, located just south of Monterey Bay on the central California mainland coast. Gonadal indices decline substantially in fall and winter, increasing again in spring. Leighton (2005) concluded from Webber and Giese's (1969) data that the peak period for spawning in black abalone at Cypress Point is probably mid-summer. Leighton (1959) and Leighton and Boolootian (1963) evaluated maturation and spawning cycles in black abalone at Pt. Dume on the southern California mainland coast near Los Angeles, finding that peak spawning season was late summer and early autumn.

Some black abalone apparently retain the ability to spawn during winter. VanBlaricom (unpublished) has noted that male black abalone at San Nicolas Island may spawn during daytime low tides in winter, often, but not always, directly following minor tactile disturbance incidental to population survey activity. In such cases spawning is most often observed in abalone that are in tide pools or otherwise submerged. Spawning by females has not been observed during winter survey work. The significance of apparent retention of mid-winter spawning capability by males is unknown.

3.3.3 Spawning density

Broadcast-spawning marine invertebrates with separate sexes, such as black abalone, must spawn in temporal and spatial synchrony in order to maximize the probability of successful production of progeny. As intertidal organisms on exposed rocky shores, black abalone typically release gametes into environments of extreme turbulence. As a consequence, eggs and sperm must be released from adults in relatively close spatial and temporal proximity in order to have any chance of union and fertilization before rapid dispersal and loss of opportunity.

Standard population models predict that a reduction in adult density should be associated with a decrease in intraspecific competition leading to an increase in growth rate, survival, and gamete production. However, these advantages may be countered by decreases in the rate of successful fertilization among sparsely distributed broadcast-spawning marine invertebrates (Levitan, 1995; Levitan and Sewell, 1998; Gascoigne and Lipcius, 2004). Fertilization success may be a limiting factor in reproduction, and hence recruitment, especially for sessile or semi-sessile broadcast-spawning species with limited larval dispersal (Smith and Rago, 2004). Since Pennington's (1985) field and laboratory experiments on fertilization success in the green sea urchin *Strongylocentrotus droebachiensis* (Müller, 1776), numerous empirical (for reviews, see Levitan, 1995; Levitan and Sewell, 1998) and modeling (see references in Lundquist and Botsford, 2004; Lauzon-Guay and Scheibling, 2007) studies have investigated the effects of spawner number and density, flow rate, and gamete age on fertilization success in broadcast-spawning marine invertebrates. However, among managers of invertebrate fisheries these types of studies "have long been considered theoretical aspects with little practical use" (Lovatelli *et al.*, 2004, p. 5).

Managers of virtually all invertebrate fisheries have long assumed that broadcast-spawners with high fecundity were capable of recovering from low adult densities and that there was little or no effective relationship between local adult density or abundance and local recruitment (Hancock, 1973; Caddy and Defeo, 2003). It has also been generally accepted that planktotrophic larvae are typically dispersed considerable distances away from adult populations and have little impact on recruitment to the natal habitat. Consequently, until recently, few studies have directly studied the impact of adult density on future recruitment in broadcast-spawning invertebrates.

The central problem for conservation of black abalone is dramatic reduction in densities over the past quarter-century in almost the entire geographic range of the species. Reductions in density are so extreme and widespread that considerable attention is now focused on assessment of critical density thresholds for successful reproduction, recruitment, and population sustainability. In our view this situation justifies an expansive consideration of the concept of critical density thresholds, including review of empirical data for other species of broadcast spawners. Here we review the literature that attempts to identify a critical threshold of adult density below which recruitment failure occurs in species other than abalone.

Sea urchins

The tropical long-spined sea urchin, *Diadema antillarum* Philippi, 1845*,* experienced mass mortalities throughout the Caribbean in 1983–1984 (presumably due to spread of an unknown pathogen) resulting in a rangewide reduction in adult densities and recruitment rates (Lessios *et al.*, 1983; Levitan, 1988). This urchin species disperses via planktotrophic echinopluteus larvae that remain in the water column for four to six weeks prior to settlement.

In the following studies population density was measured by using SCUBA. All urchins were counted at several sites using one of the following methods: (1) 15 or 1,000 m^2 transects (depending on urchin abundance) located along a 3-m depth contour (Levitan, 1988; Karlson and Levitan, 1990); (2) 1 m^2 quadrats (n=20) located randomly along a 40-m transect placed along a depth contour (Carpenter and Edmunds, 2006); or (3) a scale bar that gave a 0.4 m swath along paired transects within several survey blocks in different depths and habitats that resulted in a total survey area of either 32 or 80 m^2 per block, depending on the habitat (Chiappone *et al.*, 2002).

Evidence presented by Karlson and Levitan (1990) indicated that populations of *Diadema* continued to decline at adult densities of about 0.25 m^{-2}. The critical threshold for this species appears to lie somewhere between 0.25 m^{-2} and the pre-mortality-event densities of 5–15 m^{-2} (Quinn *et al.*, 1993; Chiappone *et al.*, 2002). In the Florida Keys (where pre-mortality adult densities were up to 5 m^{-2}), densities as of the year 2000 were no greater than 0.05 m^{-2}, which was attributed to "low numbers of larger individuals available for reproduction, reduced fertilization success due to low densities and hence, inadequate numbers of larvae available for settlement to offset post-settlement mortality from storms and predation" (Chiappone *et al.*, 2002, p. 125).

During the 1990s certain populations of *Diadema* in the southern Caribbean "reached densities sufficient to overcome" an Allee effect (Carpenter and Edmunds, 2006, p. 277) and mean densities ranging from 1.7 to 8.9 m^{-2} were observed in localized urchin zones

(Carpenter and Edmunds, 2006), indicating a region-wide recovery had begun (see also Myhre and Acevedo-Gutiérrez, 2007). Carpenter and Edmunds (2006, p. 275) reported that recruitment of *Diadema* was "not correlated with local population density" and that the combined ecological effects of "gradual larval delivery from upstream populations, episodic recruitment, and positive interactions between local population densities and larval supply … may result in nonlinear, threshold responses of recruitment as population sizes increase" (Carpenter and Edmunds, 2006, p. 277). Recent studies (Miller *et al.*, 2007) indicate that persistence of newly settled *D. antillarum* is significantly higher in the presence of high adult densities, suggesting that adult density has a potential positive effect on juveniles that escape predation under an adult spine-canopy refuge.

Sea cucumbers

Shepherd *et al*. (2004) reported on the decline in the sea cucumber (*Isostichopus fuscus* [Lugwig, 1875]; locally known as pepino) fishery in the Galápagos Islands that began in 1992-1993 when survey-derived mean densities in index areas of the western islands averaged 3.1 m^{-2}. *Isostichopus fuscus* inhabits rocky reef areas from 2 to 40 m depth, develops through a feeding auricularia larval stage, and settles and metamorphoses after 22–27 days (Hearn *et al.*, 2005). In the following studies, sea cucumber density was measured using SCUBA and by collecting all individuals present, both on and under rocks, in a circular area of 100 m^2 at depths of from 5 to 15 m (Hearn *et al.*, 2005).

Mean densities of individuals greater than 20 cm in length declined to 0.1 m^{-2} by 1998, rose to 0.35 m^{-2} in 2002 due to a recruitment event that began in 2000, and declined to 0.04 m^{-2} by 2003 (Shepherd *et al.*, 2004). Similarly, adult densities in the eastern Galápagos Islands declined to a low of only 0.06 individuals m^{-2} between 1999 and 2003, with no evidence of additional recruitment. Shepherd *et al*. (2004, p. 106) suggested that spawning aggregations of pepino were unlikely to occur at densities below about 0.1 m^{-2}, and that "mean within-patch densities to achieve 50% fertilization success were estimated to be 1.2 pepino m^{-2}." Furthermore, Shepherd et al. (2004, p. 106) stated that "the mean adult densities of pepinos on the eastern islands have been so low since 1999 that the effect of low density on fertilization success (Allee effect) is probably sufficient to have caused widespread recruitment failure." Although the strong recruitment of pepinos in 2000–2002 in the western islands supported the local fishery, based on immature animals, this cohort has subsequently been fished out with no evidence of new recruitment (Shepherd *et al.*, 2004; Toral-Granda, 2005).

Hard clams

Peterson (2002) examined density of northern quahog (aka hard clam), *Mercenaria mercenaria* (Linnaeus, 1758), adults and recruits in 1 m^2 enclosures in 11 years spanning the period from 1978 to 2001 on clam fishing grounds of central North Carolina. Statistically significant recruitment declines of 65–72% and declines in total clam densities in three representative habitats from 6.4 to 0.3 m^{-2}, 1.6 to 1.3 m^{-2}, and 9.0 to 1.1 m^{-2} over the study period "strongly implies that recruitment overfishing is the cause of unsustainable yields of hard clams in the central district of North Carolina" (Peterson, 2002, p. 102).

From data collected between 1977 and 2004, Kraeuter *et al*. (2005, p. 1045) analyzed "correlations between the average number of adults m^{-2} and the average number of 1-year-old clams m^{-2} (recruits) with the appropriate lag time" for *M. mercenaria*, in Great South Bay, New York. Average density of adult clams over this time period decreased from approximately 5 to 0.86 m^{-2}. These fisheries-independent data consisted of 350 duplicate samples taken each year with a 1 m^2 clam shell bucket. Sediment was sieved to 6.4 mm and clams of age-2 and older were considered to be the spawning stock (Kraeuter *et al.*, 2005). After analysis of appropriate spawner recruit curves (2nd order polynomial and Log), Kraeuter et al. (2005, p. 1050) suggested "that in Great South Bay under current conditions recruitment is limited at clam population densities below about 0.75 individuals m^{-2}." Hard clams are protandric hermaphrodites and produce planktotrophic veliger larvae that remain in the plankton for 12-14 days.

Scallops

Although some authors have suggested that a stock-recruitment relationship exists in some scallop species (Summerson and Peterson, 1990; Peterson and Summerson, 1992; McGarvey *et al.*, 1993; Arnold *et al.*, 1998), data are not available that could confirm or refute the concept of recruitment overfishing for sea scallops, *Placopecten magellanicus* (Gmelin, 1791), in the Northeast Atlantic (Smith and Rago, 2004). A protracted spawning period, a greater than 30 d pelagic larval period, cannibalism of larvae by filter-feeding adults, and competition for food and space with adult scallops, coupled with environmental effects on larval survival would likely obscure any relationship between stock size or density and recruitment for this species (Smith and Rago, 2004).

The bay scallop, *Argopecten irradians* (Lamarck, 1819), has planktotrophic larvae that are in the water column for no more than 2 weeks. The entire life cycle generally takes less than 18 months, and, being hermaphroditic, bay scallops may potentially self-fertilize. Even with this long larval duration, in some situations, larvae may be retained in the vicinity of the natal habitat (Arnold *et al.*, 1998). Peterson and Summerson (1992, p. 269) suggested "that the bay scallop in North Carolina may represent a collection of recruitment limited subpopulations on a scale of water basins."

Marelli *et al*. (1999) reported upon a Gulf Coast of Florida population of the bay scallop, which was abundant prior to 1990 but declined to a point where adult densities were on the order of 0.01 m^{-2} by 1997. In this study, adult scallop density was estimated at 37 randomly located survey sites by deploying a 300-m weighted transect line in a roughly equilateral triangle and having a pair of SCUBA divers count all scallops within 1 m of either side of the transect line (Marelli *et al.*, 1999). Scallop recruitment was monitored in regularly monitored recruitment traps (half-bushel citrus bags containing a bundle of polypropylene mesh suspended 0.5 m above the substrate) randomly placed in up to 20 locations (Marelli *et al.*, 1999). These researchers were unable to identify a relationship between adult density and subsequent recruitment; however, low levels of recruitment and low adult density with minor pulses of recruitment "may suggest population collapse" (Marelli *et al.*, 1999, p. 397). Marelli *et al.* (1999, p. 397) concluded that the reduced probability of fertilization success at low adult densities likely explains the "persistent low stock levels," although *A. irradians* is likely buffered from reproductive Allee effects "because they are simultaneous hermaphrodites and capable of self-fertilization" (although this may rarely occur in the wild) and also have the potential to aggregate at spawning.

Giant clams – Tridacnidae

Although the critical density threshold below which recruitment failure occurs in various species of giant clams has not been determined, Munro (1993, p. 440) stated that "it is a feature of giant clam biology that stocks will become non-sustaining when densities fall below certain undefined levels" due to a "collapse in fertilization rates and consequent reduction in recruitment rates." The larger species (*Tridacna gigas* [Linnaeus, 1758], *T. derasa* [Röding, 1819], *Hippopus hippopus* Linnaeus, 1758, and *H. porcellanus* Rosewater 1982) are highly cryptic and difficult to enumerate in diver surveys of quadrats until a shell length of about 20 cm, whereas the smaller species (*T. squamosa* Lamarck, 1819, *T. maxima* [Röding, 1798], and *T. crocea* Lamarck, 1819) can be located at a smaller size due to their conspicuous mantle coloration (Munro, 1993). On lightly exploited reefs, *T. gigas* and *T. derasa* can occur at densities of five to several hundred per hectare, whereas normal densities of *H. hippopus* range from 30–90 per hectare (0.003–0.009 m^{-2}). The smaller species can reach much higher densities, to about 1,390 ha^{-1} (0.139 m^{-2}) for *T. crocea* and *T. maxima,* and to over 3,000 ha^{-1} (0.3 m^{-2}) in exceptional cases for *T. crocea* (Munro, 1993). Tropical giant clams are likely buffered from reproductive Allee effects, because they become simultaneous hermaphrodites and may be capable of self-fertilization (Munro, 1993). Larvae are planktotrophic and larval duration ranges from 5 to 15 days.

Geoducks

Given that geoduck clams, *Panopea abrupta* (Conrad, 1849), in the Pacific Northwest have a pelagic larval phase that extends to at least 25 d, Orensanz *et al.* (2004, p. 1358) suggested that "there is virtually no connection between the reproductive contribution of a given site and recruitment to that site." Zhang and Hand (2006, p. 451) also emphasized that until more is understood concerning larval movement, links between "recruitment in one spot to stock biomass in another" cannot be made for geoducks. Data are also lacking concerning the effect of low adult density on fertilization success in geoducks; however, given their sedentary adult existence "these processes may be important depending on the concentration profile of the populations" (Orensanz *et al.*, 2004, p. 1358).

Relevance to Black Abalone

In the above review, several patterns are apparent. First, evidence for critical density thresholds has been found for broadcast-spawning species across a broad taxonomic range. Second, despite apparent risks of local extinction when critical density thresholds seem to be violated, there are several cases where combinations of circumstances allow populations to recover to densities above the critical thresholds. The potential for recovery seems most evident in species with a lengthy larval period (> ten days) and the associated ability to disperse over long distances (> 10 km). Thus, for black abalone the key conservation issues are identification of critical density thresholds and an understanding of larval longevity and capacity for dispersal across long distances.

Prince *et al*. (1988) and McShane (1992) have demonstrated correlations between densities of adult and newly recruited juvenile abalone at study locations on the South Australian coast. These patterns are consistent with models in which larval dispersal from natal populations is limited, a relatively common circumstance in broadcast-spawning marine invertebrates with lecithotrophic larvae. It follows that depleted abalone populations below critical density thresholds, and as a result unable to sustain themselves with locally based recruitment, are unlikely to benefit from larval immigration from distant populations. Available information on the genetic structure of black abalone populations is also consistent with limited dispersal beyond the immediate proximity of natal populations. Thus, black abalone populations face substantial increases in extinction probability if they fall below critical density thresholds.

Babcock and Keesing (1999) estimated critical density thresholds at 0.15-0.20 m^{-2} for *Haliotis laevigata* Donovan, 1808. Tissot (2007) reviewed recruitment patterns in three long-term data sets for black abalone in California. In each case, recruitment failed when declining population densities fell below 0.75-1.1 m^{-2}. Tissot (2007) notes that densities in most black abalone populations south of Cayucos, California, have fallen below the densities noted. Recent evidence suggests that disease-induced increases in mortality rate of black abalone continue to move northward along the mainland coast of California (e.g., Raimondi *et al.*, 2002; Miner *et al.*, 2006). Critical density thresholds may have been violated for most of the black abalone populations in California, and the number and geographic scope of populations with densities falling below sustainable levels may be increasing.

VanBlaricom (unpublished data) measured nearest neighbor distances for abalone encountered during population surveys at San Nicolas Island in annual surveys beginning in 2004. Despite dramatic disease-induced reductions in population density beginning in 1992, most animals in surveyed populations remain in close proximity to conspecifics. In the nearest neighbor sample (n=1565 total measurements from 2004-2007), 94% of measurements were within 2 m, 88% within 1 m, and 62% within 10 cm. The data indicate that black abalone have remained strongly aggregated despite reductions in density averaging nearly 99% at nine separate sites on San Nicolas Island since 1992. The mechanism for maintaining close proximity to other animals may involve behavioral responses to the presence of conspecifics, or alternatively may reflect active selection of particular microhabitat types that facilitates aggregation as a side effect. The data indicate that virtually all black abalone observed in study plots were found in crevice or cryptic microhabitats since the onset of disease-induced mass mortalities in 1992, whereas about one-third of the surveyed abalone typically occurred on open horizontal or inclined substrata prior to 1992. Regardless of the cause, it appears that persistent gregarious distributions in black abalone have the potential to forestall negative population-level effects of drastic reductions in density. These data emphasize the value of assessing the variance structure in density data as well as the mean values when considering critical density thresholds. However, the ability of given black abalone aggregations to contribute to population growth on large spatial scales is dependent on longevity and spatial dispersal capability of black abalone larvae.

As noted in sections 1.4.1 above and 3.4.3 of this Status Review, the black abalone population at one known location at San Nicolas Island may remain above a critical density threshold and is experiencing ongoing successful recruitment (VanBlaricom, unpublished data). Also noted in section 1.4.1 of this Status Review is a second location at Santa Cruz Island, where recent recruitments have occurred despite the virtual absence of local spawning adults (Richards, unpublished data). The San Nicolas Island location is known to be characterized by small local sea surface temperature anomalies, with typical temperatures slightly lower (< 1º C on average) than at other monitored sites at the Island (VanBlaricom, unpublished data). Thus, anomalous local oceanographic features may contribute in some way to local population sustainability. It is also possible that the San Nicolas Island site includes animals that have developed genetically-based resistance to withering syndrome, thereby experiencing lower mortality rates and higher probabilities of population-scale persistence. The latter possibility is currently under experimental evaluation in the laboratory of C.S. Friedman at the University of Washington, Seattle.

3.3.4 Fertilization

Cox (1962) reports that release of gametes at spawning in abalone begins with discharge from the gonad into the right renal cavity. The gametes then pass through the external renal opening, moving into the respiratory chamber from which they are expelled through the tremata into the surrounding waters.

To our knowledge, the process of fertilization has not been studied in black abalone. Recent efforts to induce spawning in laboratories have been largely unsuccessful (Friedman, personal communication). Clavier (1992) has reported laboratory experiments involving induced spawning of the ormer (*Haliotis tuberculata* Linnaeus, 1758) of coastal western Europe and Africa. Adult females were found to have instantaneous fecundities of 0.2 to 1.6 x 10^6 eggs per induced spawn, with fecundities increasing with body mass of the spawning individuals. Adult male instantaneous fecundities ranged from 0.5 to 20 x 10^{10} sperm per induced spawn, but the relationship of fecundity to body mass was unclear for males. Clavier (1992) also evaluated the relationship of sperm concentrations per unit volume of sea water to fertilization rate. Fertilizations were not observed at sperm concentrations < 10^3 cells ml^{-1}. Fertilization rate was found to increase steadily as sperm concentration increased above 10^3 cells ml^{-1}, approaching 100% fertilization at approximately 10^5 cells ml^{-1}. Fertilization rates fell to zero at sperm concentrations above 10^6 cells ml^{-1}. Apparently, excessively high sperm concentrations cause lysis of the vitelline layer of the ovum, leading to its destruction. In some cases excessively high sperm concentrations were also associated with abnormal embryonic development.

To the extent that Clavier's (1992) result may be applicable to black abalone, it seems apparent that effective fertilization at high rates in wild black abalone populations must involve a challenging problem of optimization (see also section 5.4.1.3 of this Status Review). The highly turbulent environment in which black abalone dwell demands close proximity of male and female individuals and precise temporal synchrony in gamete release. However, excessive concentrations of sperm near spawned ova may cause production of damaged embryos and larvae (polyspermy). It is likely that delivery of effective spawning pulses in black abalone reflect simultaneous and instantaneous perceptions of proximity to conspecifics, spawning status of adjacent conspecifics of the opposite sex, and pattern of water flow.

3.4 Settlement, Recruitment, and Growth

3.4.1 Settlement

Keough and Downes (1982) define settlement of the larvae of marine benthic invertebrates, including abalone, as contact with the post-larval substratum, resulting in metamorphosis from the larval to the post-larval form. A series of studies over the past two decades have provided insight to the chemical and physiological processes in abalone larvae that are associated with settlement. The work collectively involves a number of abalone species, but there is sufficient empirical evidence to suggest that the mechanisms described below apply in general form to the settlement process in black abalone.

Morse (1990) has presented evidence that abalone larvae require exogenous chemical induction for settlement and metamorphosis. Morse *et al*. (1979) and Morse and Morse (1984) reported that γ-aminobutyric acid, a simple and well-known neurotransmitter, stimulates the settlement and metamorphosis of planktonic abalone larvae. Douros (1985) showed that crustose coralline algae enhance substratum-specific settlement rates by larvae of black abalone. Douros (1985) also provided evidence that potential chemical cues associated directly with the presence of adult conspecifics, such as mucous, do not influence rates of settlement and metamorphosis by black abalone larvae. Morse and Morse (1984) suggested that settlement cues associated with crustose coralline algae are related specifically to certain chemicals present only on algal surfaces. Trapido-Rosenthal and Morse (1986) reported that specific receptors on the surfaces of abalone larvae bind to γ-aminobutyric acid mimetics produced on the surface of the algae. It is further reported that the receptors develop on the larval surface incrementally over time following fertilization, and that appearance of the receptors precedes and is required for the emergence of the capability in the larvae to respond to settlement-inducing chemicals on algal surfaces. Morse (1992) reported that the γ-aminobutyric acid-mimetic settlement cues are produced by crustose algae and not by associated microorganisms. Of 33 strains of associated microorganisms screened for chemical settlement cues, none produced positive results. Miner *et al*. (2006) suggested that presence of adult black abalone may facilitate larval settlement and metamorphosis, because the activities and presence of the abalone favor the maintenance of substantial substratum cover by crustose coralline algae.

Morse (1984) determined that optimal concentrations of γ-aminobutyric acid for induction of settlement and metamorphosis of larvae are approximately 10^{-6} mol l^{-1} for most species of abalone tested. Morse (1992) indicated that detection of γ-aminobutyric acid-mimetic chemicals by surface receptors on larvae activates signal transduction pathways that translate the chemical signal from the environment to electrochemical signals propagated by the larval nervous system. Two such pathways have been described, termed regulatory and morphogenetic (Morse, 1992). The regulatory pathway causes an increase in sensitivity in those sensors linked to the morphogenetic pathway. The morphogenetic pathway induces attachment and metamorphosis by larvae.

Morse (1992) describes metamorphosis in abalone as relatively slow compared to other gastropod mollusks, although a specific timeline is not reported. The speed of metamorphosis is said to be inversely related to the relative need for new gene expression at the time of metamorphosis. In the case of abalone, new gene expression is required for synthesis of the adult-form shell and for synthesis of digestive enzymes as the animal shifts from a non-feeding larva to a feeding juvenile.

The sequence of studies and discoveries summarized above suggests that availability of crustose coralline algae in appropriate intertidal habitats may be significant to the success of the larval recruitment process in black abalone. Although crustose coralline algae are ubiquitous in rocky benthic habitats along the west coast of North America, a mechanistic understanding of processes that sustain subject algal populations has not been established to our knowledge. If the presence of black abalone serves an important role in facilitating abundance of crustose coralline algae, it follows that the question of critical density thresholds (see section 3.2 of this Status Review) takes on a new dimension. That is, the critical density concept may apply to minimum densities needed to maintain community structure and function, including promotion of crustose coralline algal abundance, as well as to maintain minimum local abalone densities required for fertilization rates adequate to forestall local extinction.

3.4.2 Larval dispersal distances

Direct measurement of larval travel patterns typically is not tractable for broadcast-spawning marine invertebrates. Planktonic larvae generally are so small and fragile that effective methods for marking and direct tracking of movements do not exist (e.g., McShane *et al.*, 1988). Three indirect alternative methods are used to estimate larval dispersal distances empirically, and all have been applied to the problem of determining dispersal distances in abalone. The first is to use objects such as drift cards or drift bottles, labeled with appropriate identifying information, as surrogates for larvae (e.g., Tegner and Butler, 1985; Chambers *et al.*, 2005). The objects ideally are released in spatial and temporal synchrony with the spawning species of interest. Data are then collected on recovery times and locations of individual drift objects, allowing analysis and inference about larval dispersal distances. Studies of movement of surrogate objects may be strongly biased in several ways. It is rarely possible to design a surrogate object that can duplicate larval behaviors, such as directed vertical movements in the water column, that may have significant effects on dispersal rate and pathway (e.g., Forward Jr. *et al.*, 1989). Surrogate objects are in all cases much larger than the larvae they are intended to represent, also raising the potential for significant, potentially misleading scale-dependent departures from dispersal patterns in actual larvae. Finally, as with living larvae, surrogate objects have such a large range of potential destinations post-release that unbiased and comprehensive surveys to determine dispersal endpoints are rarely practical. More often, dispersal endpoints are identified by a combination of directed searches in areas thought to have a high probability of receiving dispersed objects, together with information from chance discovery of stranded objects in other locations by shoreline visitors. Reliance on data of this kind poses the risk of several types of bias.

The second approach is to use molecular tools to establish relatedness of adult populations and newly recruited cohorts, allowing inferences about dispersal pattern (e.g., Hamm and Burton, 2000; Chambers *et al.*, 2006). This type of approach has been applied using allozyme electrophoretic methods along with a number of methods involving nucleic acids, including analyses of mitochondrial DNA, nuclear DNA microsatellites, and AFLPs. Each specific method has somewhat different capabilities for resolution of population structure that reflects dispersal patterns, and each has its own potential biases (e.g., Gruenthal, 2007). Most recent research on dispersal distances in marine invertebrate larvae relies on molecular tools. The nearly continuous emergence of new molecular approaches holds the promise of an ability to measure dispersal characteristics with improved accuracy and reduced biases.

The third approach is to examine the spatial relationship of newly recruited cohorts to known aggregations of breeding adults (e.g., Prince *et al.*, 1988). Dispersal distance is estimated based on the range of distances measured between sites occupied by adults and sites occupied by groups of juveniles. This approach probably is most likely to provide accurate results along linear coastlines with relatively simple nearshore current patterns. Complex topography, such as in island archipelagos, or complex nearshore flows, such as in eastern boundary currents, have the potential to confound the interpretation of spatial relationships of adults and young cohorts as a tool for estimating dispersal distances. In this approach errors of interpretation are likely to increase as dispersal distance capability of the subject species increases.

Larval surrogates and molecular methods have been used to assess dispersal distances in black abalone. Chambers *et al*. (2005) reported the release and tracking of labeled buoyant drift cards (plywood rectangles, 70 x 100 x 7 mm) on two different dates during the black abalone breeding season at San Nicolas Island. Release dates were August 2002 (1,170 cards) and June 2003 (1,430 cards). Cards were released at high tides just beyond the surf zone at a number of shoreline locations on the Island. Fates of released drift cards were tracked by intensive post-release shoreline surveys on foot at the Island, but surveys were not possible at other locations. As a consequence, cards dispersing to shores other than San Nicolas Island were located only if they were subject to chance discovery and the requested reporting response (written on the label of each card) by shoreline visitors. Card recovery rate was 62% following the August 2002 release and 53% for the June 2003 release. A large majority of recovered cards (78% in August 2002, 99.7% in June 2003) moved directly downwind and stranded within 2 km of respective release sites on San Nicolas Island. A small proportion of released cards stranded on other southern California Islands or on the southern California mainland, as indexed by chance discovery. Cards dispersing on the larger spatial scales (> 10 km) followed pathways consistent with influence by prevailing winds and by regional-scale surface current patterns. The drift card data are consistent with primarily local dispersal, together with occasional long-distance dispersal by a few individual larvae (see also section 5.4.1.3 of this Status Review).

Molecular methods for assessment of dispersal distance in black abalone have been described in section 3.1 of this Status Review under the subheading "Population structure and genetics". Chambers *et al*. (2006) utilized allozyme electrophoresis, whereas Hamm and Burton (2000) used both allozyme data and data from mitochondrial DNA. The most recent work (Gruenthal, 2007) was based primarily on methods involving nuclear DNA. The drift card study described above, and all the molecular studies noted here and in section 3.1 of this Status Review, point to a similar perception of dispersal distances in black abalone. Larval dispersal distance is thought to be minimal, most often occurring on scales of a few km or less. Dispersal over greater distances is viewed as infrequent, but nevertheless detectable in the molecular data. As noted in section 3.1 of this Status Review, Gruenthal (2007) has characterized larval dispersal in black abalone as consistent with the stepping-stone model of dispersal (Kimura and Weiss, 1964).

Studies of the spatial juxtaposition of breeding adults and cohorts of young animals have not been applied to black abalone. Prince *et al*. (1987; 1988), McShane *et al*. (1988), and McShane (1992) have described correlations in space between adult populations and juvenile cohorts of blacklip abalone (*Haliotis rubra* Leach, 1814) along the shores of South Australia, interpreting the data as evidence of limited dispersal distances in local abalone populations.

Overall, the three indirect methods for assessing larval dispersal in abalone point to consistent results. Given that most abalone larvae are in the plankton for a period of about 3-10 days before settlement and metamorphosis (e.g., McShane, 1992), it seems clear that abalone in general and black abalone in particular have limited capacity for dispersal over distances beyond a few kilometers, and are able to do so only rarely.

3.4.3 Recruitment

In the context of our Status Review we define recruitment as the appearance in one or more locations of measurable numbers of new post-metamorphic individuals. Our definition recognizes the possibility that recruitment may occur regardless of the local presence of breeding adults. Our definition is ecologically based, and should not be confused with the traditional and familiar recruitment definition used in the context of fisheries management. In the latter, recruitment is defined as the appearance in one or more harvested populations of new individuals that have reached a size large enough for legal harvest.

Leighton (1959; 2005) reported that small (< 5 mm maximum shell diameter) juvenile black abalone can be found on the undersides of large intertidal boulders with free space below, and in small depressions in rock caused by abrasive actions of the common intertidal chiton *Nutallina californica*. These observations were made in mainland intertidal habitats of southern California. Leighton (2005) noted that juveniles in such habitats are cryptically-colored and difficult to detect visually. VanBlaricom (unpublished observations) has also observed small (< 10 mm maximum shell diameter) black abalone at San Nicolas Island in large boulder habitats similar to those described by Leighton (2005). In addition, small black abalone were observed clustered adjacent to the bases of the common epilithic intertidal anemone, *Anthopleura xanthogrammica* (Brandt, 1835), at study site 8 (see also sections 1.4.1 and 3.3.3 of this Status Review) at San Nicolas Island (VanBlaricom, unpublished observations). It is apparent that newly settled black abalone undergo ontogenetic habitat shifts as they grow, and that the sequence of habitats used by young post-metamorphic animals appears to be relatively cryptic. As a consequence, episodes of recruitment are not detected until abalone of a new cohort reach the appropriate size for emergence into more open habitats where they are readily detected in conventional sampling efforts.

Abundance surveys for black abalone rarely detect individuals less than about 20 mm in size, and relatively few abalone at less than 40 mm. For example, of 1,628 black abalone located and measured during standard population surveys at San Nicolas Island from 2001 through 2007, 15 (0.9%) were 20 mm or less and 185 (11.4%) were 40 mm or less (VanBlaricom, unpublished data). Available growth data suggest that black abalone at 20 mm are approaching 1 year of age, and at 40 mm are about 2 years of age (Leighton, 2005). Because the surveys at San Nicolas Island were typically conducted during daytime low tides in northern winter months (January through March), abalone at 20 mm were likely young of the previous summer or autumn. Because animals in the vicinity of 20 mm in size do not appear to be fully emerged on a cohort scale, the sampling protocol likely would not detect a significant recruitment at San Nicolas Island at least until the cohort's second winter post-metamorphosis. Age of emergence of black abalone to more open and readily surveyed habitats at San Nicolas Island may typically be 2-3 years.

As noted above, Prince *et al.* (1987; 1988), McShane *et al*. (1988), and McShane (1992) have presented evidence that recruitment of abalone is most likely to occur in relatively close spatial proximity to aggregations of breeding adults, at least in part a consequence of the relatively short duration of the planktonic larval phase in abalone. McShane (1992) reviewed literature emphasizing the significance of coastal current regimes, including eddies and other regional-scale flow patterns, in distributing planktonic larvae and influencing locations of settlement and recruitment. Some flow features apparently serve to concentrate larvae and may foster the development of recruited cohorts at high density in appropriate benthic habitat (e.g., McShane *et al.*, 1988). In contrast, flow patterns that disperse larvae of benthic species to inappropriate habitats, such as the open sea, may ultimately increase larval mortality rates and diminish recruitment rates (e.g., Strathmann, 1985). Predation and starvation may also influence numbers and distribution of planktonic larval abalone (Strathmann, 1985), but to our knowledge there are no data available to provide a basis for associating mortality rates to either of these processes.

An overriding problem in quantifying movement and fate of planktonic phase larvae of abalone is the virtual absence of data on abalone larval distribution in the water column, for any abalone species in any location on any scale (e.g., McShane, 1992). As a result, effects of larval-phase population dynamics on recruitment processes for abalone can be evaluated only on the basis of various indirect measures. As noted above and in previous sections, abalone recruitment appears to be influenced by distribution of breeding adults, densities of adults on a local scale, availability of benthic recruitment substrata that provide appropriate chemical cues for settlement and metamorphosis of larvae, regional and local flow regimes that control larval dispersal from natal sites, and possibly predation and starvation of larvae.

As noted in section 3.3.3 of this Status Review, Tissot (2007) has estimated empirically that successful recruitment of black abalone requires the presence of local adult populations at densities of 0.75-1.1 m^{-2} or greater, and that the number of known populations of adult black abalone at or above putative threshold densities is diminishing over time in a geographically progressive manner (see also section 5.4.1.3 of this Status Review). Tissot (2007) further noted that virtually all monitored black abalone populations continue to decrease in mean density over time. This combination of observations emphasizes the importance of critical density thresholds as a major issue in the sustainability and conservation of black abalone populations throughout their range. Patterns of aggregation may mitigate effects of decline below a critical density threshold (see section 3.3.3 of this Status Review; VanBlaricom, unpublished data). However, only one or two populations in California are known to be increasing in numbers (see sections 1.4.1 and 3.3.3 of this Status Review). Thus, a tendency for abalone to aggregate may not be sufficient to facilitate recruitment at rates or spatial scales sufficient for population sustainability under current environmental conditions.

Black abalone densities in sites monitored at San Nicolas Island since 1981 reached a minimum in 2001, and have been increasing slowly since then (VanBlaricom, unpublished data). The increase is driven almost entirely by growth of densities at study site 8 (see map in VanBlaricom, 1993). Mean densities at all sites were well above the apparent critical density threshold range of 0.75-1.1 m^{-2} (Tissot, 2007) until 1992, falling below the threshold between 1992 and 2001. Densities at all sites across all years, except for site 8, have remained below the apparent critical threshold since 2001 (range 0-0.48 m^{-2} by site). Densities at site 8 have averaged 1.22 abalone m^{-2} since 2001 (annual means have ranged from 0.70 to 1.61 m^{-2}), with evidence of significant recruitment each year since 2001. Densities doubled between 2002 and 2006 at site 8 before dropping 8% between 2006 and 2007. Densities in the most recent survey (winter 2007) were 1.39 abalone m^{-2}. Among quadrats (n=278 quadrats at 1 m^2) within site 8 in 2007, counts ranged from 0 to 26 abalone. Twenty-four of the 278 quadrats surveyed (8.6%) contained five or more abalone. Assuming equal sex ratios and a random spatial distribution of each sex among quadrats, the probability that a quadrat with five abalone will contain at least one animal of each sex is 0.96. Thus, it is plausible that there are a number of patches at site 8 that have the potential to produce larvae. In contrast, at the other eight sites combined (n=1,776 quadrats at 1 m^2) only three quadrats (0.17%) had counts of five abalone, and none had more than five. Two of the three quadrats were at site 7, and the remaining one was at site 5.

Size frequency distributions in black abalone have been monitored at all nine study sites on San Nicolas Island since 1981 (VanBlaricom, unpublished data). Evidence of nine recruitment events has been observed at sites other than site 8 at San Nicolas Island since 2001 in size frequency and density data sets, but none of the young cohorts survived into a second year. Recruitment events were detected at two locations (sites 5 and 7) in 2002 and again at the same two sites in 2003, at site 3 in 2004, at three sites in 2005 (sites 2, 5, and 7), and at site 5 in 2006. Collectively, the data suggest four patterns of particular interest:

1) Densities at site 8 appear, based on patterns of local recruitment, to have been at or above the local critical density threshold since 2001;

2) Recruitments can and do occur at sites located >10 km (along-shore distance) away from the single population (site 8) that has sustained densities at the apparent critical density threshold;

3) Recruitments have been most common at sites 5 (four events detected) and 7 (three events detected), both of which are southeastward and directly downwind of site 8 on the south shore of the Island. Given the results of drift card studies at the Island (Chambers *et al.*, 2005) it is quite plausible that recruitments at sites 5 and 7 result from larvae produced at site 8 that were transported along shore by prevailing local flow patterns. On the same basis, it is only barely plausible that recruitments at sites 2 (detected in 2005) and 3 (detected in 2004) arose from larvae produced at site 8. Local production of larvae at sites 5 and 7 is modestly plausible as variance in density is relatively high and dense local aggregations of adults can be found at both sites (both had at least one aggregation of five adult abalone within a plot of 1 m^2 during 2007 population surveys, as noted above). Local production of larvae at sites 2 and 3 is only marginally plausible because of chronically low adult densities (< 0.25 m^{-2} in all years at both sites since 2001) and the absence of substantial local adult aggregations at either site (no quadrat counts were as high as five animals since 2001; n=274 quadrats at 1 m^2 at site 2; n=300 quadrats at 1 m^2 at site 3).

4) Post-recruitment mortalities clearly are limiting the incorporation of recruited cohorts into the local breeding populations at sites other than site 8.

As noted in section 1.4.1 of this Status Review, Richards (unpublished data) has detected substantial recruitment of young abalone at Willows Anchorage, Santa Cruz Island, in the absence of significant numbers of adults. This recruitment event was first detected in 2004, and the recruited cohort has survived in significant numbers since then, with the mean maximum shell diameter at 62 mm in winter 2007. In summary, the data from studies in the California Islands indicate temporal variability in the occurrence of detectable recruitment events, the potential for long-distance recruitment, the reasonably high probability that most recruitments emerge from local or nearby adult aggregations, and spatial variability in survival in recruited cohorts post-detection. Data on population growth patterns on the Islands are generally consistent with the proposed critical density threshold values proposed by Tissot (2007).

Stock-recruitment relationships and models (e.g., Ricker, 1954; Beverton and Holt, 1957) are often a staple of fishery management research and have substantial influence on management decisions such as harvest quotas and size limits. Such models attempt to link stock size to recruitment potential in exploited populations. Application of stock-recruitment theory to marine invertebrate populations, for whatever purpose, has often been ineffective, likely because factors such as spatially and temporally variable flow regimes can disperse larvae in complex patterns, effectively confounding and possibly negating existing relationships between adult breeding population size and recruitment potential (e.g., McShane, 1992). Prince *et al*. (1988) proposed a stock-recruitment relationship for *H. rubra*, but McShane (1991) countered that patterns in data used as evidence were more likely a reflection of differences in post-settlement mortality than in stock-recruitment relationships. McShane and Smith (1988) found high temporal variance in a single population of abalone over time, despite little temporal variation in the size of the breeding stock. Thus, McShane (1992) argued that there is little quantitative incentive or value in applying stock-recruitment theory to the characterization of abalone population dynamics. To our knowledge, stock-recruitment theory has not been applied to the management of any populations of black abalone.

3.4.4 Growth rate and maximum size

In a conservation context, growth rate of abalone is important because of linkages of size, age, and reproductive potential. Growth is also important to understand because body size may be an important determinant of vulnerability to predation. Growth may also be a useful indicator of abalone health and may reflect patterns of temperature, food supply, and other environmental features that can be monitored in the interest of abalone conservation. Growth rate data are clearly of value in the context of fishery management as well (e.g., Day and Fleming, 1992).

As noted previously, young post-metamorphic abalone are often cryptic in coloration and habitat use, making direct measurements of growth rate in the field difficult. The problem is compounded by the small size of young animals, such that tag attachment is largely intractable and, if attempted, may cause disturbance, injury or death of the subject animal.

Leighton (2005) suggests that black abalone reach a size of about 20 mm during their first year. During the second year black abalone begin to emerge from highly cryptic habitats to more open locations, probably in order to improve access to detached drifting algal pieces that dominate the diet, and perhaps as well to join aggregations of other abalone for eventual breeding purposes. Once emerged, most black abalone are of sufficient size and accessibility that tagging studies for growth measurement become practical.

There are a number of studies of post-emergent black abalone growth in the published literature. Leighton (1959) and Leighton and Boolootian (1963) tagged groups of black abalone at two sites on the mainland coast of southern California in spring 1958. Relocation surveys were done quarterly through February 1959 and involved measurement of relocated individuals. Sixteen relocations were made. Growth rates were found to vary by season (highest in summer and fall), and between locations (growth at Pt. Dume higher than at the Palos Verdes Peninsula). Growth rates ranged from 0.5 to 2.6 mm month^{-1} by individual at Pt. Dume, and from 0 to 1.62 mm month^{-1} at the Palos Verdes Peninsula. Leighton (1959) and Leighton and Boolootian (1963) also estimated growth rates from size frequency distributions. A cohort of small animals (17-26 mm) at the Palos Verdes Peninsula study site grew about 15 mm between August 1958 and April 1959. Bergen (1971) and Bergen Wright (1975; same individual) reported growth rates for tagged black abalone at Santa Cruz Island over a period of 12 months. Bergen Wright (1975) indexed size by measuring the distance from the shell spire to the shell edge, rather than the maximum shell diameter. Thus, growth rate data are not directly comparable to those reported in other published studies. Bergen Wright's (1975) study involved 71 recaptures of tagged individuals. Mean asymptotic size was estimated at 125 mm (Bergen Wright, 1975, as cited in Day and Fleming, 1992). Day and Fleming (1992) estimated von Bertalanffy growth parameters from data provided in a study at Santa Cruz Island by Douros (1985) over a period of 8 months, based on 57 recaptures of tagged animals. Growth coefficients for two groups of tagged abalone were estimated at 0.37 and 0.47. Mean asymptotic sizes were estimated at 117 mm and 139 mm for the same two groups, respectively. Blecha *et al*. (1992) estimated growth coefficients to range from 0.12 to 0.23 for black abalone populations at four sites near Diablo Cove on the central California mainland, and asymptotic sizes at 97 to 150 mm for the same sites. Study duration was about 20 months and 760 recaptures were made. Haaker *et al*. (1995) measured growth at several locations on San Miguel Island and at Pt. Arguello (on the central California mainland coast just north of Pt. Conception) over periods of two (Pt. Arguello) and four years (San Miguel Island). During the study, 769 black abalone were recaptured. Growth coefficients and asymptotic sizes were estimated at 0.19 and 134 mm for San Miguel Island and 0.11 and 135 mm for Pt. Arguello. Leighton (2005) summarized unpublished data from tagging work done with black abalone at Pt. Estero, on the central California mainland, over a period of 15 months in 1972. Tag relocation was minimal, but the growth coefficient was estimated at between 0.1 and 0.2, and the asymptotic size at 140 mm.

VanBlaricom and Monti (In preparation) studied growth in 413 tagged adult black abalone at two sites (sites 1 and 7 as described in VanBlaricom, 1993) on San Nicolas Island from 1981 through 1996. The same groups of tagged animals were also used for the movement studies described in section 3.1.6 of this Status Review. Relocations totaled 3,232 (2,425 at site 1; 807 at site 7). Abalone < 10 cm in size at tagging typically grew at about 1 mm per month until size reached 11-12 cm, when growth slowed.

Abalone of 10-13 cm at tagging showed very little positive growth, even in cases of multiple relocations over a number of years (maximum longevity of an animal post-tagging was 14 years). Abalone with shell lengths > 13 cm at tagging most often showed negative growth during the study. Analyses by site of net growth per unit time as a function of length at tagging indicated statistically significant ($p<0.05$) linear regressions with negative slopes. X-intercept values for the regressions were 121 mm at both sites. The data indicate that black abalone effectively have determinant growth at San Nicolas Island. X-intercept values for linear regressions appear to be the empirical equivalent of asymptotic size estimates from fitted von Bertalanffy growth models. Growth slowed with age and size in the tagged population. The observations of negative growth indicate that individual animals may exceed a local asymptotic size temporarily, but that shell erosion rates inevitably overtake shell growth rates as animals age. The result is convergence from both directions of black abalone shell size toward a fixed value that represents the long-term maximum shell size for a given location (see also section 5.4.1.3 of this Status Review). Long-term maximum shell lengths may vary by location, although they were similar between the two study sites at San Nicolas Island.

In summary, available data on black abalone growth suggest that young animals reach maximum shell diameters of about 2 cm in their first year, then grow at rates of 1-2 cm per year for the next several years. Growth begins to slow at lengths of about 10 cm, corresponding to an age range of 4-8 yrs. Beyond this point, growth is less predictable, shell erosion may become a significant factor, and size distributions for older animals may vary according to local conditions. Growth and erosion of shells may come into equilibrium in older black abalone, such that growth can be viewed as facultatively determinant.

Maximum recorded shell length for black abalone was listed at 213 mm by Wagner and Abbott (1990). Ault (1985) reported a maximum shell length of black abalone at 215 mm. Leighton (2005) indicated a shell length of 216 mm reported by Owen (unpublished observation). At least two black abalone of approximately 220 mm maximum shell length were known to be alive at San Nicolas Island in January 2007 (VanBlaricom, Neuman, and Witting, unpublished observations), but the cryptic locations of the animals have made measurements awkward and possibly not accurate. Monitoring and measurement of these individuals will continue in association with ongoing population surveys.

3.5 Mortality

Shepherd and Breen (1992) provide an excellent review of mortality in abalone, and note that an understanding of mortality rates in the three phases of natural abalone populations (larvae, juveniles, and adults) is essential to appropriate population modeling and management. As with most marine species, the various categories of mortality rates often are poorly known in abalone.

Mortalities of abalone larvae

Mortality processes in larval abalone are particularly difficult to evaluate for wild populations in natural settings. Shepherd and Breen's (1992) review of abalone mortality lists a number of factors that may influence mortality rates and provides a number of supporting references to the published literature. Among physical oceanographic factors, fluctuation beyond species-specific tolerance ranges in temperature and salinity have been identified as possible sources of mortality. As noted previously, larvae that are distributed to inappropriate habitats by ocean currents likely experience high mortality rates as a result of physiological stress, starvation or predation, although documentation of such processes is lacking to our knowledge. Based on the drift card study of Chambers *et al*. (2005), it is also likely that larvae of nearshore abalone species may be lost as a consequence of entrainment in the surf zone and violent impacts or abrasion against solid rocky or sandy substrata. Many predators have the capacity for ingestion of abalone larvae in the marine water column, including planktivorous fishes and zooplankton, but rates of mortality associated with planktonic predation are also unknown. Given known fecundities for abalone, including black abalone (see section 3.4.4 of this Status Review), and in consideration of the largest of estimated post-metamorphic abalone population sizes, it is likely that larval mortality rates in abalone are high even in pristine settings.

Mortalities of minute newly metamorphosed abalone

As described above, available information indicates that crustose coralline algae are particularly important recruitment habitats for black abalone as well as for other abalone species. Shepherd and Breen (1992) indicate that little is known about predation on newly metamorphosed abalone in this habitat type. It is speculated that a broad range of small benthic invertebrates are capable of consuming new abalone recruits, including polychaetes, nematodes, polyclad flatworms, and anemones. Small, newly-recruited abalone may also be susceptible to mortalities associated with disturbances such as substratum movement or disruption, deposition of sediment, influx of low-salinity waters associated with heavy rainfall and river discharge, and local seawater temperature anomalies associated with local weather events or larger-scale oceanographic perturbations. To our knowledge there are no published data capable of supporting meaningful estimates of mortality rates in newly recruited juvenile abalone in response to any of the listed processes or events, or to any other form of predation or disturbance.

Mortalities of small (<40-50 mm shell length) cryptic abalone

As abalone grow, associated mortality processes become somewhat more tractable research topics. Larger animals can be more easily located and monitored in the field as compared to smaller life history phases, allowing an understanding of certain types of mortality processes based on direct observation or tagging methods. In addition, the *post mortem* persistence of robust shells typical of larger animals often provides useful information on mortality sources and rates. Post-metamorphic abalone still small enough to remain highly cryptic may require cracks or crevices of appropriate dimensions to provide refuge from foraging crabs (e.g, Shepherd, 1973). Abalone in this size range (< 40-50 mm) face predatory pressure from a number of other consumer species as well.

Ault (1985) and Shepherd and Breen (1992) list gastropods, octopuses, lobsters, sea stars, and fishes as predators capable of ingesting small abalone. At San Nicolas Island, VanBlaricom (unpublished observations) has observed directed predation on black abalone in rocky intertidal habitats by the ochre sea star *Pisaster ochraceus* (Brandt, 1835), an octopus (*Octopus bimaculatus* Verrill, 1883), a large cottid fish, the cabezon (*Scorpaenichthys marmoratus* Girard, 1854), and a shorebird, the black oystercatcher *Haematopus bachmani* Audubon, 1838. In addition, VanBlaricom (unpublished observations) has observed ingestion of small black abalone by three taxa normally viewed as herbivores: the lined shore crab *Pachygrapsus crassipes* Randall, 1839; the purple sea urchin *Strongylocentrotus purpuratus* (Stimpson, 1857); and the turban snails *Tegula* spp. Consumption of black abalone by normally herbivorous species may involve scavenging on dead or moribund animals, such as those afflicted by disease, rather than directed predatory activity. Despite the large number of identified predators on small cryptic abalone, we are aware of no studies that estimate mortality rates of black abalone in association with the predator species that have been identified. Tegner and Butler (1985) were able to provide some indication of predation rates by octopuses on outplanted small green abalone as part of a restoration study off southern California.

Cryptic abalone < 40-50 mm in size may also suffer mortalities from the same range of physical disturbances listed above for minute post-metamorphic abalone, although estimates of rates of mortality from such sources are not available for black abalone. In addition, abalone in this size range are large enough to experience illegal harvest by people in some locations. Finally, abalone in this category are susceptible to mortalities caused by the recently-emerged lethal disease known as abalone withering syndrome. Mortalities caused by human removals and diseases are reviewed in sections 3.4.5.1 and 3.4.5.2 of this Status Review.

Mortalities of emergent abalone

Mortality patterns for large, emergent abalone (> 40-50 mm in size) are reasonably well-known for some species. Identified categories of mortality include predation, variation in food supply, physical disturbance, pollution, disease, and human removal (e.g., Shepherd and Breen, 1992).

Emergent black abalone are known to be killed and consumed by sea otters, sea stars, and fishes. Predation by sea otters is considered in section 3.5.3 of this Status Review. The ochre sea star is a known predator of black abalone, and appears to be capable of killing and consuming the largest abalone typically present in populations (VanBlaricom, unpublished observations). Ault (1985) indicated that rates of abalone consumption by ochre sea stars probably are too low to be significant ecologically. The same is likely true for consumption by cabezon, also capable of ingesting large black abalone.

As noted in section 3.2 of this Status Review, the diet of black abalone is dominated by large kelps, especially the giant kelp *Macrocystis californica* in southern and central California and the bull kelp *Nereocystis leutkeana* in central and northern California. Large kelps are also known to be important in the diets of other abalone species in

California. During the second half of the twentieth century storm disturbances associated with El Niño events occurred with increasing frequency along the California coast, and with a broadening awareness of ecological consequences to nearshore ecosystems. Severe El Niño events in 1957-1959, 1982-1984, and 1997-1999, each more intensive than the previous, caused substantial temporary reductions in the sizes of kelp forests along the California coast. Published evidence indicate red and green abalone populations experienced reduced individual growth rates, reduced gonadal growth, diminished recruitment, and starvation as a consequence of the events of 1957-1959 and 1982-1984 (e.g., Cox, 1962; Dayton and Tegner, 1984; Tegner and Dayton, 1987; Shepherd and Breen, 1992). Black abalone may have suffered from nutritional deficiencies during the 1957-1959 event (Leighton, 2005). However, nutritional consequences of later events for black abalone are less clear. Data from San Nicolas Island indicate no evident change in black abalone abundance in response to the 1982-1984 event, except in association with substratum disturbances, despite obvious reductions in sizes of offshore kelp forests in the vicinity of the Island (VanBlaricom, 1993). The 1997-1999 event also reduced sizes of offshore kelp canopies near San Nicolas Island and elsewhere. Black abalone densities were in decline during the late 1990s (VanBlaricom, unpublished data), such that linkages to storm disturbance and possible food shortages are confounded by mortalities associated with disease during the same time period. As a result, the significance of variable food supply to black abalone population dynamics in California is not clear.

As noted above, substratum disturbance was observed at San Nicolas Island during the 1982-1984 El Niño event (VanBlaricom, 1993). On one permanent transect of 30 x 2 m dimensions at site 3, severe wave impacts during storms in winter 1983 caused separation of inclined sandstone beds, resulting in creation and movement (over distances of 10 m or more) of rock pieces ~2 m in thickness and up to 5 m across. Changes in configuration of the substratum caused some mortality and relocation of abalone on a small local scale. Despite the visually dramatic nature of the disturbances, changes in substratum configuration were not enough to produce a noticeable signal in the time series of density data for black abalone at the site.

Shanks and Wright (1986) described the role of breaking waves in suspending and moving pebbles and cobbles in intertidal habitats at San Nicolas Island. In moderate or larger surf conditions, the displaced stones effectively become projectiles that can damage or kill intertidal invertebrates. Chipped and fractured abalone shells, either in beach wrack or on living black abalone, have been observed in sites at San Nicolas Island where cobbles and pebbles are available for suspension as potentially destructive projectiles (VanBlaricom, unpublished observations). Rates of mortality caused by projectile impacts are probably low for black abalone using protective cryptic microhabitats, but may be significant in groups of animals using open, unprotected habitats. Quantitative estimation of black abalone mortality rates associated with projectile impacts has not been reported in the literature.

Shepherd and Breen (1992) note one published instance of abalone mortality associated with a pollution event, described by Martin *et al*. (1977). Toxic levels of copper in the cooling water effluent of a nuclear power plant near Diablo Canyon, California, were associated with abalone mortalities in a nearshore cove that received significant effluent flows. There is ongoing concern that accidentally spilled oil from offshore drilling platforms or various types of commercial vessels could occur near shore in California, could spread through a significant proportion of black abalone habitat, and could cause significant black abalone mortalities on shorelines. VanBlaricom and Jameson (1982) evaluated movement of a large quantity of lumber accidentally spilled from a barge during a winter storm off central California, using the spilled lumber as a surrogate for spilled oil. The spilled lumber was equivalent in volume to ~30,000 bbl of oil. Lumber dispersed from the Monterey Peninsula southward to San Miguel Island. Much of the spilled material stranded on shore in excellent black abalone habitat. While there is no direct published evidence of potential damage to black abalone from spilled oil, the lumber surrogate study emphasized the significant risk of potential damage to black abalone populations on a large spatial scale, should a large spill occur.

3.5.1 Competitive interactions and anthropogenic mortality

Abalone and sea urchins often share habitats and food preferences. Tegner *et al*. (1992) noted that sea urchins can have negative effects on other herbivorous marine invertebrates in cases of limited food supply. Tegner and Levin (1982) evaluated possible competitive interactions of red abalone and red sea urchins (*Strongylocentrotus franciscanus* Agassiz, 1879), finding minimal evidence for strong competition for food resources. Tegner (1989) noted that purple sea urchins may also be abundant in red abalone habitats in California, and may be capable of destructive overgrazing of kelp populations at a level that could be nutritionally detrimental to abalone, potentially contributing to increased mortality rates.

In California's rocky intertidal habitats, high densities of purple sea urchins and small numbers of red sea urchins often occur in close proximity (< 1 m) to black abalone. Purple urchin aggregations may reach several hundred individuals or more per m^2 in tidepools in high-quality black abalone habitat on the islands off southern California, and urchins are commonly seen holding and ingesting drift fragments of the same kelp species used as food by black abalone (Richards and VanBlaricom, unpublished observations). Thus, the potential for food competition between black abalone and sea urchins is plausible. To our knowledge, potential competitive interactions of black abalone and purple sea urchins have not been investigated. VanBlaricom (unpublished observations) observed that purple urchins were quite abundant in rocky intertidal habitats at San Nicolas Island during years (1981-1991) of high black abalone abundance. The decline in black abalone densities from 1992 to 2001 was not accompanied by noticeable changes in distribution or densities of purple sea urchins. These observations are consistent with insignificant competitive interactions between black abalone and purple sea urchins, but are not definitive. The strength of the potential interaction remains unresolved.

Mortalities associated with human removals

Mortalities of black abalone associated with human removals fall into five major categories:

a. Subsistence harvest by indigenous peoples;
b. Commercial harvest;
c. Recreational harvest;
d. Purposeful illegal harvest;
e. Accidental lethal injury.

There is a substantial technical literature on harvests of black abalone by indigenous peoples, particularly for the southern California Islands where extensive shell middens have survived, in many cases with minimal disturbance (see also section 3.1.5.1 of this Status Review). There are also informative technical reports on commercial harvest and at least one report relevant to the issue of accidental lethal injury to black abalone resulting from human activity in rocky intertidal habitats. To our knowledge there are no published data detailing direct effects of legal recreational harvests or of purposeful illegal harvests of black abalone, although it is plausible that both have been important sources of black abalone mortality in the recent past. One study considered the effects of legal recreational harvest by contrasting abundances and recruitment frequencies among black abalone populations in locations with varying levels of formal and *de facto* prohibition of harvest.

1. Subsistence harvest by indigenous peoples

Well-preserved shell middens are common in the southern California islands. Many of the middens contain large numbers of black abalone shells, particularly at sites of ages less than ~4,500 calendar years before present (Glassow, 1993). In earlier sites the predominant abalone is the red abalone. Red abalone occur in habitats with lower seawater temperatures than black abalone. Glassow *et al*. (1994) have used oxygen isotope data from middens on Santa Cruz Island to support the argument that the shift in favor of black abalone was associated with an ocean warming event of about 2.5º C at the time of the shift. Salls (1992) and Sharp (2002) claimed instead that available evidence favors cultural changes in hunting practices by native people as the explanation for the shift.

Middens with large numbers of black abalone present have been reported for San Miguel (e.g., Vellanoweth *et al.*, 2002), Santa Rosa (e.g., Orr, 1967), Santa Cruz (e.g., Douros, 1993), Santa Catalina (e.g., Meighan, 1959), and San Nicolas Islands (e.g., Reinman, 1964), and likely occur on the other southern California islands as well. The striking abundance of black abalone in middens is evidence of large populations of black abalone at the Islands and high harvest rates of black abalone by native human communities, at least episodically if not continuously. However, none of the indigenous human communities of the islands survived the immigration of European cultures to western North America in the latter part of the second millennium AD. Mainland native communities in coastal California also harvested shellfish from nearshore environments, but the mainland communities likewise suffered cultural disruption and population reduction, such that subsistence indigenous harvest of black abalone and other nearshore marine invertebrates was effectively terminated by the early twentieth century.

In some regions of the U.S., traditional native rights to shellfish harvests have been argued in the U.S. federal court system, and in some cases the courts have ruled in favor of tribal claims. The best-known example is a ruling in 1994 by a U.S. District Court, commonly known as the Rafeedie Decision (U.S. v. Washington, 873 F. Supp. 1422, W.D. Wa 1994), and a related subsequent federal District Court order and judgement (U.S. v. Washington, 898 F. Supp. 1453, W.D. Wa 1995). The ruling pertained to a claim by native tribes in Washington State of traditional rights of access to shellfish resources on a commercial scale. The favorable ruling for the tribes was made on the basis of a Treaty signed by tribal representatives and the U.S. federal government in the middle nineteenth century. The ruling established protocols for sharing of harvest quotas among tribal and non-tribal entities, marking a significant shift in shellfishery management at the State level, and modifying the impact of human harvests on shellfish populations in coastal waters of Washington.

To our knowledge, surviving tribal entities in California have not formally indicated an interest in exploring legal options for restoration of traditional harvest activity on black abalone or other marine invertebrate species. However, there can be no argument regarding the importance of black abalone as a traditional food resource for some indigenous communities in California. The extent to which tribal harvests of black abalone may emerge in the future likely will turn on perceptions by the court system of formal agreements, if any, among tribal and U.S. territorial and federal authorities regarding the disposition of resource harvest rights at the time tribes were displaced from traditional harvest locations.

In the case of Washington State, agreements in question were in the form of treaties, viewed by the court as having the same authority as any international treaty. Often, however, such agreements have more ambiguous status and may be documented in vague language subject to a wide variety of interpretations. It has been noted that U.S. federal courts traditionally interpret such agreements as they were perceived, or thought to have been perceived, by tribal parties to the agreements. This protocol acknowledges the disadvantageous position of signatory tribes because of language barriers. The courts have further ruled that it is within the rights of tribal fishers to use modern techniques (e.g., scuba diving) that may not have been available during pre-Columbian times, and to pursue commercial as well as subsistence harvests (VanBlaricom, 1996). Thus, it is at least plausible that substantial tribal fisheries for black abalone will again emerge in the future.

2. Commercial harvest

Commercial-scale harvests for black abalone began in about 1850 (see also sections 3.1.5.1 and 5.4.1.1 of this Status Review). The earliest harvesters were primarily of Chinese ancestry, using intertidal and shallow subtidal habitats to take black and green abalone in the San Diego area, in Baja California, and in several of the southern

California islands (Parker *et al.*, 1992). Harvest of intertidal and shallow subtidal abalone populations was soon prohibited by local governments in response to concern about stock depletion. The ban led to a shift in the ethnic composition of the abalone fishing community in favor of Japanese fishers, whose knowledge of newly emerging diving technologies allowed a stronger focus on larger and more marketable pink abalone in subtidal habitats. Cox (1962) reported that 1,860 mt of abalone were taken by Chinese fishers in 1879, but we are aware of no other harvest data available for either the Chinese or Japanese periods of commercial harvest of black abalone. Commercial harvests of all abalone species were banned throughout southern California in 1913, primarily by local jurisdictions concerned about possibly excessive harvest rates.

The modern era of commercial black abalone harvesting began in 1956. Black abalone were not popular with domestic markets for several reasons: they are relatively smaller in size; the meat is tougher than other species and requires extra work to tenderize; and the meat is oddly colored (gray-green as compared to the more appealing beige-white of other species). However, markets for black abalone products were found in Asia and export product demand remained strong through the life of the fishery. The State of California permitted legal commercial harvest of black abalone from 1956 through 1993. The fishery was regulated by issuance of permits to commercial fishers, a size limit (minimum shell diameter of 5.5 inches or 140 mm, increased to 5.75 inches or 146 mm in 1974), and seasonal closures. In 1974, harvest quotas and areas closed to harvest were added as management tools for black abalone harvests. All harvest rate data described here were provided by the California Department of Fish and Game, in units of pounds harvested per year. Harvests were small in 1956 (0.3 mt) and 1957 (0.9 mt). No black abalone were taken commercially from 1958 through 1967 because of weak domestic market demand. Commercial harvest activity resumed in 1968, when laws prohibiting export of abalone products were repealed, and increased rapidly over the next few years. Peak annual harvest rates in the fishery were in 1972 (459 mt), 1973 (868 mt), and 1974 (523 mt). Harvest totals in 1973 and 1974 were higher for black abalone than for any other abalone species harvested in California. Harvest rates for black abalone averaged about 181 mt per year from 1975 through 1983 and about 68 mt per year from 1984 through 1988, after which the harvest rate declined to near zero by the early 1990s. The fishery was closed in 1993 in response to concern about stock sustainability relating to the significant mortalities caused by withering syndrome. The closure was followed by a moratorium on commercial fisheries for abalone of all species in California in 1997. The moratorium remained in effect at completion of this document. However, at this writing (January 2008) there are plans for opening a limited red abalone fishery in a portion of the waters of the Channel Islands National Marine Sanctuary in the near future.

The commercial black abalone harvest was pursued largely on the Islands of southern California. The five harvest blocks with the largest reported landings were at San Miguel, San Clemente, Santa Rosa, and San Nicolas islands, listed in order of harvest quantity. The total harvest for these blocks, over the life of the commercial fishery, was 4,082 mt. The most heavily harvested block, incorporating the western three-quarters of San Miguel Island, produced 1,541 mt over the life of the commercial fishery. Small harvests were recorded at Santa Cruz, Anacapa, Santa Barbara, and Santa Catalina

Islands, and at Cortez Banks, all located off southern California. Minor harvests were also reported in scattered mainland harvest blocks from Pt. Estero, on the central California coast, southward to the U.S.-Mexico border.

Black abalone was the last of the five species of commercial abalone in California to be harvested intensively in an unfortunate process common to multi-species fisheries, known as "serial depletion" (Estes and VanBlaricom, 1985; Parker *et al.*, 1992; Karpov *et al.*, 2000). Serial depletion typically begins with harvest effort focused on the most desirable species as defined by harvest efficiency and marketing criteria. In the case of California species, the red abalone was the first species to be emphasized during commercial harvests in the twentieth century, and sustained the fishery almost exclusively until World War II when harvest effort dropped to near zero. Following the War, demand for abalone products increased, and harvests of red abalone likewise increased. Red abalone harvest rates began to drop steadily in the late 1960s, and the fishery began exploiting pink, then green, then white (*Haliotis sorenseni* Bartsch, 1940) abalone, moving to a new focal species as an existing focal species became depleted. Pink, green, and white abalone were all highly marketable, but unexploited stocks were smaller, less widely distributed, and less efficiently harvested than red abalone. Thus, the industry pursued harvests for pink, green, and white abalone only after catch per unit effort of red abalone became unattractive to commercial fishers.

It was only after the four other major commercial abalone species were substantially depleted that the industry began to emphasize harvest of black abalone, the species producing the lowest price range to fishers and the greatest challenge to marketers. Serial depletion of this form is facilitated by a tendency for fishery managers to evaluate status of harvestable stocks based on catch data summed across species and summed across exploited spatial harvest blocks. When the data are considered only in summed format, serial depletion in space and by species is masked, and management decisions may be made with protocols that are blind to the actual status of individual species. The problem is intensified by the traditional reliance on harvest data rather than fishery-independent population assessment data. With the benefit of hindsight it is clear that the California abalone fishery was managed without the necessary consideration of population dynamics at the species level. Although a number of factors have contributed to unsustainable levels of mortality in California's abalone fisheries, it appears that commercial harvest may have been broadly excessive, contributing to depletion of all commercially significant species, to a listing of white abalone as endangered, and to circumstances leading to the petition for listing of black abalone.

To our knowledge there are no current plans in development for resumption of commercial harvests of black abalone in California. Should commercial harvests resume, risks of damage to the sustainability of exploited populations will immediately increase, particularly if the lessons of serial depletion are not incorporated into future management strategies.

3 & 4. Legal recreational harvest and purposeful illegal harvest

Harvest of black abalone for individual use on a recreational scale was permitted in California for a number of decades prior to the 1990s. Harvests were traditionally limited by bag limits (typically a maximum of four abalone in possession, reduced to two in the period just before suspension of the fishery), size limits (harvest allowed only for animals with shell diameters of 5.0 inches (127 mm) or more), and seasonal closures. To our knowledge there are no data available, either statewide or by harvest block, for quantities of recreational take of black abalone in California, because the State did not have a system in place for statewide monitoring of legal non-commercial take. As a consequence, it is not possible to estimate the role of recreational harvest in the long-term dynamics of black abalone populations. Recreational harvest might have influenced the sustainability of black abalone populations along the California mainland because of the ready access of mainland rocky intertidal habitats to human visitation. Confirmation of effects would require harvest data and reasonable estimates of other sources of mortality, such as illegal harvest or predation by sea otters, none of which are known. Legal recreational harvests of black abalone were suspended by the State of California in 1993, in response to concern about the drastic demographic effects of withering syndrome.

Micheli *et al*. (In review) examined densities of black abalone in intertidal habitats of the central California coast in Monterey County in 2002 (see also section 5.3 of this Status Review). Although densities were relatively low (overall mean = 0.39 m^{-2}; range of means by site = 0.01-0.77 m^{-2}), the populations examined were found to have experienced regular recruitment and were said to be stable through time. Examination of annuli in shells collected in 2005 indicated regular annual recruitment across the previous decade. Micheli *et al*. (in review) suggested that a key to sustainability of the subject black abalone populations was the presence of several formal marine protected areas in the region that explicitly prohibit removal of black abalone by people. Micheli *et al*. (in review) also suggested that areas with good abalone habitat that were difficult for humans to visit, either because of hazardous terrain or because of obstacles associated with placement of lands in private ownership, served as *de facto* marine protected areas and provided a level of protection to black abalone populations comparable to that of formally designated marine protected areas. Sea otters were present in the vicinity of the study areas and are known to take black abalone as prey. Mortalities due to the spreading influence of withering syndrome had not occurred in study sites at the time of data collection. The authors concluded that black abalone populations free of disease effects survive in sustainable status in the study locations despite sea otter predation if human removal is prevented. In the study sites surveyed by Micheli *et al*. (In review), only one had mean densities within the range of the critical density threshold (0.75-1.1 m^{-2}) proposed by Tissot (2007). Thus, it is possible that black abalone recruitment can be sustained at lower adult densities in the absence of local disease activity than in locations with active disease-induced mortality.

Purposeful illegal harvest, typically termed poaching, clearly has been a source of mortality for black abalone throughout their range since the establishment of harvesting regulations by the State of California. The chronic virtual absence of black abalone populations from highly accessible intertidal habitats near human population centers in California during the twentieth century can plausibly be viewed as evidence for the importance of poaching as a contributing source of abalone mortality.

From 1993 to 2003 a number of black abalone poaching cases were documented by the CDFG along the California mainland coast, particularly in the northern portion of the black abalone's geographic range (Taniguchi, unpublished data). Some of these cases resulted in well-publicized arrests and trials of black abalone poachers. These events often involved removals of tens to hundreds of abalone, across all size categories present in the exploited populations, and without regard to harvest size limits in effect prior to commercial and recreational fishery closures (Table 1). Enforcement effort varied over the ten-year time period, increasing in 2000 because of coordinated efforts between CDFG marine and coastal regions and planned overflights along the central California coast during low tides (Table 1). CDFG wardens estimate that 80% of seized abalone were returned alive to the wild. At this time, the utility of these data for calculating poaching-induced mortality estimates for black abalone has not been explored. The problem of poaching clearly persists, but the relative impact of poaching-related mortality is poorly understood.

5. Accidental lethal injury

Accidental lethal injury may occur in habitats where human visitation rates are high enough to expose black abalone to risks from trampling, overturning of rocks, and other forms of disturbance from people interested in legal viewing of intertidal organisms but overzealous in their activities. Direct documentation of black abalone mortality rates associated with such activities is not available to our knowledge. Inferences about rates of accidental lethal injury can be made by comparing black abalone populations among otherwise similar intertidal locations, each with good quality black abalone habitat but varying in human visitation rate.

Kimura and Steinbeck (2003) collected size frequency data for black abalone in intertidal habitats at Pt. Piños and several nearby sites on the Monterey Peninsula in coastal central California in 2002 (see also section 5.3 of this Status Review). The goal of the study was to assess effects of high rates of recreational visitation by people in intertidal biological communities. Removal of black abalone by people is prohibited at all study sites surveyed. Anticipated effects of high visitation rate included trampling and localized substratum disturbance. Data from the high-use area at Pt. Piños were compared with data from nearby sites with lesser visitation rates by people. Size distributions were found to be dominated by small individuals at all sites. The average size was 57 mm (n=129) at Pt. Piños, and 58 mm (n=136) at nearby sites with lesser use. Densities of black abalone were not estimated in the study. It was concluded that high recreational use at Pt. Piños was not having substantially greater effects on black abalone size distributions than more modest use rates at other nearby sites. No black abalone symptomatic for withering syndrome were found during the study. Data from this study suggest that black abalone populations in the region can survive even in the presence of heavy visitation by people, as long as harvest of abalone is prohibited and disease effects are absent. Sea otters were common in the vicinity of the study areas at the time of the study, and may have been contributing to the overall total rate of mortality in black abalone.

3.5.2 Mortalities associated with disease

Prior to the appearance of withering syndrome (Haaker *et al.*, 1992) there was little evidence of significant diseases in black abalone. Growth and reproduction of black abalone were reported to have been impaired on the Palos Verdes Peninsula in the late 1950s and early 1960s, in association with apparent combined effects of a significant El Niño event and poor water quality resulting from large-volume domestic sewage discharge by Los Angeles County (Leighton, 1959; Cox, 1962; Young, 1964; Miller and Lawrenz-Miller, 1993).

There is now substantial concern among scientists and marine resource managers about the emergence of virulent disease processes in marine organisms on a global scale, in association with ocean warming in recent decades (e.g., Harvell *et al.*, 1999; Harvell *et al.*, 2002). Recent surveys of the literature suggest that the frequency of reporting of new diseases has increased for several major marine taxa, including mollusks (e.g., Ward and Lafferty, 2004). The appearance of withering syndrome in black abalone is consistent with the reported pattern. As described below, mortality rates associated with withering syndrome often correlate to positive anomalies in sea surface temperature. There is, however, no explicitly documented causal link between the existence of withering syndrome and global climate change.

Evidence of effects of withering syndrome on black abalone was first noticed along the south shore of Santa Cruz Island in 1985 (see also sections 3.1.5.2 and 5.4.1 of this Status Review), when a fisherman noticed large numbers of dying black abalone and empty shells (Lafferty and Kuris, 1993). The primary symptoms of disease noted at the time included pedal atrophy and a diminished ability to maintain a grip on rocky substrata. Haaker *et al.* (1992) and Richards and Davis (1993) described the first observations of mass mortalities of black abalone in previously monitored populations on the island shores of Channel Islands National Park in 1986, and broadened the list of recognized symptoms to include epipodial and mantle discoloration, and lack of response to tactile stimulation. Haaker *et al*. (1992) were the first authors to apply the term “withering syndrome” to the suite of symptoms and consequent mass mortalities observed in the field. Between 1985 and 1992, mass mortalities occurred at San Miguel, Santa Rosa, Anacapa, Santa Barbara, and San Clemente Islands, in all cases with symptoms indicating withering syndrome (Davis *et al.*, 1992; Haaker *et al.*, 1992; Lafferty and Kuris, 1993; Richards and Davis, 1993). Evidence of withering syndrome was first seen at San Nicolas Island in spring 1992 (VanBlaricom *et al.*, 1993), and was followed by widespread mass mortalities at the Island from 1992 to 1996 (Tissot, 2007). The delayed appearance of withering syndrome at San Nicolas Island, as compared to the other southern California Islands, remains unexplained but may have reflected patterns of dispersal by disease propagules. To our knowledge, no effort has been made to assess effects of withering syndrome at Santa Catalina Island, although the Island historically supported significant black abalone populations (e.g., Meighan, 1959).

The first reported occurrence of significant numbers of black abalone with symptoms of withering syndrome on the California mainland was at Diablo Canyon, near Port San Luis in San Luis Obispo County, in 1988 (Steinbeck *et al.*, 1992). Afflicted animals were found primarily within Diablo Cove, which receives warmed effluent seawater from the cooling system of a nearby nuclear power plant. A mass mortality of black abalone occurred at the site between 1988 and 1989, with mortality rates correlating well to local patterns of sea temperature elevation associated with power plant effluent. Evidence of infection of red abalone with withering syndrome has been found in wild populations south of San Francisco along the California mainland coast, and in farmed red abalone throughout California (Friedman and Finley, 2003).

Since the middle 1990s withering syndrome has appeared sequentially in progressively more northward populations of black abalone on the mainland California coast (Altstatt *et al.*, 1996; Raimondi *et al.*, 2002; Miner *et al.*, 2006). The most recent observations available suggest that significant mortalities associated with withering syndrome have occurred at least as far north as Pt. Piedras Blancas, near San Simeon in northern San Luis Obispo County (see also section 5.4.1.2 of this Status Review). Surveys for the microorganism responsible for withering syndrome have found positive results as far north as San Francisco (Finley and Friedman, 2000; Friedman and Finley, 2003). In addition, positive results have been found at two sites in northern California known to be locations of red abalone outplanted from shellfish hatcheries (Friedman and Finley, 2003). However, red abalone symptomatic for withering syndrome have not been observed in natural habitats north of San Francisco.

Early efforts to identify the cause of withering syndrome focused on endoparasites, pollution, and reduced food supply. Infestations of renal coccidian parasites were identified in black abalone soon after mass mortalities were observed, and were initially suspected to be the cause of the disease. However, evidence linking coccidian infestation intensity with symptoms of withering syndrome could not be established (e.g., Haaker *et al.*, 1992; Steinbeck *et al.*, 1992; Friedman *et al.*, 1993). Efforts to link mass mortalities and symptoms of withering syndrome to pollutant concentrations likewise produced negative results (Gardner *et al.*, 1995). Davis *et al.* (1992) suggested that mass mortalities caused by withering syndrome in black abalone were but one symptom of a broad-scale collapse of coastal ecosystems in southern California resulting from excessive anthropogenic impacts on marine species and habitats, occurring in temporal synchrony with the severe El Niño event of the early 1980s. Davis *et al.* (1992) posited that a key consequence of ecosystem disruption was reduced food supply for black abalone. Although reductions in kelp abundance occurred in the early 1980s (see section 3.1 of this Status Review), subsequent studies (e.g., Friedman *et al.*, 1997) have suggested that reduced food supply probably did not trigger the mass mortalities caused by withering syndrome in black abalone. Kelp abundances had recovered from El Niño effects in southern California by the time withering syndrome was first observed in 1985, and the abundant black abalone populations at San Nicolas Island showed no response in density to the 1982-1984 El Niño disturbances, despite dramatic reductions in kelp abundance near the Island (VanBlaricom, 1993).

It is now broadly accepted that withering syndrome in black abalone is caused by a *Rickettsia*-like prokaryotic organism, '*Candidatus* Xenohaliotis californiensis' (Gardner *et al.*, 1995; Friedman *et al.*, 1997; Friedman *et al.*, 2000; Friedman *et al.*, 2002). The pathogen is described as a gram-negative, pleomorphic, obligatorily intracellular species that occurs in membrane-bound vacuoles in the cytoplasm of epithelial cells of the gastrointestinal tract. Symptomatic infected animals are unable to transfer digested food materials from the gut lumen into the epithelial cells and beyond, resulting in malnutrition, dramatic loss of tissue mass, and eventual death. Physiological manifestations of withering syndrome include reduced food intake and oxygen consumption, and increased ammonia excretion (Kismohandaka *et al.*, 1993). The same pathogen is known to cause symptoms of withering syndrome in red abalone, and mortality rate is positively associated with water temperature in red abalone as it is in black abalone (Moore *et al.*, 2000a, b; Vilchis *et al.*, 2005). Andree *et al.* (2000) have developed a polymerase chain reaction assay for rapid DNA-based detection of '*Candidatus* X. californiensis', allowing detection of infections prior to onset of clinical symptoms in both black and red abalone. Moore *et al.* (2001) have developed a histological method for rapid quantification of the intensity of infections by '*Candidatus* X. californiensis'.

In wild animals symptomatic for withering syndrome, weakness resulting from the disease may cause the individual to lose the typically secure grip on the rocky substratum in response to wave impacts, allowing attack by predators or scavengers before the individual succumbs to the disease itself. Transfer of pathogens from animal to animal is fecal to oral on a local scale, and is therefore likely facilitated by aggregation of abalone in natural habitats. Transmission pathways on large spatial scales are entirely unknown at present. The pathogen for withering syndrome is now reported to be endemic to all the coastal marine waters of central (Friedman and Finley, 2003) and southern California (Moore *et al.*, 2002) south of San Francisco. Information from Isla de Cedros and Islas San Benito, Baja California, Mexico, on pink (known as "yellow" in Mexico) and green ("blue" in Mexico) abalone indicated the presence of abalone symptomatic for withering syndrome, and the presence of '*Candidatus* Xenohaliotis californiensis' in tissue samples, for both species (Tinajero *et al.*, 2002). Recent data indicate the presence of '*Candidatus* X. californiensis' and abalone (*Haliotis tuberculata*) symptomatic for withering syndrome at a number of locations in the coastal marine waters of western Europe, including both farmed and wild animals (Balseiro *et al.*, 2006).

Mortality rates caused by withering syndrome appear to be sensitive to fluctuations in local sea surface temperatures (Friedman *et al.*, 1997; Raimondi *et al.*, 2002; Harley and Rogers-Bennett, 2004; Vilchis *et al.*, 2005). There is evidence that, in the short term, population-scale mortality rates vary in space and time from near zero to high proportions of local populations. The available evidence suggests that mortality rates driven by withering syndrome are highest during periods following elevations in sea surface temperature (e.g., Raimondi *et al.*, 2002). Over the long term, all available evidence indicates substantial increases in mortality rates, and consequent reductions in densities, in populations of black abalone afflicted by withering syndrome (e.g., Tissot, 2007).

In the vast majority of cases where long-term monitoring data are available, the appearance of animals symptomatic for withering syndrome in a population lead inevitably to rapid and dramatic declines in population size, most often in excess of 90% (Tissot, 2007). The pattern has been documented for black abalone populations throughout the range in California. Reports indicate similar trends for black abalone populations in Mexico. As noted previously, the exceptions are at one location each on Santa Cruz and San Nicolas islands. At Santa Cruz Island, a recruitment event at Willows Anchorage in 2004 produced an increase in local densities that persisted at least until this writing (January 2008). There were no adult abalone present in the Willows Anchorage site prior to the 2004 recruitment. At San Nicolas Island, black abalone numbers at site 8 (as described by VanBlaricom, 1993) have increased since reaching a low point in 2001 following a mass mortality associated with presence of withering syndrome, except for a small decline between surveys in 2006 and 2007, with recruitment observed each year. The pattern at site 8 can be plausibly interpreted as a possible result of genetically-based disease resistance on a local scale. These observations are exceptions that suggest potential for localized resilience and recovery in populations reduced dramatically by withering syndrome. However, Tissot's (2007) synopsis of negative impacts of withering syndrome, in multiple locations across the entire range of the species, and with evidence of increasing geographic scope of impact, indicates that exceptional cases are rare. Given that black abalone apparently have short larval durations and limited larval dispersal capability in space, the potential for exceptional locations to facilitate a large-scale reversal of trends identified by Tissot seems quite small. The preponderance of evidence indicates that withering syndrome continues to damage the size and sustainability of black abalone populations on a large scale, with little plausible basis for any predictions of reversal except in localized, spatially isolated cases.

3.5.3 Mortalities associated with foraging sea otters

Sea otters (*Enhydra lutris* [Linnaeus, 1758]) are known to feed preferentially on red abalone in California (Lowry and Pearse, 1973; Estes *et al.*, 1981; Hines and Pearse, 1982; Ostfeld, 1982; Estes and VanBlaricom, 1985). Through the application of innovative behavioral attributes and the use of stones as hammers during foraging, sea otters impose significant constraints on red abalone abundances, size frequencies, and microhabitat distributions (Lowry and Pearse, 1973; Cooper *et al.*, 1977; Wendell, 1994; Fanshawe *et al.*, 2003). The reduction of abundance and modification of size distributions of red abalone by sea otters effectively eliminate the possibility of sustainable harvests of red abalone by people in locations where sea otters occur.

Sea otters once ranged throughout the North Pacific Rim from southern Baja California to northern Japan, but were reduced to near extinction by excessive hunting for the fur trade during the eighteenth, nineteenth, and early twentieth centuries. A small sea otter population survived near Big Sur, California, when sea otter hunting was terminated by international treaty in 1911. The virtual removal of sea otters from coastal habitats during the fur trade era facilitated growth of red abalone populations, and possibly other abalone populations as well (Estes and VanBlaricom, 1985). Patterns described above have been recognized largely as a consequence of the return of sea otters to former habitats in California following the imposition of protected status. Sea otters presently occur from San Mateo County to Santa Barbara County on the California mainland, and at San Nicolas Island off southern California (see below). Thus, most previously occupied sea otter habitat in southern California currently lacks sea otters. The California sea otter population currently numbers between 2,500 and 3,000 individuals and is listed as "threatened" pursuant to the ESA, and as "depleted" pursuant to the Marine Mammal Protection Act of 1972 as amended (16 U.S.C. 1361 *et seq*.).

Despite the well-documented effects of sea otter predation on red abalone, there are few data available to evaluate relationships of sea otters with other species of abalone in California. Given that pink and green abalone overlap substantially in habitat use, size distributions, and ecological attributes with red abalone, it is plausible that sea otters may affect populations of these species much as they do red abalone, if sea otters become more broadly established in southern California coastal waters. Relationships of sea otters with white and black abalone are less apparent because of lesser overlap in habitat characteristics, especially water depth, with those of red abalone. Sea otters are known to feed on black abalone, but the quantitative ecological strength of the interaction has not been directly investigated and remains poorly known.

Because black abalone are primarily found in intertidal habitats, use of the intertidal zone as foraging habitat by sea otters warrants consideration. Foraging by sea otters is known to influence abundance and size distribution of intertidal mussels in Prince William Sound, Alaska (VanBlaricom, 1987), and to produce episodic localized clearings in the cover of rocky intertidal mussel populations along the coast of central California (VanBlaricom, 1988). However, the use of intertidal habitats as foraging locations by sea otters is difficult to predict. Sea otters are known to vary at the individual level with regard to foraging behavior and prey preference (Lyons, 1991; Estes *et al.*, 2003). VanBlaricom (1988) presented evidence that use of exposed rocky intertidal habitats on the central California coast by foraging sea otters varies substantially over time because individual sea otters with differing foraging habits may shift among coastal locations. Thus, the use of a particular intertidal prey species in a particular location by foraging sea otters depends on the presence nearby of individual sea otters with a preference for the subject prey species. From 1978-1984 at Pt. Piedras Blancas, California, the use of intertidal habitats and prey by sea otters in given locations varied from intensive in some years to entirely absent in others, in association with apparent movement by sea otters with varying individual foraging preferences (VanBlaricom, 1988).

Sea otters were relocated to San Nicolas Island beginning in 1987 (e.g., Hatfield, 2005) as part of a federal ESA Recovery Plan in effect at that time. Numbers of sea otters remaining at the Island were initially quite low because of unexpected dispersal of released otters away from the Island. Despite the fact that sea otters were occasionally seen feeding on black abalone at the Island (VanBlaricom, unpublished observations), a sea otter signature could not be seen in the time series of density data for black abalone. Since 1992, the ability to detect a sea otter effect at San Nicolas Island has been preempted by the confounding effects of sharp declines in black abalone abundances caused by disease. Presently there are about forty sea otters at San Nicolas Island, with evidence of recent growth in numbers (Hatfield, 2005). Continued growth of the sea otter population at the Island, coupled with continued monitoring of sea otter foraging and black abalone populations, may lead to a better understanding of interactions between sea otters and black abalone.

4.0 Existing Regulatory Mechanisms

4.1 Federal

4.1.1 National Marine Fisheries Service

Black abalone was added to NMFS' Candidate Species list on 23 June 1999 (64 FR 33466). The NMFS' Candidate Species List was revised and redefined and the NMFS' Species of Concern List was created on 15 April 2004 (69 FR 19975). Black abalone was transferred to the Species of Concern List at that time. Species of Concern are those species about which NMFS has some concerns regarding status and threats, but for which insufficient information is available to indicate a need to list the species under the ESA. On 17 October 2006 (71 FR 61021), NMFS formally announced initiation of a black abalone status review and at that time the species became a Candidate Species. Shortly thereafter, on 27 December 2006, NMFS received a petition from the CBD requesting that the agency list black abalone as either an endangered or threatened species under the ESA and designate critical habitat for the species concurrently with any listing determination. Candidate Species are those petitioned species that are actively being considered for listing as endangered or threatened under the ESA, as well as those species for which NMFS has initiated an ESA status review that it has announced in the Federal Register. Designation as a "Candidate Species" or a "Species of Concern" carries no procedural or substantive protections under the ESA. Thus, no ESA-mandated federal measures that provide protection for black abalone are currently in place.

4.1.2 National Marine Sanctuaries

Three coastal national marine sanctuaries in California contain intertidal habitat suitable for black abalone: Channel Islands National Marine Sanctuary (CINMS), Monterey Bay National Marine Sanctuary (MBNMS), and Gulf of the Farallones National Marine Sanctuary (GFNMS) (Figure 6). These sanctuary sites, administered by the National Oceanic and Atmospheric Administration, are protected by federal regulations pursuant to the National Marine Sanctuaries Act of 1972 as amended (16 U.S.C. 1431 *et seq.*). The regulations, which are similar at all three sites, provide protection against some of the threats to black abalone. At all three sanctuaries, the inshore boundary extends to the mean high water line, thus encompassing intertidal habitat.

Direct disturbance to or development of the intertidal habitat of black abalone is regulated at all three national marine sanctuaries by way of a prohibition on the alteration of, construction upon, drilling into, or dredging of the seabed (including the intertidal zone), with exceptions for anchoring, installing navigation aids, special dredge disposal sites (MBNMS only), harbor-related maintenance, and with bottom tending fishing gear in areas not otherwise restricted.

Water quality impacts to black abalone habitat are regulated by strict discharge regulations at all three national marine sanctuaries. Essentially, regulations provide that no discharge or deposit of pollutants is allowed within these sanctuaries, except for effluents required for normal boating operations (e.g., vessel cooling waters, effluents from marine sanitation devices, fish wastes and bait).

Although these national marine sanctuaries do not regulate the take of black abalone, networks of marine reserves and marine conservation areas have been established by the CDFG within the CINMS and along portions of the MBNMS. Within these areas, especially within CINMS where the protected areas have been in place since 2003 and are within the Channel Islands National Park, multi-agency patrols provide elevated levels of enforcement presence that increase protection against poaching of black abalone.

Full texts of the current CINMS, MBNMS and GFNMS regulations discussed above can be found at 15 Code of Federal Regulations (CFR), Parts 922.71, 922.132, and 922.91, respectively. However, all of these sanctuary sites are currently undergoing management plan review processes, which include reviews of and updates to regulations. Although the regulations are expected to be modified, with finalization expected in 2008, the level of protection provided to black abalone is not expected to decrease from that described above, and possibly may increase should proposed prohibitions be adopted for the release of introduced species, and should stricter regulations be adopted regarding large vessel discharges[1].

4.2 State/Local

The CDFG Abalone Recovery and Management Plan (ARMP) provides a cohesive framework for the recovery of depleted abalone populations in central and southern California, and for the management of the northern California fishery and future fisheries. All of California's abalone species are included in this plan: red, green, pink, white, pinto (*Haliotis kamtschatkana* Jonas, 1845, including *H.k. assimilis*), black, and flat abalone.

The depleted condition of abalone resources prompted the California Fish and Game Commission to eventually close all abalone fisheries south of San Francisco by 1997, beginning with the black abalone fishery in 1993. The southern abalone fisheries were closed indefinitely with the passage of the Thompson bill (AB 663) in 1997. This bill created a moratorium on taking, possessing, or landing abalone for commercial or

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[1] For more information on proposed regulatory changes, see the management plan sections of these web sites: channelislands.noaa.gov, montereybay.noaa.gov, and farallones.noaa.gov.

recreational purposes in ocean waters south of San Francisco, including all offshore islands.

The Thompson bill also mandated the creation of an Abalone Recovery and Management Plan (ARMP) which was finalized in December 2005. The bill further required the Fish and Game Commission to undertake abalone management in a manner consistent with the ARMP. Passage of the Thompson bill and the resultant passage in the California State Fish and Game Code (FGC §5522[a]) specifically calls for the following items in an ARMP:

- **Scientific Background:** An explanation of the current scientific knowledge of the biology, habitat requirements, and threats to abalone
- **Interim and Long-term Goals**: A summary of recovery goals, including alternative conservation and management goals and activities. The Department will report why it prefers the recommended activities
- **Alternatives for Allocation**: Alternatives for allocating harvest between recreational and commercial abalone harvesters
- **Costs**: An estimate of time and costs required for meeting interim and long-term recovery goals for each species
- **Time Frame**: An estimate of the time necessary to meet interim recovery goals, and a description of triggers for review and amendment of strategies
- **Evaluation Criteria**: A description of objective, measurable criteria by which to determine whether the goals and objectives of the recovery strategy are being met.

Recovery of at-risk abalone species and management of abalone fisheries are separate but continuous and complementary processes in the ARMP. The recovery portion of the plan addresses all abalone species that are subject to the fishing moratorium. The management portion of the plan applies to populations considered sustainable and fishable, such as the current northern California red abalone fishery. Abalone in California vary in status from populations bordering on extinction (white abalone) to a sustainable population with a harvestable margin of animals that is still being fished (northern California red abalone). The ultimate goal of recovery is to move species from a perilous condition to a sustainable one with a harvestable margin of abalone available for fishing. The ultimate goal of management is to maintain sustainable fisheries under a long-term management plan that can be adapted quickly to respond to environmental or population changes.

4.3 International

The IUCN publishes a Red List of species that are at high risk of extinction and, when data are sufficient, categorizes species as either Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, or of Least Concern (IUCN 2001). There are five quantitative IUCN criteria for placing a species in the relevant IUCN category and meeting any one criterion is justification for a threat level listing (IUCN, 2001, 2006). The five criteria are:

A. Declining population (past, present and/or projected);
B. Geographic range size and fragmentation, decline, or fluctuations;
C. Small population size and fragmentation, decline, or fluctuations;
D. Very small population or very restricted distribution;
E. Quantitative analysis of extinction risk (e.g., Population Viability Analysis).

In 2003 the IUCN, based on an assessment by Smith *et al*. (2003), placed black abalone on the Red List as Critically Endangered under criterion A4e. Under criterion A4, a species may be classified as Critically Endangered, Endangered, or Vulnerable when its population size, measured over the longer of 10 years or three generations**,** has declined ≥80%, ≥50%, or ≥30%, respectively, due to an "observed, estimated, inferred, projected or suspected population reduction (up to a maximum of 100 years) where the time period must include both the past and the future, and where the causes of reduction may not have ceased or may not be understood or may not be reversible, based on any of the following:

(a) direct observation;
(b) an index of abundance appropriate to the taxon;
(c) a decline in area of occupancy, extent of occurrence and/or quality of habitat;
(d) actual or potential levels of exploitation;
(e) the effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites" (IUCN, 2006, p. 10).

Smith *et al*. (2003, web document with unnumbered pages) stated that "If no action is taken, it is estimated that *H. cracherodii* will decline by at least 80% over a period of three generations (from approximately 1975 to 2015), extending into the past and the future, and consequently, the species qualifies for Critically Endangered under criterion A4." The IUCN population reduction criteria call for measuring decline "over the longer of 10 years or 3 generations" (IUCN, 2006, p. 10). A simple definition of generation time is the average age of the total number of parents (spawners) in the population. Smith *et al*. (2003, web document with unnumbered pages) stated that:

> "Generation time [in black abalone] is not easy to determine. Individuals do not display the same growth rate and older individuals may cease to grow altogether (B. Tissot, Washington [State] University, pers. comm.). Reproductive maturity is reached between three and seven years (when they are approximately 130-150 mm in length), but life expectancy ranges from 25 to 75 years. Taking an average of these provides only a very rough estimate for the average age of parents, especially since the relationship between age and fecundity is unknown. Nonetheless, generation time is estimated to be between 14 and 41 years, thus a minimum three generation period would be 42 years (Smith et al. 2001 [unpublished])."

Smith *et al*. (2003) listed major threats to black abalone, as described in the IUCN threats format, as:

1) habitat loss/degradation - infrastructure development - human settlement (ongoing);
2) habitat loss/degradation - infrastructure development - transport (water) (ongoing);
3) harvesting (hunting/gathering) - food (ongoing);
4) harvesting (hunting/gathering) - materials (ongoing);
5) pollution (affecting habitat and/or species) - water pollution - domestic (ongoing);
6) pollution (affecting habitat and/or species) - water pollution - commercial/industrial (ongoing); and
7) changes in native species dynamics - pathogens/parasites (ongoing).

More specifically, Smith *et al*. (2003) declared that the main threat to black abalone is withering syndrome, followed by the large human population inhabiting southern California, coastal development, large ocean discharges of municipal and industrial wastes, and past commercial and recreational fishing.

5.0 Approaches to Evaluating Risk of Extinction

5.1 The "Extinction Risk" Question

After the composition of an ESA species is determined, the next question to address is, "Is the 'species' threatened or endangered?" As stated in Section 1.2.2, the ESA defines the term "endangered species" as "any species which is in danger of extinction throughout all or a significant portion of its range." The term "threatened species" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." Neither NMFS nor the USFWS have developed any formal policy guidance about how to interpret the definitions of threatened or endangered species in the ESA.

A variety of information is considered in evaluating the level of risk faced by a species. According to the ESA, the determination of whether a species is threatened or endangered should be made on the basis of the best scientific information available regarding its current status, after taking into consideration conservation measures that are proposed or are in place. During the Status Review process, the team does not evaluate likely or possible effects of conservation measures except to the extent they are reflected in metrics of population or species viability; these measures are taken into account in a separate process by the NMFS regional offices prior to making any listing determinations. Therefore, the SRT does not make recommendations as to whether the species should be listed as threatened or endangered, because that determination requires evaluation of factors not considered by the team. Rather, the BRT draws scientific conclusions about the risk of extinction faced by the species under the assumption that present conditions will continue into the future (recognizing that existing trends in factors affecting populations and natural demographic and environmental variability are inherent features of "present conditions").

5.2 Factors for Decline

According to Section 4 of the ESA, the Secretary (of Commerce or the Interior) determines whether a species is threatened or endangered as a result of any (or a combination) of the following factors: destruction or modification of habitat, overutilization, disease or predation, inadequacy of existing regulatory mechanisms, or other natural or man-made factors. Collectively, these are often referred to as "factors for decline."

In Section 5.4.2 of this Status Review, we examine these five factors for their historic, current, and/or potential impact on black abalone. Current and potential threats, along with current species distribution and abundance, help determine the species' present vulnerability to extinction. We include information regarding historic threats to assist in our interpretation of population trends. The relationship between historic threats and population trends also provides insights that may help project future population changes in response to current and potential threats.

5.3 Available Data

A long-term trends analysis for black abalone was conducted by Tissot (2007). These data and the corresponding analysis (Tissot, 2007) were used by the SRT to evaluate black abalone risk of extinction. A summary of these fishery-dependent and fishery-independent data sources follows.

California fishery data were obtained from the CDFG for 1940-1993. Data included the total annual landed weight of black abalone per CDFG fishing block region, defined by 10 minute (latitude and longitude) geographic grids. Because catch data prior to 1969 were low in value (<0.5 mt) and sporadic, these data were not analyzed.

Fishery-independent data were obtained from six studies, which included all major long-term monitoring studies in California (Table 2) and included surveys that occurred from 1975-2006 at 36 study sites (Figure 7). Data were collected using a variety of techniques, including randomly allocated plots, fixed quadrats along transects, variably shaped plots, and band transects (Table 3). Study locations were chosen based either on the presence of abalone aggregations (studies by VanBlaricom, Tissot, Raimondi, and the National Park Service) or by selecting a location within appropriate intertidal habitat (studies by Miller and Tenera Environmental). Data from each study were selected for the longest continuous monitoring efforts in areas where black abalone were normally present and not disturbed by major human impacts (Table 4). This process excluded newer established sites in the Channel Islands and some sites adjacent to the thermal discharge of the Diablo Canyon Power Plant in Central California.

The SRT also reviewed available data from three sources of population data for black abalone in the vicinity of the Monterey Peninsula. These data, however, were not incorporated into the long-terms trends analysis either because they were not long-term studies (Kimura and Steinbeck, 2003; Micheli *et al.*, in review) or they were not available in a form amenable to the Tissot (2007) analysis (J.S. Pearse, unpublished data). These data sources are summarized in Table 5.

Kimura and Steinbeck (2003) evaluated the effects of visitor use on rocky intertidal habitats at Pt. Piños (see also section 3.4.5.1 of this Status Review). The black abalone component of the project involved collection of size frequency data and an assessment of the presence of animals showing symptoms of withering syndrome. Densities of black abalone were not estimated because of variable plot size and irregular substratum configuration. Size frequencies for abalone indicated that most animals were relatively small. In high use sites at Pt. Piños (n=8), the overall mean size was 57 mm, with a maximum length of 147 mm (n=129 abalone). In the lesser use sites near Pt. Piños (n=9), the overall mean size was 58 mm and the maximum 129 mm (n=136 abalone). No abalone in either site category were found to have symptoms of withering syndrome. It was concluded that high visitation rates at Pt. Piños were not causing elevated black abalone mortality rates, as compared to mortality rates at the lesser use reference sites.

Micheli *et al*. (in review) evaluated the persistence and possible recovery of two abalone species, black and red, in response to the presence of no-take marine protected areas. Black abalone studies were conducted at eight rocky intertidal sites along a 35 km segment of the coastline of Monterey County, California (see also section 3.4.5.1 of this Status Review). Four of the sites were either no-take marine protected areas that varied by time since establishment (5-71 years) or *de facto* protected areas (i.e., areas with limited access due to adjacent private property or precipitous local geomorphologies). Four sites were open-access sites. The study also assessed age distributions using counts of shell annuli, in order to assess recruitment frequency in black abalone. Finally, the study provided data on patterns of occurrence and aggregation by black abalone in preferred crevice microhabitats.

Densities of black abalone were highly variable among sites, and there was no statistically significant difference in mean density among sites. The overall mean was 0.36 m^{-2} (range 0 - 1.98 m^{-2} among individual swath counts). Size frequency distributions of black abalone varied significantly among sites. Black abalone larger than 80 mm were more abundant in no take areas than in open access areas.

Shell annuli data indicate that black abalone had experienced successful recruitments in each of the ten years preceding shell collection. Estimated ages ranged from 2 to 19 years for shells analyzed for annulus count. Black abalone were found to be non-randomly distributed in space, with statistically significant aggregation the common pattern. Aggregations of three or more abalone were found more often than expected in crevices, based on Poisson distributional models. Crevices with narrow openings contained black abalone more often than would be expected for a randomly-distributed spatial pattern. Of black abalone encountered in surveys, 97% occurred in crevice microhabitats, primarily in crevices with narrow openings. The majority of black abalone located in surveys were found close to other black abalone.

Micheli *et al*. (in review) concluded that black abalone populations are surviving along the Monterey County shoreline because of persistently high recruitment rates, despite relatively low spatial densities and relatively high mortality rates. It is suggested that marine protected areas are a substantial benefit to the persistence of black abalone by limiting harvest and poaching, thereby maintaining overall mortality rates at levels necessary for population sustainability. The authors note that sustainability of black abalone populations is occurring in the absence of effects of withering syndrome and other diseases.

Dr. John S. Pearse, at the University of California, Santa Cruz (UCSC), conducted quarterly surveys of intertidal biota from autumn 1971 through summer 2002 at 20 rocky intertidal sites on the shorelines of San Mateo, Santa Cruz, and Monterey counties, California. The survey data have not been analyzed and are not published in a peer-reviewed outlet, but a portion is available at: http://www.mbnms-simon.org/sections/rockyShores/project_info.php?pid=100281&sec=rs. The data set includes two kinds of information. The “quantitative” portion provides counts of abalone in four permanent quadrats at each of the 20 sites. The “qualitative” portion provides three density characterizations (“rare”, “moderate”, and “abundant”) at each of three tidal levels (“low”, “middle”, and “high”).

Black abalone data in the quantitative portion of the Pearse data set are sparse. Abalone counts greater than zero were recorded only for two surveys in the data set, both at Davenport Landing in Santa Cruz County. Two abalone were recorded in spring 1983, and one in spring 1991.

Although the Pearse data set is a continuous time series from 1971 to 2002, only a small subset of the “qualitative” portion of the data are shown on the subject website. Data are available for two periods, 1971-1973, and 1996-1997. Information from the spring 1994 survey is also included. Black abalone data in the qualitative portion of the data set suggest the following general patterns: 1) most abalone were observed in the low or middle intertidal during the surveys; and 2) black abalone were most commonly seen at sites in the northern portion of the range of sites, including Pigeon Pt., Pt. Año Nuevo, Año Nuevo Cove, Scott Creek, and Davenport Landing.

5.4 Risk Assessment Methods

5.4.1 Trends in Abundance: Summary of Tissot (2007)

Tissot’s (2007) long-term trends analysis used the fishery-dependent and fishery independent data described above in section 5.3 and Tables 2, 3, and 4 of this Status Review. CDFG Fisheries data were analyzed from catches that occurred adjacent to the shore along the mainland or offshore islands and were grouped by decade and geographic region to illustrate patterns of change in fishery landings. Data from long-term fishery-independent monitoring studies were converted to density (m^{-2}) and analyzed across the time period of the study to detect trends in abundance. Each time series was divided into pre-withering syndrome and post-withering syndrome time periods by noting when marked changes in abundance occurred. The percent change in population density was calculated by comparing the mean density in all pre-withering syndrome years to the last 2-3 post-withering syndrome years using equation 1:

$$\textbf{Percent change} = ([D_{post\text{-}ws} - D_{pre\text{-}ws}] / D_{pre\text{-}ws}) \times 100 \qquad (1)$$

where D = density (m^{-2}).

The percent changes were examined geographically to detect patterns in changes in abundance. Several studies were also examined for the incidence of newly recruited abalone (≤ 20 mm in length) and the relationship between recruitment and adult density (Miller, Tissot, Tenera). The density of adults was noted when recruitment failure was observed.

5.4.1.1 Results: Fishery data

Commercial landings for black abalone began to increase rapidly in the early 1970s, peaking in 1973 and 1983, then declining until the fishery was closed in 1993 by CDFG (Figure 8; see also section 3.4.5.1 of this Status Review). The catch was historically greatest in the islands offshore of southern California, particularly San Miguel, San Clemente, and San Nicolas islands (Figure 9). During the 1970s the catch was centered in the northern California Channel Islands (San Miguel, Santa Rosa, and Santa Cruz islands) as well as San Clemente Island. In the 1980s this shifted to San Miguel, San Clemente, and San Nicolas islands. In the 1990s, landings came primarily from San Miguel and San Nicolas islands. The average annual catch declined from 290 mt in the 1970s, to 175 mt in the 1980s, and 14 mt in the 1990s (Figure 10).

Although there are few data available from black abalone populations in Mexico, existing studies suggest similar fishery declines to those in California. Overall, black abalone are a very small portion of the commercial fishery and account for about 1.2% of the catch in the Zone 1 Fishery Cooperatives which extend north of Punta Eugenia to the US border (Palleiro, cited in Hobday and Tegner, 2000). Based on the data published in Hobday and Tegner (2000), the catch of black abalone declined from a high of 28 mt in 1990, to <1 mt in 1998, an overall decline of >95% (Figure 11). Thus, patterns of decline in the black abalone harvests in Mexico were similar to trends observed in California during the same time period.

5.4.1.2 Results: Fishery-Independent data

Long-term monitoring has been done at sites from Año Nuevo Island to the U.S.-Mexico border, representing most of the geographic range of black abalone in California (Figure 1). Long-term monitoring data were compiled for 37 sites. Black abalone have not been seen at an additional 19 sites established in southern California in the 1990s (Tissot, 2007).

At Laguna Beach in Orange County, abalone were present at relatively constant low densities in 1983-1985, but went locally extinct on transects in 1986 (Figure 12). Data from the Palos Verdes Peninsula, Los Angeles County, showed declines in abundance beginning the year the surveys started in 1975 and continuing until the local extinction of abalone on transects in 1987 (Portuguese Bend), 1990 (Abalone Cove 2), and 1993 (Pt. Vicente). Small numbers of abalone (0.30 m^{-2}) persisted in 2006 at the Abalone Cove 1 site (Figure 13).

In the southern California Islands, major abalone declines occurred at Anacapa Island from 1985-1990, at Santa Rosa Island from 1986-1990, at Santa Barbara Island from 1987-1990, and at San Miguel Island from 1990-1993 (Figure 14; see also section 3.4.5.2 of this Status Review). In 1993, abalone went locally extinct at Santa Barbara Island, at Ford Point on Santa Rosa Island, and at Harbor Seal Arch on Anacapa Island. They went locally extinct in 1996 at Johnson's Lee on Santa Rosa Island; in 1998 at Cat Rock on Anacapa Island and at Fossil reef on Santa Rosa Island; and in 1999 at the NW Talcott site at Santa Rosa Island (Figure 14). Abalone persisted at low densities (0.08-0.10 m^{-2}) at Crook Point, Harris Point, and Otter Harbor on San Miguel Island.

At Santa Cruz Island, major declines occurred from 1987-1990 at Forney Cove and from 1987-1991 at Fraser Point (Figure 15). Abalone went locally extinct at two of three sites at Fraser Point in 1997 and at two of four sites at Forney Cove in 1999 and 2001. At San Nicolas Island, major declines in abundance occurred in 1992-1996 with abalone in 2006 at low densities varying from < 0.01-1.1 m^2 (Figure 16). In central California, the patterns of decline began in 1992 near Government Point, Santa Barbara County, and spread northward as far as Pt. Piedras Blancas, northern San Luis Obispo County, in 2003 (Figure 17; see also section 3.4.5.2 of this Status Review). Major declines occurred at Government Pt. in 1992-1993, at Boathouse from 1994-1998, at Stairs from 1995-1999, and at Purisima Point from 1997-1999. Abalone occurred at low densities (0.06-0.47 m^{-2}) at the Government Point, Boathouse, Stairs, and Purisima Point study sites (all in Santa Barbara County) in 2006.

At Diablo Canyon in San Luis Obispo County, trends in abundance were complex with several periods of fluctuation (Figure 18). At North Control site 1, abundance was relatively stable from 1976-1991, but declined from 1991 to 2006, falling to low densities (0.10 m^{-2}). At North Control site 2, declines occurred from 1977-1983, between 1987-1989, and from 1993-2004 until black abalone went locally extinct. At Field's Cove, declines occurred from 1980-1985 and from 1989-2000 when abalone went locally extinct. At the South Control site, abalone declined from 1978-2005 when they went locally extinct (Figure 18).

Declines of 99.9% occurred at Cayucos, San Luis Obispo County, from 1998-2005. Rancho Marino (San Luis Obispo County) and Pt. Piedras Blancas showed a moderate decline (~50%) in abundance from 2002-2006 and densities remain around 1.1-1.3 m^{-2} at these sites. All other sites in central California north of Pt. Piedras Blancas show no evidence of declines and were either stable or showed increases, some as high as 131% (Figure 19). At these sites abalone density varies from 3.8-10.3 m^{-2}. At Año Nuevo

Island in southern San Mateo County, which is not currently being monitored but is included for its historical baseline, abalone were relatively constant in abundance from 1987-1990 but showed a decline between 1990 and 1995 (Figure 20).

Overall, excluding the two sites that have not been monitored recently (Laguna Beach and Año Nuevo Island), black abalone have gone locally extinct at 13 of the 34 study sites (38%), have declined between 90-99% at an additional 13 (38%) study sites, and have declined between 47-67% at two sites (Figure 21). At six sites (18%), all north of Pt. Piedras Blancas in central California, there have been no declines in abundance and abalone have increased in abundance by an average of 56%. The current status of two of the 36 sites (Laguna Beach and Año Nuevo Island) is unknown. Thus, significant declines (>90%) have occurred at the majority (76%) of study sites, including all sites in southern California (Figure 21).

5.4.1.3 Results: Density and mortality patterns

The size distribution of abalone at many sites showed a pattern similar to that at Point Vicente near Long Beach in Los Angeles County (Figure 22). Initially, abalone were present in a range of sizes from 20 mm up to the legal minimum size (127 mm) for recreational harvest. A size distribution truncated near the legal minimum for harvest should be interpreted with caution, given observations that growth may be effectively determinant at between 120 and 130 mm in shell length (see section 3.4.4 of this Status Review). Peak size classes at Point Vicente occurred at the 40-60 mm size range. As populations declined in abundance, small abalone became less abundant, eventually disappearing altogether, with the population shifting to larger individuals, and eventually going locally extinct.

The relationship between adult density and recruitment failure was fairly consistent in three geographically separate studies. At Point Vicente, newly recruited abalone disappeared when adult density declined below 1.1 m^{-2} (Figure 23). At Forney Cove on Santa Cruz Island this threshold occurred at an adult density of 0.75 m^{-2} (Figure 24). At Diablo Canyon in central California (Field's Cove) it occurred at an adult density of 0.80 m^{-2} (Figure 25). Overall, abalone density was below the 0.75-1.1 m^{-2} threshold at all sites in southern California except at site 8 at San Nicolas Island and at all sites in central California south of Rancho Marino (near Cambria) (Figure 26). However, it should be noted that the reported densities include all abalone size classes. Thus, adult densities could be even lower at all sites. All sites north of Rancho Marino had densities greater than the threshold range, with the range of densities at 3.8-10.3 m^{-2} (Figure 26). Sections 3.3.3 and 3.4.3 of this Status Review provide further discussion of the importance of considering the scale at which density data is measured and the variance structure of density data when drawing conclusions about critical density thresholds for successful spawning and overall population viability.

Black abalone have experienced major declines in abundance as evidenced by declining trends and eventual closure of the commercial fishery and by major declines, local extinctions and low densities in the majority of long-term monitoring studies in California. Significantly, these declines have been particularly severe in the southern California Islands which have historically been major foci of the commercial fishery from 1970-1993, with high abalone densities (> 40 m^{-2}) as late as the mid-1980s. Although the geographic range of black abalone extends to northern California and perhaps southern Oregon (Geiger, 2000), the vast majority of abalone populations have historically occurred south of Monterey, particularly in the southern California Islands (Cox, 1960; Karpov *et al.*, 2000). Thus, black abalone have been severely reduced in more than half of its geographic range, and these areas have historically included >90% of the commercial fishery catch and the majority of the adult abalone stock in California.

Both the commercial fishery trends and long-term monitoring studies indicate that significant declines of black abalone stocks began in southern California in the mid-1980s. The first evidence of this decline is present at Palos Verdes in the late 1970s and early 1980s and at Laguna Beach in 1985-1986 (Tissot, 1988). However, in the case of Palos Verdes much of the decline may have been due to illegal poaching (Miller and Lawrenz-Miller, 1993). The first mass mortality associated with withering syndrome was observed at Santa Cruz Island in 1985 (Lafferty and Kuris 1993). By 1986, declining populations and associated observations of withering syndrome had spread to Anacapa, Santa Rosa, and Santa Barbara Islands, and then to San Miguel Island in 1989 (Tissot, 1991; Davis *et al.*, 1992; Tissot, 1995). By the early 1990s, withering syndrome had spread to San Nicolas Island (VanBlaricom *et al.*, 1993) and to Government Point, just south of Pt. Conception, on the mainland (Altstatt *et al.*, 1996). During the 1990s withering syndrome was observed at Boathouse and Stairs, near Pt. Arguello, in 1994-1997 and moved north to Purisima Point and Cayucos in 1998-1999 (Altstatt *et al.*, 1996; Raimondi *et al.*, 2002). Withering syndrome was also observed in central Baja California around Bahia Tortugas during El Niño events in the late 1980's and 1990s (Altstatt *et al.*, 1996; Pedro Sierra-Rodriquez, personal communication) and may be linked to declines in the fishery that occurred in the 1990s. Thus, the spread of withering syndrome is strongly associated with declines in abundance, with a pattern of increased northward expansion of the disease co-occurring with increasing coastal warming and El Niño events (Tissot, 1995; Altstatt *et al.*, 1996; Raimondi *et al.*, 2002) (Figure 27).

To our knowledge there are no data available on black abalone populations north of San Mateo County on the mainland coast of California. As a consequence, we lack information on the remaining stocks of black abalone not influenced by withering syndrome (Figure 1). The two northernmost sites have either not been studied since 1995 (Año Nuevo; Tissot, 1995) or have only been recently established in large, dispersed areas (Pigeon Point; Raimondi and Miner, personal communication). Establishment of long-term monitoring studies in northern California (e.g., in San Francisco County and north of the Golden Gate) would serve an important need in documenting northward progression of withering syndrome and mass mortality as far as the northern limit in the geographic range of black abalone.

Natural recovery of severely-reduced abalone populations can be a very slow process (e.g., Tegner, 1992). This is largely due to the low reproductive efficiency of widely dispersed adult populations, coupled with short larval dispersal distances. Abalone reproduce using synchronous broadcast fertilization (see section 3.3.4 of this Status Review). Sperm and eggs are mixed together in the water column, resulting in current-borne larvae which eventually settle to become juveniles (Cox, 1962). Therefore, overharvested populations, in addition to providing few reproductive adults, also experience reduced effectiveness of fertilization and eventual recruitment of larval abalone.

Moreover, many studies have shown that abalone larvae are generally not widely dispersed (see section 3.4.2 of this Status Review). For example, Prince et al. (1988) and McShane (1992) showed a strong correlation between the abundances of adult and newly recruited abalone at several sites in South Australia, which suggests that larvae are not dispersed very far from their point of origin. Similarly, Tegner (1992) showed that recruitment of juvenile green abalone was rare in Palos Verdes, California, where adult abalone were very uncommon even though abundant adult stocks were found less that 30 km away in the Channel Islands. Thus, although more abundant black abalone populations occur in central and perhaps northern California, decimated stocks in southern California are unlikely to receive significant recruitment from these distant populations (Hamm and Burton, 2000).

Studies indicate that a local adult "threshold" exists which influences local recruitment. Recovery will largely depend on the density of local brood stocks and whether this density is below the critical value necessary for successful recruitment (Tegner, 1992). Based on field experiments, Babcock and Keesing (1999) showed that recruitment failure occurred in *Haliotis laevigata* at adult densities of 0.15-0.20 m^{-2}. Based on empirical data from three long-term studies of black abalone in California, recruitment failure occurred below adult densities of 0.75-1.10 m^{-2} (see also section 3.4.3 of this Status Review). Given that the majority of populations south of Cayucos in central California are below this threshold, many significantly so, it seems unlikely that these populations will be able to recover naturally to their former abundances, at least in the near future. Moreover, given the continued decline of most populations and the continued northward expansion of withering syndrome with warming events (Raimondi *et al.*, 2002), it seems likely that black abalone populations will continue to decline on a large scale.

5.4.2 Assessment of Threats

The potential role that nine limiting factors have played in the decline of wild populations of black abalone in California and Mexico was examined by the SRT (Table 6). Within the limiting factor categories, specific threats were qualitatively ranked according to severity, geographic scope, level of certainty that black abalone is affected, and overall current and future (30 years) risk imposed by that threat. Team members then provided an overall ranking for each of the nine limiting factors. Also noted is the ESA factor for decline within which falls each limiting factor and threat (see Section 5.2 of this Status Review).

The terms used in Table 6 are defined as follows:

- **Factors for Decline =** according to Section 4 of the ESA, NMFS determines whether a species is threatened or endangered as a result of any (or a combination) of the following five factors for decline: destruction, modification or curtailment of habitat; overutilization; disease or predation; inadequacy of existing regulatory mechanisms; or other natural or man-made factors.
- **Limiting Factors** = the specific condition that causes stress to the organisms (e.g., elevated temperature or sediment runoff).
- **Threats** = natural or anthropogenic processes that create stressful conditions for organisms (e.g., climate change or coastal development).
- **Key Ecological Attributes Affected** = response of the organisms to the stressor, usually in the form of altered physiological processes (e.g., reduced reproductive potential or growth) or mortality.
- **Life Stage Affected** = the life stage (i.e. adult, juvenile, larval) of black abalone directly or indirectly affected by a threat.
- **Historic Threats** = threats that occurred in the past and may or may not be occurring presently.
- **Current Threats** = threats that are occurring now.
- **Future Threats** = threats that are likely to affect black abalone over the next 30 years (duration chosen as a reasonable approximation of average black abalone life span, and as a reasonable horizon for projecting current conditions into the future).
- **Severity** = the level of damage to the species that can reasonably be expected within 30 years under the current circumstances (i.e., given the continuation of the existing management/conservation situation). Specific rankings for this category are defined as follows:
    - **Very High:** The threat is *likely to destroy or eliminate* the populations over some portion of the of the species' range.
    - **High:** The threat is *likely to seriously degrade* populations over some portion of the species' range.
    - **Medium:** The threat is *likely to moderately degrade* the population over some portion of the species' range.
    - **Low:** The threat is *likely to only slightly impair* the population over some portion of the species' range.
- **Geographic Scope** = the geographic scope of impact on the species that can reasonably be expected within 30 years under the current circumstances (i.e. given the continuation of the existing situation). Specific rankings for this category are defined as follows:
    - **Very High:** The threat is *likely to be very widespread or pervasive* in its scope and affect the species *throughout its entire* range.
    - **High:** The threat is likely to be widespread in its scope and affect the species at *many locations within its range*.
    - **Medium:** The threat is *likely to be localized* in its scope and affect the species at *some locations within its range*.

    - **Low:** The threat is *likely to be very localized* in its scope and affect the species in a *limited portion of its range*.
- **Level of Certainty That Species Is Affected** = the level of certainty that the threat will affect the species with the severity and geographic scope ascribed in the next 30 years. Specific rankings for this category are defined as follows:
    - **High:** There is *definitive* published and unpublished data to support the conclusion that this threat is likely to affect the species with the severity and geographic scope ascribed (please specific references).
    - **Medium:** There is *some* published and unpublished data to support the conclusion that this threat is likely to affect the species with the severity and geographic scope ascribed (please provide specific references).
    - **Low:** There is *little* published and unpublished data to support the conclusion that this threat is likely to affect the species with the severity and geographic scope ascribed.
- **Overall Threat Level Currently and Into the Future (over the next 30 years)** = the current and future risk that this threat will contribute to the decline of the species over the next 30 years. Specific rankings for this category are defined as follows:
    - **High:** This threat is likely to *destroy, eliminate, or seriously degrade* black abalone populations at *many locations within the species' range* and there is *definitive* published data to suggest that the threat will affect the species.
    - **Medium:** This threat is likely to *moderately degrade* black abalone populations at *some locations within the species' range* and there is *some* published data to suggest that the threat will affect the species.
    - **Low:** This threat is likely to *only slightly impair* black abalone populations in a *limited portion of the species' range* and there is *little* published data to suggest that the threat will affect the species.
- **Overall Ranking of Limiting Factor** = the current and future risk that this limiting factor will contribute to the decline of the species over the next 30 years. Specific rankings for this category are defined as follows:
    - **High:** This limiting factor encompasses *a high number (>65%)* of threats that are likely to contribute to the decline of black abalone populations at many locations within the species' range.
    - **Medium:** This limiting factor encompasses *an intermediate number (35-65%)* of threats that are likely to contribute to the decline of black abalone populations at many locations within the species' range.
    - **Low:** This limiting factor encompasses *a low number (< 35%)* of threats that are likely to contribute to the decline of black abalone populations at many locations within the species' range.

The factors that are believed to have contributed to the decline of black abalone are: (1) the present or threatened destruction, modification or curtailment of its habitat or range (i.e., suboptimal water temperatures associated with effluents, El Niño-Southern Oscillation events, and global climate change, and, to a lesser extent, substrate destruction and reduced food quality and/or quantity); (2) overutilization (i.e., poaching and historical overfishing); (3) disease or predation (i.e., withering syndrome and predation); and (4) other natural and manmade factors (i.e., environmental pollutants and toxins).

Most of the threats that result in substrate destruction, such as coastal development, recreational access, cable repairs, nearshore military operations and benthic community shifts, occur infrequently, have a narrow geographic scope, or have uncertain or indirect effects on black abalone. Some exceptions may exist in the cases of sedimentation and sea level rise in that these threats have the potential to produce more widespread impacts, but the certainty that these factors will affect black abalone are low. For example, sea level rise may result in loss of suitable habitat in a preferred depth range because of increased erosion, turbidity and siltation, but we currently lack information to determine whether these habitat changes will be important factors for further decline.

Suboptimal water temperatures are likely to have contributed to the decline of black abalone and pose a serious threat to the ability of the species to persist because elevated water temperatures are correlated with accelerated rates of withering syndrome transmission and disease-induced mortality. Water temperatures can become elevated because of anthropogenic sources of thermal effluent and long-and short-term climate change (e.g., global climate change and El Niño – Southern Oscillation). For example, discharge from the Diablo Canyon nuclear power plant in San Luis Obispo County, California and recent El Niño – Southern Oscillation oceanographic events in the Pacific Ocean have produced short-term periods of ocean warming and are associated with increased rates of mortality due to withering syndrome over relatively small spatial scales. Although there is no explicitly documented causal link between the existence of withering syndrome and global climate change, patterns observed over the past three decades suggest that progression of ocean warming associated with large-scale climate change may facilitate further and more prolonged vulnerability of black abalone to effects of withering syndrome.

Throughout most of the species' range, local densities are below the critical threshold density required for successful spawning and recruitment. This predicament has occurred because of mass mortalities due to withering syndrome and overutilization for commercial and recreational purposes (i.e. prior to the fishery closure in 1993). Data from abalone fisheries in California and Baja California, Mexico indicate a decline in landings of at least 93 percent during the 1990s. These reductions, however, may not be indicative of declines due only to fishing activities because mass mortalities due to withering syndrome had begun in many locations at approximately the same time. Nonetheless, Rogers-Bennett et al. (2002) estimate that 3.5 million black abalone were taken during commercial and recreational abalone fishing and these removals likely contributed to the decline of local densities. This threat no longer exists in California because the black abalone fisheries were closed in 1993. The limited information we have from Mexico makes it difficult to ascertain the relative importance of fishing to overall species decline.

We conclude that the disease known as withering syndrome has been and continues to be the primary threat contributing to the decline of black abalone. The disease has caused mass mortality and near extirpation of populations throughout most of the species' range and the disease continues to spread to populations in Monterey County and to the north. The rate at which the disease is spreading northward will likely be exacerbated by suboptimal (i.e. warmer) water temperatures that may result due to a variety of factors.

Abalone face non-anthropogenic predatory pressure from a number of consumer species such as gastropods, octopuses, lobsters, sea stars, fishes and sea otters (Ault 1985; Estes and VanBlaricom, 1985; Shepherd and Breen 1992). Black abalone have been exposed to varying predation pressure through time and this pressure is likely to continue. However, in the past black abalone populations were much more robust and able to absorb losses due to predation without compromising viability. Now that the few remaining populations are smaller, more isolated, and still declining throughout the range, predation may pose risk to the future survival of the species. In addition, non-anthropogenic predation could limit the effectiveness of future recovery efforts by interacting with other limiting factors.

There is evidence suggesting that aquaculture operations have provided a pathway for the spread of withering syndrome and unless the industry is carefully regulated in the future, may continue to do so. Past State and federal regulations were not adequate to prevent the spread of the disease within and outside the USA through importation of infected animals from one aquaculture facility to another and outplanting of infected animals from aquaculture facilities to the wild. It is through the latter pathway that the etiological agent of withering syndrome was introduced to two healthy populations of black abalone north of San Francisco (Friedman and Finley, 2003). While spread of the disease outside the State does not threaten the continued existence of black abalone per se, suspected within-State transmission of abalone rickettsia to two populations north of San Francisco has put those populations at higher risk of extinction. Recent State regulations to carefully monitor the health of abalone at aquaculture facilities and control the importation/exportation of abalone between facilities will likely reduce the threat that the aquaculture industry poses in the future. Currently, the State monitors aquaculture facilities for introduced organisms and disease on a regular basis. There is also a restriction on out-planting abalone from facilities which have not met certification standards. If new State regulations to carefully monitor aquaculture facilities are effective, the future threat that they pose to black abalone will be limited. In fact, aquaculture may emerge as being an important, and possibly the only effective recovery tool for restoring black abalone populations through captive propagation and enhancement efforts.

Poaching has been a source of mortality for black abalone throughout their range since the establishment of harvesting regulations by the State of California (see section 3.5.1 Competitive interactions and anthropogenic mortality above for further discussion). The problem of poaching clearly persists and there is no evidence that existing regulatory mechanisms have effectively reduced the risks posed by illegal take. Inadequate regulatory mechanisms are likely to have contributed to the decline of black abalone and pose a serious threat to the ability of the species to recover.

Environmental pollutants and toxins are likely present in areas where black abalone have occurred and still do occur, but evidence suggesting causal and/or indirect negative effects on black abalone due to exposure to pollutants or toxins is lacking. There is one instance of abalone mortality associated with a pollution event, described by Martin et al. (1977). Toxic levels of copper in the cooling water effluent of the Diablo Canyon nuclear power plant were associated with abalone mortalities in a nearshore cove that received significant effluent flows. Growth and reproduction of black abalone were reported to have been impaired on the Palos Verdes Peninsula (Los Angeles County, California) in the late 1950s and early 1960s, in association with apparent combined effects of a significant El Niño event and poor water quality resulting from large-volume domestic sewage discharge by Los Angeles County (Leighton, 1959; Cox, 1962; Young, 1964; Miller and Lawrenz-Miller, 1993). There is ongoing concern that accidentally spilled oil from offshore drilling platforms or various types of commercial vessels could occur near shore in California and could affect a significant proportion of black abalone habitat, however, at this time we are uncertain how such an event would impact the species' overall status. The overall risk that environmental pollutants and toxins have posed is probably low given their limited geographic scope and uncertain effects on black abalone, however, a single event in the future, depending on where it occurs, could irreparably damage the few remaining viable populations of black abalone.

5.4.3 Assessment of Demographic Risk

The information considered in evaluating a species' status can generally be grouped into two categories: (1) demographic information reflecting the past and present condition of populations (e.g., data on population abundance or density, population trends and growth rates, the number and distribution of populations, exchange rates of individuals among populations, and the ecological, life-history, or genetic diversity among populations); and (2) information on past factors for decline as well as present and future threats faced by the species (e.g., habitat loss and degradation, overutilization, disease, climate change; see sections 5.2 and 5.4.2 of this Status Review). Conducting an overall assessment of extinction risk involves consideration of a wide variety of qualitative and quantitative information concerning the threats and demographic risks affecting a species' persistence. Moreover, the type and spatial-temporal coverage of the information available often varies within and among populations. This presents a substantial challenge of integrating disparate types of information into an assessment of a species' overall level of extinction risk. Usually such assessments necessitate qualitative evaluations based on informed professional judgment.

In previous NMFS status reviews, SRTs have used a "risk matrix" as a method to organize and summarize the professional judgment of a panel of knowledgeable scientists. This approach is described in detail by Wainright and Kope (1999) and has been used for over 10 years in Pacific salmonid status reviews (e.g., Good *et al.*, 2005), as well as in reviews of West Coast rockfishes (Stout *et al.*, 2001b), Pacific herring (Stout *et al.*, 2001a; Gustafson *et al.*, 2006), and Pacific groundfish (Gustafson *et al.*, 2000). In this risk matrix approach, the collective condition of individual populations is summarized at the "species" level according to four demographic risk criteria:

abundance, growth rate/productivity, spatial structure/connectivity, and diversity. These viability criteria, reviewed in McElhany et al. (2000), reflect concepts that are well founded in conservation biology and are generally applicable to a wide variety of species. These criteria describe demographic risks that individually and collectively provide strong indicators of extinction risk. The risk matrix approach also considers analyses of current and future threats (see section 5.4.2 “Assessment of Threats”) and any mitigating biological factors that may not be manifested in the current demographic status of the species. The summary of demographic risks and other pertinent information obtained by this approach is then considered by the SRT in determining the species’ overall level of extinction risk (see section 5.5 “Risk Determination”). In the following paragraphs we briefly summarize the demographic risk criteria as they relate to a species’ extinction risk, and overview the risk scoring method employed in the risk matrix approach.

5.4.3.1 Demographic Risk Criteria

Evaluating extinction risk of a species includes considering the available information concerning the abundance, growth rate/productivity, spatial structure/connectivity, and diversity of a species and assessing whether demographic risks are such that it is nearing extinction or likely to become so in the foreseeable future. A species at very low levels of abundance and with few populations will be less tolerant to environmental variation, catastrophic events, genetic processes, demographic stochasticity, ecological interactions, and other processes (e.g., Gilpin and Soule, 1986; Meffe and Carroll, 1994; Caughley and Gunn, 1996). A rate of productivity that is unstable or declining over a long period of time may reflect a variety of causes, but indicates poor resiliency to future environmental variability or change (e.g., Lande, 1993; Foley, 1997; Middleton and Nisbet, 1997). For species at low levels of abundance, in particular, declining or highly variable productivity confers a high level of extinction risk. A species that is not widely distributed across a variety of well-connected habitats will have a diminished capacity for recolonizing locally extirpated populations, and is at increased risk of extinction due to environmental perturbations and catastrophic events (Schlosser and Angermeier, 1995; Hanski and Gilpin, 1997; Tilman and Lehman, 1997; Cooper and Mangel, 1999). A species that has lost locally adapted genetic and life-history diversity may lack the raw resources necessary to endure short- and long-term environmental changes (e.g., Groot and Margolis, 1991; Wood, 1995).

The demographic risk criteria described above are evaluated based on the present species status in the context of historical information, if available. However, there may be current or future threats, or other relevant biological factors, that might alter the determination of the species’ overall level of extinction risk. These threats or other risk factors are not yet reflected in the available demographic data because of the time lags involved, but are nonetheless critical considerations in evaluating a species’ extinction risk (Wainwright and Kope, 1999). Forecasting the effects of threats and other risk factors into the foreseeable future is rarely straightforward, and usually necessitates qualitative evaluations and the application of informed professional judgment. This evaluation highlights those factors that may exacerbate or ameliorate demographic risks so that all relevant information may be integrated into the determination of overall extinction risk for the species. Examples of such threats or other relevant factors may include: climatic regime shifts that portend favorable temperature and marine productivity conditions; an El Niño event that is anticipated to result in reduced food quantity or quality; recent or anticipated increases in the range and/or abundance of predator populations; or population age-structure information indicating that a significant proportion of the reproductive population will soon become senescent.

5.4.3.2 Risk Matrix Approach

The risk matrix (Table 7) integrates the consideration of the four demographic risk criteria (abundance, growth rate/productivity, spatial structure/connectivity, and diversity) and other key risks (e.g., threats) into the determination of a species' overall extinction risk. After reviewing all relevant biological information for the species, each SRT member assigns a risk score (see below) to each of the four demographic criteria. The scores are tallied (mean score and range of scores), reviewed, and the range of perspectives discussed by the SRT before making its overall risk determination (see section 5.5 of this Status Review). Although this process helps to integrate and summarize a large amount of diverse information, there is no simple way to translate the risk matrix scores directly into a determination of overall extinction risk. For example, a species with a single extant population might be at a high level of extinction risk because of high risk to spatial structure/connectivity, even if it exhibited low risk for the other demographic criteria. Another species might be at risk of extinction because of moderate risks to several demographic criteria.

Scoring Population Viability Criteria—Risks for each demographic criterion are ranked on a scale of 1 (very low risk) to 5 (very high risk):

1. ***Very Low Risk***. Unlikely that this factor contributes significantly to risk of extinction, either by itself or in combination with other factors.

2. ***Low Risk***. Unlikely that this factor contributes significantly to risk of extinction by itself, but some concern that it may, in combination with other factors.

3. ***Moderate Risk***. This factor contributes significantly to long-term risk of extinction, but does not in itself constitute a danger of extinction in the near future.

4. ***High Risk***. This factor contributes significantly to long-term risk of extinction and is likely to contribute to short-term risk of extinction in the foreseeable future.

5. ***Very High Risk***. This factor by itself indicates danger of extinction in the near future.

Considering Threats and Other Risks—The "Threats and Other Risks" category considers events that have predictable consequences for the species' status in the foreseeable future but have occurred too recently to be reflected in the past or present demographic data. This category allows for SRT members to highlight those components of the threats analysis (see section 5.4.2 of this Status Review) that, although not reflected in the current demographic status of the species, may pose significant risks in the foreseeable future. This category is scored as follows:

++ : expect a strong improvement in the status of the species;
+ : expect some improvement in status;
0 : neutral effect on status;
- : expect some decline in status;
-- : expect strong decline in status.

5.4.4 Population Modeling: Geographic Spread of Disease and Disease Resistance

Calculating the probability of extinction with time is usually done with a model that attempts to account for all threats. Here we use a simple formula (equation 2) to account for withering syndrome, viewed by the SRT as the primary threat to the sustainability of black abalone populations throughout their geographic range, as a function of two parameters, using the logic that if this threat alone results in a high enough risk of extinction in a short time then that may suffice to address whether the species is in danger of extinction currently or in the foreseeable future.

$$P(x) = (1 - S)(1 - R) = 1 - S - R + (RS) \qquad (2)$$

where **P(x)** = probability of effective extinction very soon, **S** = probability that the northward spread of disease (withering syndrome) will cease very soon for reasons of the suitable geographic range and environmental tolerances of the agent, and **R** = probability that resistance will emerge very soon in the host. In turn we define the following terms for S, R, and P(x):

- Very soon = 30 years (expected life span of black abalone).
- Effective extinction = density less than spawning threshold density, or there are no reproducing individuals, over a SPOIR.
- Resistance = positive population growth that persists through temperature fluctuations ("true" resistance, as opposed to healthy, reproducing animals that have not yet been exposed to withering syndrome or to temperatures needed to trigger withering syndrome).
- Emerge = resistance emerges at some locations throughout the current range (Point Arena, CA, to Punta Eugenia, Northern Baja California).

The range of probabilities chosen for R was 0 to 0.15, and for S was 0 to 0.10. These ranges were chosen to completely span what SRT members felt was plausible. In other words, no one felt that there was a greater than 10% chance of the spread of withering syndrome ceasing in the next 30 years (S) or a greater than 15% chance of the emergence of resistance (R) on a significant spatial scale. Thus, the most optimistic probability of extinction in 30 years is 77%. However, the most optimistic probability is not a realistic assessment. To give a more detailed assessment of the implications of the SRT members' beliefs about the probabilities of the quantities bearing on the chance of extinction in 30 years, SRT members were asked to assign relative probabilities to each of the values considered in the ranges for R and S. These probabilities can be summed across SRT members and normalized across the range of values for each parameter to give a rough aggregate distribution of degree of belief for each value of the parameter. These probabilities were: P(S=0.00) = 0.74, P(S=0.05) = 0.21, P(S=0.1) = 0.05, P(R=0.00) = 0.48, P(R=0.02) = 0.28, P(R=0.07) = 0.14, P(R=0.10) = 0.0875, P(R=0.15) = 0.025 (Table 8). Assuming R and S are independent, the degree of belief in each cell in Table 8 can be calculated as the product of the corresponding degree of belief for the respective S and R. This can be used as a weight applied to the probability of extinction associated with that cell in Table 8 to obtain values which can be summed over the cells of the table for a single belief-weighted probability of extinction. This gives the overall probability of effective extinction in 30 years based on the SRT members' opinions as 0.957. Effective extinction includes all the definitions imbedded in R and S concerning densities less than the threshold required for successful recruitment, resistance being indicative of a population with positive growth and emergence being resistant populations across the range. Thus, this probability should not be interpreted as a prediction of the demise of the *last* individual black abalone within 30 yrs. Nevertheless, the collective view of the SRT is that the risk is clearly high and at a level where ultimate extinction without active management has a very high likelihood.

5.5 Overall Risk Determination

The SRT's analysis of overall risk to the species used categories that correspond to definitions in the ESA: in danger of extinction; likely to become endangered in the foreseeable future; or neither (as noted above, these evaluations do not consider protective efforts, and therefore are not recommendations regarding ESA listing status). The overall determination of extinction risk reflected informed professional judgment by each SRT member. This assessment was guided by the results of the risk matrix analysis, integrating information about demographic risks with expectations about likely interactions with threats and other factors.

To allow individuals to express uncertainty in determining the overall level of extinction risk facing the species, the SRT adopted a "likelihood point" method, often referred to as the "FEMAT" method because it is a variation of a method used by scientific teams evaluating options under the Northwest Forest Plan (Forest Ecosystem Management Assessment Team (FEMAT), 1993). In this approach, each SRT member distributes ten likelihood points among the three species extinction risk categories, reflecting their opinion of how likely that category correctly reflects the true species status. Thus, if a SRT member were certain that the species was in the "not at risk" category, he or she could assign all ten points to that category. A SRT member with less certainty about the species' status could split the points among two or even three categories. This method has been used in all status review updates for anadromous Pacific salmonids since 1999, as well as in reviews of West Coast rockfishes (Stout *et al.*, 2001b), Pacific herring (Stout *et al.*, 2001a; Gustafson *et al.*, 2006), Pacific groundfish (Gustafson *et al.*, 2000), and North American green sturgeon (Adams *et al.*, 2002; Adams *et al.*, 2006).

The results of the overall risk determination are summarized in section 7.0 of this Status Review. The majority and minority opinions of the SRT are summarized, as well as the key demographic risks, threats, and other risks underlying the majority and minority opinions.

6.0 Results and Conclusions: Risk Assessment

The SRT concluded that black abalone face high levels of risk in each of the four demographic risk criteria (abundance, growth rate/productivity, spatial structure/connectivity, and diversity; Table 7). The SRT unanimously scored the species' abundance at high risk due to critically low population abundance and density levels. Severe declines in abundance (>90%) have occurred at the majority (76%) of long-term monitoring sites, including all sites in southern California (Tissot 2007). Additionally, the high risk scored for abundance is attributable to populations declining to densities below the minimum threshold density for successful fertilization success (0.75 – 1.1 m^{-2}). All mainland areas surveyed south of Cayucos (California) are below this threshold, as are all offshore island areas with the exception of only two small isolated populations.

The majority of the SRT concluded that the species' growth and productivity is at very high risk. Population growth is negative in all areas south of Cayucos. Except for two isolated island populations, all monitored populations have exhibited recruitment failure. The majority of the SRT concluded that black abalone are at high to very high risk due to compromised spatial structure and poor population connectivity. Dispersion data among local populations indicates that there is poor connectivity among populations. Such limited connectivity reduces the likelihood that disease resistance to withering syndrome, if it exists, will spread to other populations. Furthermore, the poor connectivity among populations makes it unlikely that populations extirpated by disease or local catastrophic events will be recolonized in the foreseeable future.

The SRT unanimously concluded that black abalone are at high risk due to low genetic diversity. Black abalone populations show hetergenous genetic structure among populations, and much of the localized genetic diversity has likely been lost in areas where populations have declined to extremely low levels. The apparent loss of genetic diversity in mainland and island populations severely limits the species' capacity for adapting to environmental change and or responding to the rapid spread of disease. The loss of populations in the southern extent of the species' range will likely impede the re-colonization of aggregations adapted to the environmental conditions in the region. This risk factor, in combination with low spatial connectivity between populations suggests that even if the local genetic diversity exists for disease resistance to have emerged or to emerge in the future, any resistance is not likely to spread and establish itself in other extant populations.

With respect to recent threats and other risks that may exacerbate the appraised risks to the species' abundance, productivity, spatial structure, or diversity, the SRT unanimously underscored the severe threat posed by the manifestation and continuing spread of withering syndrome disease. The SRT also expressed concern that increasing sea surface temperatures in the future will facilitate the spread of the disease to the remaining uninfected populations. Additionally, increased temperatures may increase the virulence of the disease in many of the northern, more abundant populations where the pathogen is present. Some SRT members expressed concern about likely future habitat degradation due to ongoing coastal development. Some SRT members were concerned about the possibility of an oil spill causing local mortality events and further habitat damage. Poaching and predation on black abalone was also noted as posing future threats and exacerbating demographic risks.

7.0 Results and Conclusions: Risk Determination

The SRT unanimously concluded that black abalone is in danger of extinction (Table 9). All SRT members placed the vast majority of their likelihood points in the "in danger of extinction" category, and a minority of points in the "likely to become endangered in the foreseeable future." One SRT member placed all their likelihood points in the "in danger of extinction" category. High to very high risks to the species' abundance, growth/productivity, spatial structure/connectivity, and diversity contributed to the SRT's assessment that the species' is at high risk of extinction in the long and short terms. Other threats posed by disease (i.e. withering syndrome), suboptimal water temperatures; and illegal take exacerbate the risk of extinction faced by the species. The SRT estimated that there is approximately a 95% probability that black abalone will be effectively extinct in 30 years due to the progression of withering syndrome and the limited prospects for disease resistance becoming established. The threat posed by withering syndrome is worsened for certain local populations by thermal effluents, and throughout the species' range by El Niño events and increasing sea surface temperatures associated with global climate change. Illegal take, and the limited resources afforded enforcement agencies, likely will intensify demographic risks already facing populations with critically low densities, and further aggravate the species' risk of extinction.

8.0 Significant Portion of the Range of the Species Question

The ESA defines an "endangered" species as "any species which is in danger of extinction throughout all or a significant portion of its range," and a "threatened" species as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range" (emphasis added). The statutory phrase "throughout all or significant portion of its range" is not defined in the ESA, explained in the Congressional record, the ESA implementing regulations for NMFS or the U.S. Fish and Wildlife Service, nor in interpretive policies issued by these two agencies charged with implementing the ESA. The requirement to give appropriate consideration of this statutory phrase was underscored by a 2001 ruling by the Ninth Circuit Court of Appeals (Defenders of Wildlife v. Norton, 258 F .3d 1136 (9th Cir. 2001)) rejecting the U.S. Fish and Wildlife Service's interpretation of the phrase in its decision not to list the flat-tailed horned lizard (*Phrynosoma mcallii* [Halliwell, 1852]). The Ninth Circuit's ruling has subsequently been adopted by seven district courts, including a decision to reject NMFS' decision not to list North American green sturgeon (*Acipenser medirostris* Ayres, 1854) under the ESA (Env. Protection Info. Center v. NMFS, No. C-02-5401 EDL (N.D. Cal. Mar. 1, 2004). For an agency to determine that a species does not warrant listing, it must demonstrate that The Ninth Circuit held that the "significant portion of its range" phrase is a "substantive standard for determining whether a species is an endangered or threatened species". Under the court's interpretation, there are two situations in which a species must be listed: (1) where the species is threatened or endangered in all of its range; or (2) where the species is threatened or endangered throughout a significant portion of its range. In determining what constitutes a significant portion of a species range, several interpretations have been proposed (DOI 2007; Waples 2007; Vucetich 2006), but as yet NMFS has yet to adopt an approach or provide policy guidance.

8.1 Approaches to the "Significant Portion of its Range" Question

The SRT concluded that black abalone is at risk throughout all of its range, rendering the question of whether black abalone is at risk throughout a significant portion of its range moot.

9.0 References

Abbott, R. T. 1974. American Seashells, second edition. Van Nostrand Reinhold, New York.

Adams, P. B., C. B. Grimes, J. E. Hightower, S. T. Lindley, M. L. Moser, and M. J. Parsley. 2006. Population status of North American green sturgeon, *Acipenser medirostris*. Environmental Biology of Fishes Online Edition:DOI 10.1007/s10641-10006-19062-z.

Adams, P. B., C. B. Grimes, S. T. Lindley, and M. L. Moser. 2002. Status review for North American green sturgeon, *Acipenser medirostris*. NOAA, National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, CA. 50 p.

Altstatt, J. M., R. F. Ambrose, J. M. Engle, P. L. Haaker, K. D. Lafferty, and P. T. Raimondi. 1996. Recent declines of black abalone *Haliotis cracherodii* on the mainland coast of central California. Marine Ecology Progress Series 142:185-192.

Andree, K. B., C. S. Friedman, J. D. Moore, and R. P. Hedrick. 2000. A polymerase chain reaction assay for the detection of genomic DNA of a Rickettsia-like prokaryote associated with withering syndrome in California abalone. Journal of Shellfish Research 19:213-218.

Arnold, W. S., D. C. Marelli, C. P. Bray, and M. M. Harrison. 1998. Recruitment of bay scallops *Argopecten irradians* in Floridan [sic] Gulf of Mexico waters: scales of coherence. Marine Ecology Progress Series 170:143-157.

Ault, J. S. 1985. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest) -- black, green, and red abalones. U.S. Fish & Wildlife Service Biological Report 82 (11.32), U.S. Army

Corps of Engineers, TR EL-82-4. U.S. Department of the Interior, Washington, D.C.

Babcock, R. and J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: Laboratory and field studies. Canadian Journal of Fisheries and Aquatic Sciences 56:1668-1678.

Balseiro, P., R. Aranguren, C. Gestal, B. Novoa, and A. Figueras. 2006. *Candidatus* Xenohaliotis californiensis and *Haplosporidium montforti* associated with mortalities of abalone *Haliotis tuberculata* cultured in Europe. Aquaculture 258:63-72.

Bartsch, P. 1940. The west American *Haliotis*. Proceedings of the United States National Museum 89:49-58.

Bergen, M. 1971. Growth, feeding, and movement in the black abalone, *Haliotis cracherodii* Leach 1814. Master's thesis. University of California, Santa Barbara. 59 pages.

Bergen Wright, M. 1975. Growth in the black abalone. Veliger 18:194-199.

Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fisheries Investigations (London) 19:1-533.

Blecha, J. B., J. R. Steinbeck, and D. C. Sommerville. 1992. Aspects of the biology of the black abalone (*Haliotis cracherodii*) near Diablo Canyon, central California. Pages 225-236 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U.K.

Bonnot, P. 1930. Abalones in California. California Fish and Game 16:15-23.

---. 1948. The abalones of California. California Fish and Game 34:141-168.

Boolootian, R. A., A. Farmanfarmaian, and A. C. Giese. 1962. On the reproductive cycle and breeding habitats of two western species of *Haliotis*. Biological Bulletin (Woods Hole) 122:183-193.

Burton, R. S. and M. J. Tegner. 2000. Enhancement of red abalone *Haliotis rufescens* stocks at San Miguel Island: Reassessing a success story. Marine Ecology Progress Series 202:303-308.

Caddy, J. F. and O. Defeo. 2003. Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources. United Nations Food and Agricultural Organization Fisheries Technical Papers 448.

Campbell, J. L. 1949. The structure and function of the alimentary canal of the black abalone, *Haliotis cracherodii* Leach. Master's thesis. University of California, Berkeley.

Carpenter, R. C. and P. J. Edmunds. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecology Letters 9:271-280.

Carpenter, P. P. 1872. The mollusks of western North America. Smithsonian Miscellaneous Collections 252. Smithsonian Institution, Washington, DC. Available at http://www.archive.org/details/manualconch12tryorich. Accessed: December 2007.

Caughley, G. and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts. xii + 459 pp.

Chambers, M. D., H. Hurn, C. S. Friedman, and G. R. VanBlaricom. 2005. Drift card simulation of larval dispersal from San Nicolas Island, California, during black abalone spawning season. Pages 421-434 *in*: D. K. Garcelon and C. A. Schwemm (editors). Proceedings of the Sixth California Islands Symposium, December 1-3, 2003, Ventura, CA. National Park Service Technical Publication CHIS-05-01, Institute for Wildlife Studies, Arcata, CA.

Chambers, M. D., G. R. VanBlaricom, L. Hauser, F. Utter, and C. S. Friedman. 2006. Genetic structure of black abalone (*Haliotis cracherodii)* populations in the California islands and central California coast: Impacts of larval dispersal and decimation from withering syndrome. Journal of Experimental Marine Biology and Ecology 331:173-185.

Chiappone, M., D. W. Swanson, and S. L. Miller. 2002. Density, spatial distribution, and size structure of sea urchins in Florida Keys coral reef and hard-bottom habitats. Marine Ecology Progress Series 235:117-126.

Clavier, J. 1992. Fecundity and optimal sperm density for fertilization in the ormer (*Haliotis tuberculata* L.). Pages 86-92 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U.K.

Cooper, A. B. and M. S. Mangel. 1999. The dangers of undetected metapopulation structure for the conservation of salmonids. Fishery Bulletin 97:213-226.

Cooper, J., M. Weiland, and A. Hines. 1977. Subtidal abalone populations in an area inhabited by sea otters. Veliger 20:163-167.

Cox, K. W. 1960. Review of the abalone of California. California Department of Fish and Game, Marine Resources Operations.

---. 1962. California abalones, family Haliotidae. California Department of Fish and Game, Fish Bulletin 118:1-132.

Croker, R. S. 1931. Abalones. Division of Fish and Game, Fish Bulletin 30:58-72.

Davis, G. E., D. V. Richards, P. L. Haaker, and D. O. Parker. 1992. Abalone population declines and fishery management in southern California. Pages 237-249 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalones of the world: Biology, fisheries, and culture. Blackwell Scientific Publications Ltd., Oxford, U.K.

Day, R. W. and A. E. Fleming. 1992. The determinants and measurement of abalone growth. Pages 141-168 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U. K.

Dayton, P. K. and M. J. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. Science 224:283-285.

Douros, W. J. 1985. Density, growth, reproduction, and recruitment in an intertidal abalone: Effects of intraspecific competition and prehistoric predation. Master's thesis. University of California, Santa Barbara. 112 pages.

---. 1987. Stacking behavior of an intertidal abalone: An adaptive response or a consequence of space limitation? Journal of Experimental Marine Biology and Ecology 108:1-14.

---. 1993. Prehistoric predation on black abalone by Chumash Indians and sea otters. Third California Islands Symposium: Recent advances in research on the California Islands.

Erlandson, J. M., D. J. Kennett, B. L. Ingram, D. A. Guthrie, D. P. Morris, M. A. Tveskov, G. J. West, and P. L. Walker. 1996. An archaeological and paleontological chronology for Daisy cave (CA-SMI-261), San Miguel Island, California. Radiocarbon 38:355-373.

Estes, J. A., R. J. Jameson, and A. M. Johnson. 1981. Food selection and some foraging tactics of sea otters. Pages 606-641 *in*: J. A. Chapman and D. Pursley (editors).

The worldwide furbearer conference proceedings. Worldwide Furbearer Conference, Frostberg, Maryland, USA.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual prey selection by sea otters: Patterns, causes, and implications. Journal of Animal Ecology 72:144-155.

Estes, J. A. and G. R. VanBlaricom. 1985. Sea otters and shellfisheries. Pages 187-235 *in*: R. Beverton, J. Beddington, and D. Lavigne (editors). Conflicts between marine mammals and fisheries. George, Allen, and Unwin, London, U.K.

Fanshawe, S., G. R. VanBlaricom, and A. A. Shelly. 2003. Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: A case study with red abalones and sea otters. Conservation Biology 17:273-283.

FEMAT. 1993. Forest ecosystem management: An ecological, economic, and social assessment. USDA Forest Service, BLM, USFWS, NOAA, EPA, and National Park Service, Portland, Oregon.

Finley, C. A. and C. S. Friedman. 2000. Examination of the geographic distribution of a Rickettsia-like prokaryote in red abalone, *Haliotis rufescens,* in northern California. Journal of Shellfish Research 19:512-513.

Foley, P. 1997. Extinction models for local populations. Pages 215-246 *in*: I. Hanski and M. E. Gilpin (editors). Metapopulation biology. Academic Press, New York.

Forward Jr., R. B., C. A. Wellins, and C. U. Buswell. 1989. Behavioural responses of larvae of the crab *Neopanope sayi* to hydrostatic pressure. Marine Ecology Progress Series 57:267-277.

Friedman, C. S., K. B. Andree, K. A. Beauchamp, J. D. Moore, T. T. Robbins, J. D. Shields, and R. P. Hedrick. 2000. '*Candidatus Xenohaliotis californiensis*', a newly described pathogen of abalone, *Haliotis* spp., along the west coast of North America. International Journal of Systematic and Evolutionary Microbiology 50:847-855.

Friedman, C. S., W. Biggs, J. D. Shields, P. L. Haaker, C. Chun, and R. P. Hedrick. 1997. An examination of four potential etiologies of WS: Temperature, food availability, renal coccidia, and Rickettsiales-like procaryotes. Third International Abalone Symposium: Biology, fisheries, and culture, Monterey, CA, October 26-31, 1997.

Friedman, C. S., W. Biggs, J. D. Shields, and R. P. Hedrick. 2002. Transmission of withering syndrome in black abalone, *Haliotis cracherodii,* Leach. Journal of Shellfish Research 21:817-824.

Friedman, C. S. and C. A. Finley. 2003. Anthropogenic introduction of the etiological agent of withering syndrome into northern California abalone populations via conservation efforts. Canadian Journal of Fisheries and Aquatic Sciences 60:1424-1431.

Friedman, C. S., W. Roberts, G. Kismohandaka, and R. P. Hedrick. 1993. Transmissibility of a coccidian parasite of abalone, *Haliotis* spp. Journal of Shellfish Research 12:201-205.

Gardner, G. R., J. C. Harshbarger, J. L. Lake, T. K. Sawyer, K. L. Price, M. D. Stephenson, P. L. Haaker, and H. A. Togstad. 1995. Association of prokaryotes with symptomatic appearance of withering syndrome in black abalone *Haliotis cracherodii*. Journal of Invertebrate Pathology 66:111-120.

Gascoigne, J. and R. N. Lipcius. 2004. Allee effects in marine systems. Marine Ecology Progress Series 269:49-59.

Geiger, D. L. 1998. Recent genera and species of the family Haliotidae Rafinesque, 1815 (Gastropoda: Vetigastropoda). The Nautilus 111:85-116.

Geiger, D. L. 1999. A total evidence cladistic analysis of the Family Haliotidae (Gastropoda: Vetigastropoda). PhD Dissertation. University of Southern California. xix, 423 pp.

---. 2000. Distribution and biogeography of the Haliotidae (Gastropoda: Vetigastropoda) world-wide. Bollettino Malacologico 35:57-120.

---. 2004. AbMap: The abalone mapping project. http://www.vetigastropoda.com/ABMAP/text/index.htm. Accessed:

Gilpin, M. E. and M. E. Soule. 1986. Minimum viable populations: process of species extinctions. Pages 19-34 *in*: M. E. Soule (editor). Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Glassow, M. A. 1993. The occurrence of red abalone shells in northern Channel Island archaeological middens: Implications for climate reconstruction. Pages 567-578 *in*: F. G. Hochberg (editor). Proceedings of the Third California Islands Symposium: Recent advances in California Islands research. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Glassow, M. A., D. J. Kennett, J. P. Kennett, and L. R. Wilcoxon. 1994. Confirmation of middle Holocene ocean cooling inferred from stable isotope analysis of prehistoric shells from Santa Cruz Island, California. Pages 223-232 *in*: W. L. Halvorson and G. J. Meander (editors). The Fourth California Islands

Symposium: Update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Gonzales, J. G. and Q. M. Ortiz. 1986. Estudios sobre madurez, indice gonadal y fecundidad en abulon negro, *Haliotis cracherodii* (Mollusca: Gasteropoda) a partir de muestras colectadas en la Isla de Cedros, Baja California, en Junio 1982. Instituto Nacional de Pesca. CRIP Ensenada. Doc. Tec. Inf. 1: 54-72. Cited in: Leighton, D. L. 2005. Status review for the black abalone, *Haliotis cracherodii* Leach 1814. Unpublished document produced for the Black Abalone Status Review Team, Office of Protected Resources, Southwest Region, National Marine Fisheries Service, Long Beach, CA, USA.

Good, T. P., R. S. Waples, and P. Adams (editors). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-66.

Groot, C. and L. Margolis (editors). 1991. Pacific salmon life histories. UBC Press, Vancouver, British Columbia.

Gruenthal, K. M. 2007. Conservation genetics of California abalone species. Doctoral dissertation. University of California, San Diego. 249 pages.

Gustafson, R. G., J. Drake, M. J. Ford, J. M. Myers, E. E. Holmes, and R. S. Waples. 2006. Status review of Cherry Point Pacific herring (*Clupea pallasii*) and updated status review of the Georgia Basin Pacific herring distinct population segment under the Endangered Species Act. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-76. 182 pp.

Gustafson, R. G., W. H. Lenarz, B. B. McCain, C. C. Schmitt, W. S. Grant, T. L. Builder, and R. D. Methot. 2000. Status review of Pacific hake, Pacific cod, and walleye pollock from Puget Sound, Washington. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-44.

Haaker, P. L., K. C. Henderson, and D. O. Parker. 1986. California abalone. California Department of Fish and Game, Marine Resources Division, Long Beach, CA.

Haaker, P. L., D. O. Parker, and C. S. Y. Chun. 1995. Growth of black abalone, *Haliotis cracherodii* Leach, at San Miguel Island and Point Arguello, California. Journal of Shellfish Research 14:519-525.

Haaker, P. L., D. O. Parker, H. Togstad, D. V. Richards, G. E. Davis, and C. S. Friedman. 1992. Mass mortality and withering syndrome in black abalone, *Haliotis cracherodii,* in California. Pages 608 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U.K.

Hamm, D. E. and R. S. Burton. 2000. Population genetics of black abalone, *Haliotis cracherodii*, along the central California coast. Journal of Experimental Marine Biology and Ecology 254:235-247.

Hancock, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer, 164:113-131.

Hanski, I. A. and M. E. Gilpin (editors). 1997. Metapopulation biology. Academic Press, San Diego.

Harley, C. D. G. and L. Rogers-Bennett. 2004. The potential synergistic effects of climate change and fishing pressure on exploited invertebrates on rocky intertidal shores. CalCOFI Reports 45:98-110.

Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann, E. K. Lipp, A. D. M. E. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith, and G. R. Vasta. 1999. Emerging marine diseases - climate links and anthropogenic factors. Science 285:1505-1510.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296:2158-2162.

Hatfield, B. B. 2005. The translocation of sea otters to San Nicolas Island: An update. Pages 473-475 *in*: D. K. Garcelon and C. A. Schwemm (editors). Proceedings of the Sixth California Islands Symposium, Ventura, California, December 1-3, 2003. Institute for Wildlife Studies, Arcata, California, USA.

Hearn, A., P. Martínez, M. V. Toral-Granda, J. C. Murillo, and J. Polovina. 2005. Population dynamics of the exploited sea cucumber *Isostichopus fuscus* in the western Galápagos Islands, Ecuador. Fisheries Oceanography 14:377-385.

Hellberg, M. E., R. S. Burton, J. E. Neigel, and S. R. Palumbi. 2002. Genetic assessment of connectivity among marine populations. Bulletin of Marine Science 70 (suppl.):273-290.

Hines, A. H. and J. S. Pearse. 1982. Abalones, shells, and sea otters: dynamics of prey populations in central California. Ecology 63:1547-1560.

Hobday, A. J. and M. J. Tegner. 2000. Status review of white abalone (*Haliotis sorenseni*) throughout its range in California and Mexico. NOAA Technical Memorandum NOAA-TM-SWR-035, U.S. Department of Commerce, National Oceanic and Atmospheric Administration. National Marine Fisheries Service, Long Beach, CA, USA.

Howorth, P. C. 1978. The abalone book. Naturegraph Publishers, Inc., Happy Camp, CA.

IUCN. 2001. IUCN Red List categories and criteria: Version 3.1. IUCN. Available at http://intranet.iucn.org/webfiles/doc/SSC/RedList/redlistcatsenglish.pdf. Accessed: September 2007

---. 2006. Guidelines for using the IUCN Red List categories and criteria. Version 6.2. Prepared by the Standards and Petitions Working Group of the IUCN SSC Biodiversity Assessments Sub-Committee in December 2006. Available at http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf. Accessed: September 2007

Karlson, R. H. and D. R. Levitan. 1990. Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. Oecologia 82:40-44.

Karpov, K. A., P. L. Haaker, I. K. Taniguchi, and L. Rogers-Bennett. 2000. Serial depletion and the collapse of the California abalone fishery. Pages 11-24 *in*: A. Campbell (editor). Workshop on rebuilding abalone stocks in British Columbia. Canadian Special Publications, Fish and Aquatic Sciences.

Keough, M. J. and B. J. Downes. 1982. Recruitment of marine invertebrates: The role of active larval choices and early mortality. Oecologia 54:348-352.

Kimura, M. and G. H. Weiss. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49:561-576.

Kimura, S. and J. R. Steinbeck. 2003. A comparative intertidal study and user survey, Point Pinos, California. Tenera Environmental, San Luis Obispo, California, USA.

Kismohandaka, G., C. S. Friedman, W. Roberts, and R. P. Hedrick. 1993. Investigation of physiological parameters of black abalone with withering syndrome. Journal of Shellfish Research 12:131-132.

Kraeuter, J. N., S. Buckner, and E. N. Powell. 2005. A note on a spawner-recruit relationship for a heavily exploited bivalve: The case of northern quahogs (hard clams), *Mercenaria mercenaria* in Great South Bay New York. Journal of Shellfish Research 24:1043-1052.

Lafferty, K. D. and A. M. Kuris. 1993. Mass mortality of abalone *Haliotis cracherodii* on the California Channel Islands: tests of epidemiological hypotheses. Marine Ecology Progress Series 96:239-248.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911-927.

Lauzon-Guay, J. S. and R. E. Scheibling. 2007. Importance of spatial population characteristics on the fertilization rates of sea urchins. Biological Bulletin 212:195-205.

Leach, W. E. 1814. The zoological miscellany; being descriptions of new, or interesting animals. B. McMillan and E. Nodder & Son, London. 263 pp.

Leighton, D. and R. A. Boolootian. 1963. Diet and growth in the black abalone, *Haliotis cracherodii*. Ecology 44:227-238.

Leighton, D. L. 1959. Diet and its relation to growth in the black abalone, *Haliotis cracherodii* Leach. Master's thesis. University of California, Los Angeles. 61 pages.

---. 2005. Status review for the black abalone, *Haliotis cracherodii* Leach 1814. Unpublished document produced for the Black Abalone Status Review Team, Office of Protected Resources, Southwest Region, National Marine Fisheries Service, Long Beach, CA, USA. 32 pp.

Lessios, H. A., P. W. Glynn, and D. R. Robertson. 1983. Mass mortalities of coral reef organisms. Science 222:715.

Lessios, H. A., B. D. Kessing, and D. R. Robertson. 1998. Massive gene flow across the world’s most potent marine biogeographic barrier. Proceedings of the Royal Society of London B 265:583-588.

Levitan, D. R. 1988. Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands. Journal of Experimental Marine Biology and Ecology 119:167-178.

---. 1995. The ecology of fertilization in free-spawning invertebrates. Pages 123-156 *in*: L. McEdward (editor). Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL.

Levitan, D. R. and M. A. Sewell. 1998. Fertilization success in free-spawning marine invertebrates: review of the evidence and fisheries implications. Pages 159-164 *in*: G. S. Jamieson and A. Campbell (editors). Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Canadian Special Publications in Fisheries and Aquatic Sciences 125.

Lovatelli, A., C. Conand, S. Purcell, S. Uthicke, J. F. Hamel, and A. Mercier. 2004. Advances in sea cucumber aquaculture and management. United Nations Food and Agricultural Organization Fisheries Technical Paper 463.

Lowry, L. F. and J. S. Pearse. 1973. Abalones and sea urchins in an area inhabited by sea otters. Marine Biology 23:213-219.

Lundquist, C. J. and L. W. Botsford. 2004. Model projections on the implications of the Allee effect in broadcast spawners. Ecological Applications 14:929-941.

Lundy, A. 1997. The California abalone industry - A pictorial history. Best Publishing Company, Flagstaff, Arizona.

Lyons, K. J. 1991. Foraging behavior of California sea otters: The importance of individual variation. Doctoral dissertation. University of California, Santa Cruz.

Marelli, D. C., W. S. Arnold, and C. Bray. 1999. Levels of recruitment and adult abundance in a collapsed population of bay scallops (*Argopecten irradians*) in Florida. Journal of Shellfish Research 18:393-399.

Martin, M., M. D. Stephenson, and J. H. Martin. 1977. Copper toxicity experiments in relation to abalone deaths observed in a power plant's cooling waters. California Fish and Game 63:95-100.

McCauley, J. E., and L. D. Marriage. 1955. The intertidal mussel, piddock, and abalone resources of Oregon's outer coast. Fish Commission of Oregon Research Briefs 6:4-13.

McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-42.

McGarvey, R., F. M. Serchuk, and I. A. McLaren. 1993. Spatial and parent-age analysis of stock recruitment in the Georges Bank sea scallop (*Placopecten magellanicus*) population. Canadian Journal of Fisheries and Aquatic Sciences 50:564-574.

McShane, P. E. 1991. Density dependent mortality of recruits of the abalone *Haliotis rubra* (Mollusca: Gastropoda). Marine Biology 110:385-389.

---. 1992. Early life history of abalone: A review. Pages 120-138 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world. Biology, fisheries, culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U. K.

McShane, P. E., K. P. Black, and M. G. Smith. 1988. Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. Journal of Experimental Marine Biology and Ecology 124:175-203.

McShane, P. E. and M. G. Smith. 1988. Measuring recruitment of abalone *Haliotis rubra* Leach (Gastropoda: Haliotidae): Comparison of novel method with two other methods. Australian Journal of Marine and Freshwater Research 39:331-336.

Meffe, G. and R. Carroll. 1994. Principles of conservation biology. Sinauer Associates, Inc., Sunderland, Massachusetts. 600 pp.

Meighan, C. W. 1959. The Little Harbor site, Catalina Island: An example of ecological interpretation in archaeology. American Antiquity 19:109-125.

Micheli, F., A. O. Shelton, S. M. Bushinsky, A. L. Chiu, A. J. Haupt, K. W. Heiman, C. V. Kappel, M. C. Lynch, R. G. Martone, and J. Watanabe. In review. Persistence of depleted marine invertebrates in marine reserves of central California. Biological Conservation.

Middleton, D. A. J. and R. M. Nisbet. 1997. Population persistence time: estimates, models, mechanisms. Ecological Applications 7:107-117.

Miller, A. C. and S. E. Lawrenz-Miller. 1993. Long-term trends in black abalone, *Haliotis cracherodii* Leach, 1814, populations along the Palos Verdes Peninsula, California. Journal of Shellfish Research 12:195-200.

Miller, R. J., A. J. Adams, J. P. Ebersole, and E. Ruiz. 2007. Evidence for positive density-dependent effects in recovering *Diadema antillarum* populations. Journal of Experimental Marine Biology and Ecology 349:215-222.

Miner, C. M., J. M. Altstatt, P. T. Raimondi, and T. E. Minchinton. 2006. Recruitment failure and shifts in community structure following mass mortality limit recovery prospects of black abalone. Marine Ecology Progress Series 327:107-117.

Moore, J. D., G. N. Cherr, and C. S. Friedman. 2001. Detection of '*Candidatus* Xenohaliotis californiensis' (Rickettsiales-like prokaryote) inclusions in tissue squashes of abalone (*Haliotis* spp.) gastrointestinal epithelium using a nucleic acid fluorochrome. Disease of Aquatic Organisms 46:147-152.

Moore, J. D., C. A. Finley, C. S. Friedman, and T. T. Robbins. 2002. Withering syndrome and restoration of southern California abalone populations. CalCOFI Reports 43:112-119.

Moore, J. D., T. T. Robbins, and C. S. Friedman. 2000a. The role of a Rickettsia-like prokaryote in withering syndrome in California red abalone, *Haliotis rufescens*. Journal of Shellfish Research 19:525-526.

---. 2000b. Withering syndrome in farmed red ablone *Haliotis rufescens*: Thermal induction and association with a gastrointestinal Rickettsiales-like prokaryote. Journal of Aquatic Animal Health 12:26-34.

Morris, R. H., D. L. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, Palo Alto, CA.

Morse, A. N. C. and D. E. Morse. 1984. Recruitment and metamorphosis of *Haliotis* larvae are induced by molecules uniquely available at the surfaces of crustose red algae. Journal of Experimental Marine Biology and Ecology 75:191-215.

Morse, D. E. 1990. Recent progress in larval settlement and metamorphosis: Closing the gaps between molecular biology and ecology. Bulletin of Marine Science 46:465-483.

---. 1992. Molecular mechanisms controlling metamorphosis and recruitment in abalone larvae. Pages 107-119 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U.K.

Morse, D. E., N. Hooker, H. Duncan, and L. Jensen. 1979. γ-aminobutyric acid, a neurotransmitter, induces planktonic abalone larvae to settle and begin metamorphosis. Science 204:407-410.

Munro, J. L. 1993. Giant clams. Pages 431-449 *in*: A. Wright and L. Hill (editors). Nearshore marine resources of the South Pacific. Information for fisheries development and management. Institution of Pacific Studies, Suva; Forum Fisheries Agency, Honaira; and International Centre Ocean Development, Canada.

Myhre, S. and A. Acevedo-Gutiérrez. 2007. Recovery of sea urchin *Diadema antillarum* populations is correlated to increased coral and reduced macroalgal cover. Marine Ecology Progress Series 329:105-110.

Oldroyd, I. S. 1927. The marine shells of the west coast of North America. Stanford University Publications, Geological Sciences, Vol. II, Part 3.

Orensanz, J. M., C. M. Hand, A. M. Parma, J. Valero, and R. Hilborn. 2004. Precaution in the harvest of Methuselah's clams — the difficulty of getting timely feedback from slowpaced dynamics. Canadian Journal of Fisheries and Aquatic Sciences 61:1355-1372.

Orr, P. C. 1967. Geochronology of Santa Rosa Island, California. Pages 317-325 *in*: R. N. Philbrick (editor). Proceedings of the Symposium on the Biology of the

California Islands. Santa Barbara Botanic Garden, Santa Barbara, California, USA.

Ostfeld, R. S. 1982. Foraging strategies and prey switching in the California sea otter. Oecologia 53:170-178.

Parker, D. O., P. L. Haaker, and H. A. Togstad. 1992. Case histories for three species of California abalone, *Haliotis corrugata, H. fulgens,* and *H. cracherodii*. Pages 384-394 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U.K.

Pennington, J. T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. Biological Bulletin (Woods Hole) 169:417-430.

Peterson, C. H. 2002. Recruitment overfishing in a bivalve mollusk fishery: hard clams (*Mercenaria mercenaria*) in North Carolina. Canadian Journal of Fisheries and Aquatic Sciences 59:96-104.

Peterson, C. H. and H. C. Summerson. 1992. Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. Marine Ecology Progress Series 90:257-272.

Phillips, J. B. 1937. Abalone. Division of Fish and Game, Fish Bulletin 49:107-113.

Pilsbry, H. A. 1890. Manual of Conchology, Structural and Systematic with Illustrations of the Species, Vol. 12, Stomatellidae, Scissurellidae, Pluerotomariidae, Haliotidae, Scutellinidae, Addisoniidae, Cocculinidae, Fissurellidae. Academy of Natural Sciences, Philadelphia, 323 p. Available at http://www.archive.org/details/manualconch12tryorich. Accessed: December 2007.

Prince, J. D., T. L. Sellers, W. B. Ford, and S. R. Talbot. 1987. Experimental evidence for limited dispersal of haliotid larvae (genus: *Haliotis*: Gastropoda: Gastropoda). Journal of Experimental Marine Biology and Ecology 106:243-263.

---. 1988. Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). Journal of Experimental Marine Biology and Ecology 122:91-104.

Quinn, J. F., S. R. Wing, and L. W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. American Zoologist 33:537-550.

Raimondi, P. T., C. M. Wilson, R. F. Ambrose, J. M. Engle, and T. E. Minchinton. 2002. Continued declines of black abalone along the coast of California: are mass mortalities related to El Niño events? Marine Ecology Progress Series 242:143-152.

Reinman, F. M. 1964. Marine adaptation on San Nicolas Island, California: A preliminary and speculative evaluation. Pages 50-84 *in*: University of California, Los Angeles, Archaeological Surveys, Annual Report 1963-1964.

Richards, D. V. and G. E. Davis. 1993. Early warnings of modern population collapse in black abalone *Haliotis cracherodii,* Leach, 1814 at the California Channel Islands. Journal of Shellfish Research 12:189-194.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559-623.

Rogers-Bennett, L., P. L. Haaker, T. O. Huff, and P. K. Dayton. 2002. Estimating baseline abundances of abalone in California for restoration. CalCOFI Reports 43:97-111.

Salls, R. A. 1992. Prehistoric subsistence change in California's Channel Islands: Environmental or cultural. Pages 157-172 *in*: T. Jines (editor). Essays on the prehistory of maritime California. Center for Archaeological Research at Davis, University of California, Davis, California, USA.

Schlosser, I. J. and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392-401 *in*: J. L. Nielsen (editor). Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Shanks, A. L. and W. G. Wright. 1986. Adding teeth to wave action - the destructive effects of wave-borne rocks on intertidal organisms. Oecologia 69:420-428.

Sharp, J. 2002. Shellfish analysis from a Santa Cruz Island red abalone midden: Re-evaluating the marine cooling hypothesis. Pages 563-572 *in*: D. Browne, K. Mitchell, and H. Chaney (editors). Proceedings of the Fifth California Islands Symposium, March 29 - April 1, 1999. Pacific OCS Region, Minerals Management Service, Los Angeles, California, USA.

Shepherd, S. A. 1973. Studies on southern Australian abalone (genus *Haliotis*). I. Ecology of five sympatric species. Australian Journal of Marine and Freshwater Research 24:217-257.

Shepherd, S. A. and P. A. Breen. 1992. Mortality of abalone: Its estimation, variability, and causes. Pages 276-304 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Blackwell Scientific Publications Ltd., Oxford, U.K.

Shepherd, S. A., P. Martinez, M. V. Toral-Granda, and G. J. Edgar. 2004. The Galapagos sea cucumber fishery: management improves as stocks decline. Environmental Conservation 31:102-110.

Sierra-Rodriguez, P., M Muciño Díaz, J.L. Gutiérrez González, and J.R. Turribates Morales. 2006. La Pesquería de Abulón. Pages 3-38 *in*: J. Cueller P. and C.O. Cadena (editors). Sustentabilidad y Pesca Responsable en México. Evaluación y Manejo. Instituto Nacional de la Pesca. México, D.F., México.

Smith, G., C. Stamm, and F. Petrovic. 2003. *Haliotis cracherodii*. *In* IUCN 2006 Red List of threatened species. Available at http://www.iucnredlist.org/search/details.php/41880/all (accessed May 2007).

Smith, S. J. and P. Rago. 2004. Biological reference points for sea scallops (*Placopecten magellanicus*): the benefits and costs of being nearly sessile. Canadian Journal of Fisheries and Aquatic Sciences 61:1338-1354.

Steinbeck, J. R., J. M. Groff, C. S. Friedman, T. McDowell, and R. P. Hedrick. 1992. Investigations into a mortality among populations of the California black abalone, *Haliotis cracherodii*, on the central coast of California. Pages 203-213 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo, editors. Abalone of the world: biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U.K.

Stout, H. A., R. G. Gustafson, W. H. Lenarz, B. B. McCain, D. M. Van Doornik, T. L. Builder, and R. D. Methot. 2001a. Status review of Pacific herring in Puget Sound, Washington. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-45.

Stout, H. A., B. B. McCain, R. D. Vetter, T. L. Builder, W. H. Lenarz, L. L. Johnson, and R. D. Methot. 2001b. Status review of copper rockfish, quillback rockfish, and brown rockfish in Puget Sound, Washington. U.S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-46.

Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life history evolution in marine invertebrates. Annual Review of Ecology and Systematics 16:339-361.

Summerson, H. C. and C. H. Peterson. 1990. Recruitment failure of the bay scallop, *Argopecten irradians concentricus*, during the first red tide, *Ptychodiscus brevis*, outbreak recorded in North Carolina. Estuaries 13:322-331.

Tegner, M. J. 1989. Chapter 17: The California abalone fishery: Production, ecological interactions, and prospects for the future. Pages 401-420 *in*: J. F. Caddy (editor). Marine invertebrate fisheries: Their assessment and management. J. Wiley and Sons, New York.

---. 1992. Brood-stock transplants as an approach to abalone stock enhancement. Pages 461-473 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Proceedings of the 1st International Symposium on Abalone. Blackwell Scientific Publications Ltd., Oxford, U.K.

Tegner, M. J. and R. A. Butler. 1985. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) in the Southern California Bight: Implications for recovery of depleted populations. Marine Ecology Progress Series 26:73-84.

Tegner, M. J. and P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. Advances in Ecological Research 17:243-279.

Tegner, M. J., J. D. DeMartini, and K. A. Karpov. 1992. The California red abalone fishery: A case study in complexity. Pages 370-383 *in*: S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Próo (editors). Abalone of the world: Biology, fisheries, and culture. Blackwell Scientific Publications Ltd., Oxford, U.K.

Tegner, M. J. and L. A. Levin. 1982. Do sea urchins and abalones compete in California kelp forest communities? Pages 265-271 *in*: J. M. Lawrence (editor). International Echinoderms Conference, Tampa Bay, 14-17 September 1981, Tampa Bay, Florida, USA.

Thompson, W. F. 1920. The abalones of northern California. California Fish and Game 6: 45-50.

Tilman, D. and C. L. Lehman. 1997. Habitat destruction and species extinctions. Pages 233-249 *in*: D. Tilman and P. Kareiva (editors). Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, New Jersey.

Tinajero, M. D., J. Caceres-Martinez, and J. G. G. Aviles. 2002. Histopathological evaluation of the yellow abalone *Haliotis corrugata* and the blue abalone *Haliotis fulgens* from Baja California, Mexico. Journal of Shellfish Research 21:825-830.

Tissot, B. N. 1988. Morphological variation along intertidal gradients in a population of black abalone *Haliotis cracherodii* Leach 1814. Journal of Experimental Marine Biology and Ecology 117:71-90.

---. 1991. Geographic variation and mass mortality in the black abalone: the roles of development and ecology. PhD Dissertation. Oregon State University. 271 pp.

---. 1995. Recruitment, growth, and survivorship of black abalone on Santa Cruz Island following mass mortality. Bulletin of the Southern California Academy of Sciences 94:179-189.

---. 2007. Long-term population trends in the black abalone, *Haliotis cracherodii*, along the eastern Pacific coast. Unpublished report for the Office of Protected Resources, Southwest Region, National Marine Fisheries Service, Long Beach, CA. 43 pp.

Toral-Granda, M. V. 2005. Requiem for the Galápagos sea cucumber fishery? SPC Beche-de-mer Information Bulletin 21:5-8. Available at http://www.spc.int/coastfish/news/BDM/21/Toral-Granda.pdf.

Trapido-Rosenthal, H. G. and D. E. Morse. 1986. Availability of chemosensory receptors is down-regulated by habituation of larvae to a morphogenetic signal. Proceedings of the National Academy of Sciences USA 83:7658-7662.

VanBlaricom, G. R. 1987. Regulation of mussel population structure in Prince William Sound, Alaska. National Geographic Research 3:501-510.

---. 1988. Effects of foraging by sea otters on mussel-dominated intertidal communities. Pages 48-91 *in*: G. R. VanBlaricom and J. A. Estes (editors). The community ecology of sea otters. Ecological studies, volume 65. Springer-Verlag, Heidelberg, Germany.

---. 1993. Dynamics and distribution of black abalone populations at San Nicolas Island, California. Pages 323-334 *in*: F. G. Hochberg (editor). Third California Islands Symposium: Recent advances in research on the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

---. 1996. Saving the sea otter in California: Contemporary problems and future pitfalls. Endangered Species Update 13:85-91.

---. 2003. Diet of black abalones (*Haliotis cracherodii*) at San Nicolas Island, California: Selective detritivores or shameless omnivores? Oral presentation. Sixth California Islands Symposium, Ventura, CA, 1-3 December 2003.

VanBlaricom, G. R. and S. L. Ashworth. In preparation. Patterns of movement in adult black abalones (*Haliotis cracherodii* Leach, 1814) at San Nicolas Island, California. Journal of Shellfish Research.

VanBlaricom, G. R. and R. J. Jameson. 1982. Lumber spill in central California waters: Implications for oil spills and sea otters. Science 215:1503-1505.

VanBlaricom, G. R. and R. A. Monti. In preparation. Patterns of individual growth in adult black abalones (*Haliotis cracherodii* Leach, 1814) at San Nicolas Island, California. Journal of Shellfish Research.

VanBlaricom, G. R., J. L. Ruediger, C. S. Friedman, D. D. Woodard, and R. P. Hedrick. 1993. Discovery of withering syndrome among black abalone *Haliotis cracherodii* Leach, 1814, populations at San Nicolas Island, California. Journal of Shellfish Research 12:185-188.

VanBlaricom, G. R. and B. S. Stewart. 1986. Consumption of pelagic red crabs by black abalone at San Nicolas and San Miguel Islands, California. Veliger 28:328-329.

Vellanoweth, R. L., T. C. Rick, and J. M. Erlandson. 2002. Middle and late Holocene maritime adaptations on northeastern San Miguel Island, California. Pages 607-614 *in*: D. Browne, K. Mitchell, and H. Chaney (editors). Proceedings of the Fifth California Islands Symposium, March 29 - April 1, 1999. Pacific Outer Continental Shelf Region, Minerals Management Service, Los Angeles, California, USA.

Vilchis, L. I., M. J. Tegner, J. D. Moore, C. S. Friedman, K. L. Riser, T. T. Robbins, and P. K. Dayton. 2005. Ocean warming effects on growth, reproduction, and survivorship of southern California abalone. Ecological Applications 15:469-480.

Vucetich, J.A., M.P. Nelson, and M.K. Phillips. 2006. The normative deimansion and legal meaning of *Endangered* and *Recovery* in the U.S. Endangered Species Act. Conservation Biology 20(5): 1383-1390.

Wainwright, T. C. and R. G. Kope. 1999. Short Communication: Methods of extinction risk assessment developed for U.S. West Coast salmon. ICES Journal of Marine Science 56:444-448.

Waples, R. S., P. B. Adams, J. Bohnsack, and B. L. Taylor. 2007. A biological framework for evaluating whether an ESA species is threatened or endangered in a "significant portion of its range." Conservation Biology 21: 964-974.

Waples, R. S. 1998. Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species. The Journal of Heredity 89:438-450.

Ward, J. R. and K. D. Lafferty. 2004. The elusive baseline of marine disease: Are diseases in ocean ecosystems increasing? Public Library of Science Biology 2:542-547.

Webber, H. H. and A. C. Giese. 1969. Reproductive cycle and gametogenesis in the black abalone *Haliotis cracherodii* (Gastropoda: Prosobranchiata). Marine Biology 4:152-159.

Wendell, F. E. 1994. Relationship between sea otter range expansion and red abalone abundance and size distribution in central California. California Fish and Game 80:45-56.

Wood, C. C. 1995. Life history variation and population structure in sockeye salmon. Pages 195-216 *in*: J. L. Nielsen (editor). Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Young, P. H. 1964. Some effects of sewer effluent on marine life. California Fish and Game 50:33-41.

Zhang, Z. and C. Hand. 2006. Recruitment patterns and precautionary exploitation rates for geoduck (*Panopea abrupta*) populations in British Columbia. Journal of Shellfish Research 25:445-453.

Table 1. Black abalone poaching cases documented by the California Department of Fish and Game from 1993-2003 (Taniguchi, unpublished data). The number of black abalone seized and the number of poaching cases (indicated parenthetically) are shown by county for each year.

Black Abalone Poaching Cases						
Year	**San Mateo**	**Santa Cruz**	**Monterey**	**San Luis Obispo**	**Santa Barbara**	**Total**
1993	0	0	0	43 (3)	0	**43 (3)**
1994	0	0	0	115 (8)	15 (5)	**130 (13)**
1995	0	0	154 (5)	102 (6)	85 (4)	**341 (15)**
1996	0	0	8 (2)	88 (9)	78 (5)	**174 (16)**
1997	0	0	33 (2)	414 (27)	98 (7)	**545 (36)**
1998	0	0	0	34 (3)	0	**34 (3)**
1999	0	0	13 (3)	120 (12)	0	**133 (15)**
2000	7 (2)	0	170 (11)	51 (6)	1 (1)	**229 (20)**
2001	5 (1)	40 (1)	422 (23)	1 (1)	0	**468 (26)**
2002	0	0	532 (33)	24 (2)	0	**556 (35)**
2003	0	6 (2)	11 (1)	0	12 (3)	**29 (6)**
Total	**12 (3)**	**46 (3)**	**1343 (80)**	**992 (77)**	**289 (25)**	**2682 (188)**

Table 2. Data sources and contact for long-term monitoring studies in California used for long-term data analysis.

Location	**Years**	**Source**
Palos Verdes (4 sites)	1975-2006	Alan & Susanne Miller (Cal. State. U. Long Beach)
San Nicolas Is. (9 sites)	1981-2006	Glenn VanBlaricom (Univ. Washington & U.S. Geological Survey)
Channel Islands National Park (10 sites)	1985-2006	Dan Richards (National Park Service)
Laguna Beach (1 site)	1983-1986	Brian Tissot (Washington State Univ.)
Santa Cruz Is. (7 sites)	1986-2003	
Año Nuevo Is. (4 sites)	1987-1995	
Diablo Canyon (4 sites)	1976-2006	John Steinbeck (Tenera Environmental)
Central California (13 sites)	1992-2006	Pete Raimondi (Univ. Calif. Santa Cruz)

Table 3. Field methods for long-term monitoring studies in California used for long-term data analysis.

Data source	**Survey technique**
Alan & Susanne Miller (Cal. State. U. Long Beach)	Thirty, randomly allocated 1m^2 quadrats per study site
Glenn VanBlaricom (Univ. Washington & USGS)	Two to seven, fixed plots of varying size (14-80 m^2) per study site
National Park Service (Dan Richards)	Five, fixed plots of varying sizes (0.9-11.2 m^2) per study site
Brian Tissot (Washington State University)	Three to five, fixed 2-m wide band transect of variable length (11-30 m^2) per study site
Tenera Environmental (John Steinbeck)	Ten, fixed 1m^2 quadrats per study site
Pete Raimondi (Univ. Calif. Santa Cruz)	Three, fixed plots of varying sizes (2-34.6 m^2) per study site

Table 4. Study sites for long-term monitoring studies in California used for long-term data analysis.

Site #	Location	Study site	Data source
1	Laguna Beach	near Emerald Bay	Tissot
2	Palos Verdes	Abalone Cove 1	Miller
3	Palos Verdes	Abalone Cove 2	Miller
4	Palos Verdes	Pt. Vicente	Miller
5	Palos Verdes	Portuguese Bend	Miller
6	Santa Barbara Is.	Sea Lion Rookery	Richards
7	Anacapa is.	Harbor Seal Arch	Richards
8	Anacapa is.	Cat Rock	Richards
9	Santa Rosa Is.	NW Talcott	Richards
10	Santa Rosa Is.	Johnson's Lee	Richards
11	Santa Rosa Is.	Fossil Reef	Richards
12	Santa Rosa Is.	Ford Point	Richards
13	San Miguel Is.	Otter Harbor	Richards
14	San Miguel Is.	Harris Point	Richards
15	San Miguel Is.	Crook Point	Richards
16	Santa Cruz Island	Near Fourney Cove	Tissot
17	Santa Cruz Island	Fraser Point	Tissot
18	San Nicolas Is.	Sites 1-9	VanBlaricom
19	Government Point	near Point Conception	Raimondi
20	Boathouse	near Point Arguello	Raimondi
21	Stairs	between Pt. Arguello and Purisima Pt.	Raimondi
22	Purisima Pt.		Raimondi

Site #	Location	Study site	Data source
23	Diablo Canyon	Station 1 (North Control) +1 ft transect	Steinbeck
24	Diablo Canyon	Station 2 (North Control) +1 ft transect	Steinbeck
25	Diablo Canyon	Station 6 (Field's Cove) +1 ft transect	Steinbeck
26	Diablo Canyon	Station 19 (South Control) +1 ft transect	Steinbeck
27	Cayucos Pt.		Raimondi
28	Rancho Marino	near Cambria	Raimondi
29	Piedras Blancas		Raimondi
30	Pt. Sierra Nevada		Raimondi
31	Mill Creek		Raimondi
32	Andrew Molera State Park		Raimondi
33	Mal Paso	south of Pt. Lobos	Raimondi
34	Pt. Lobos		Raimondi
35	Stillwater Cove		Raimondi
36	Año Nuevo Is.		Tissot

Table 5. Three sources of population data for black abalone in the vicinity of theMonterey Peninsula.

Location	**Years**	**Source**
Pt. Pinos (16 sites)	June-July 2002	Kimura and Steinbeck 2003
Monterey (8 sites)	2002 and 2005	Micheli et al. in review
San Mateo, Santa Cruz, and Monterey Counties (22 sites)	1971-2002	John Pearse, unpublished data

Table 6. Threats assessment table for the wild population of black abalone in the USA and Mexico. Life stages affected are: A=adult (settled and > 45 mm shell length), J=juvenile (settled and between 10-45 mm shell length, L=larval (< 10 mm shell length). The relative time frame over which the threat was/is/will occur: H=historic, C=current, F=future. Severity of threat, geographic scope of threat, and level of certainty that the species is affected by the threat are ranked as VH=very high, H=high, M=medium, L=low. Overall threat level currently and into the future (over the next 30 years) are ranked as H=high, M=medium, and L=low. An overall ranking for each limiting factor is provided by scoring each as H=high, M=medium, or L=low.

ESA Listing Factor	Limiting Factors	Threats	Key Ecological Attributes	Life Stage Affected	Historic/ Current/ Future	Severity	Geographic Scope	Level of Certainty	Overall Threat Level	Overall Ranking
Habitat Destruction, Modification, or Curtailment	Substrate Destruction	Coastal development	Mortality Reduced growth	A, J, L	C, F	M	M	M	M	L/M
		Recreational access		A	H, C, F	M	M	M	M	
		Sea level rise		A, J	F	M	VH	L	M	
		Oil spills		A, J	C, F	M	M	M	M	
		Cable Repairs		A, J	C, F	L	L	L	L	
		Nearshore military operations		A, J	C, F	L	L	L	L	
		Benthic community shifts		A, J	H, C, F	M	H	M	M	
	Suboptimal water temperatures	Anthropogenic thermal (+ or -) effluent	Mortality Reduced Growth	A, J, L	H, C, F	M	L	M	M	M/H
		Long- and short-term climate change		A, J, L	C, F	H	VH	H	H	
	Reduced food quantity and quality	Long- and short-term climate change	Mortality Reduced growth	A	F	M	H	M	M	L
		Kelp harvest		A	F	L	L	L	L	
		Competition		A, J	H, C, F	L	M	L	L	
		Invasive species		Unknown	F	Unknown	Unknown	Unknown	Unknown	
Overutilization	Low density	Historic overfishing	Reproductive potential	A	H	H	H	H	H	M/H
		Current distribution pattern		A, J, L	C, F	VH	VH	H	H	
	Reduced genetic diversity	Historic overfishing	Mortality Reproductive potential	A, J, L	H	M	H	M	M	M
		Current distribution pattern		A, J, L	C, F	M	H	M	H	
Disease and Predation	Disease	Endemic bacterium and unknown	Mortality	A, J	H, C, F	VH	VH	H	H	H
		Aquaculture		A, J	C, F	M	M	L	M	
		Invasive species		Unknown	F	Unknown	Unknown	Unknown	Unknown	
	Predation	Sea Otter	Mortality Behavior Reduced growth	A	H, C, F	H	M	M	M	M
		Marine fishes and invertebrates		A, J, L	H, C, F	L	VH	M	M	
		Terrestrial mammals and seabirds		A	H, C, F	L	H	L	M	
		Invasive species		Unknown	F	Unknown	Unknown	Unknown	Unknown	

Inadequate Regulatory Mechanisms	Illegal Take	Poaching	Mortality Reproductive potential	A	H, C, F	H	H	H	H	M/H
		Accidental take		A, J	H, C, F	M	M	L	M	
		Inadequate law enforcement		A	H, C, F	H	H	M	H	
		Aquaculture		A, J	C, F	M	M	L	M	
Other Natural or Man-made Factors	Environmental pollutants/toxins	Agricultural and urban runoff	Mortality Reduced growth	A, J, L	H, C, F	M	M	L	M	L/M
		Industrial waste		A, J, L	H, C, F	L	L	L	L	
		Power plant effluent		A, J, L	H, C, F	M	L	M	M	
		Liquefied natural gas terminals		A, J, L	F	L	L	L	L	
		Desalination plants		A, J, L	C, F	L	L	L	L	
		Heavy metals		A, J, L	F	L	M	L	M	
		Environmental estrogens		A	F	L	M	L	M	
		Oil spills		A, J	C, F	M	M	M	M	

Table 7. Demographic "risk matrix" evaluation worksheet for black abalone (Haliotis cracherodii). Mean risk (standard deviation) are reported for each demographic risk category on a 5-point scale (1-very low risk; 2-low risk; 3-moderate risk; 4-moderate/high risk: 5-high risk). Threats and other risks are rated from a double plus (++) strong benefit to double minus (--) strong detriment.

Risk category	**Mean Score (STD)**
Abundance Severe declines in abundance (>90%) have occurred at the majority (76%) of long-term monitoring sites, including all sites in southern California (Tissot 2007). Additionally, the high risk scored for abundance is attributable to populations declining to densities below the minimum threshold density for successful fertilization success (0.75 – 1.1 m^{-2}).	4(0)
Growth and Productivity Population growth is negative in all areas south of Cayucos. Except for two isolated island populations, all monitored populations have exhibited recruitment failure.	4.25 (0.88)
Diversity The loss of genetic diversity in mainland and island populations severely limits the species' capacity for adapting to environmental change and or responding to the rapid spread of disease. The loss of populations in the southern extent of the species' range will likely impede the re-colonization of aggregations adapted to the environmental conditions in the region. Poor connectivity between populations suggests that even if the local genetic diversity exists for disease resistance, any resistance is not likely to spread and establish itself in other extant populations.	4(0)
Spatial Structure and Connectivity Dispersion data among local populations indicates that there is poor connectivity among populations. Such limited connectivity reduces the likelihood that disease resistance to withering syndrome, if it exists, will spread to other populations. Poor connectivity among populations makes it unlikely that populations extirpated by disease or local catastrophic events will be recolonized in the foreseeable future	4.25 (0.46)
Threats and Other Risks[2] Severe threat is posed by the manifestation and continuing spread of withering syndrome. Increasing sea surface temperature will facilitate the spread of the disease to the remaining uninfected populations and may increase the virulence of the disease in many of the northern, more abundant populations where the pathogen is present. There is also concern about likely future habitat degradation due to ongoing coastal development and the possibility of an oil spill causing local mortality events and further habitat damage. Poaching and predation on black abalone was also noted as posing future threats and exacerbating demographic risks.	--

Table 8. The probability of effective extinction in 30 years for combinations of a range of values of S and R. Where S = probability that the northward spread of disease (withering syndrome) will cease very soon for reasons of the suitable geographic range and environmental tolerances of the agent, and R = probability that resistance will emerge very soon in the host. Each SRT member assigned an uncertainty to the S and R values using 10 votes to distribute among values of S (0, 5, 10%) and R (0, 2, 7, 10%).

	S			
R	0.00	0.05	0.10	subtotal
0.00	0.350	0.096	0.021	0.468
0.02	0.199	0.054	0.012	0.265
0.07	0.094	0.026	0.006	0.126
0.10	0.058	0.016	0.004	0.078
0.15	0.016	0.004	0.001	0.021
subtotal	0.717	0.196	0.044	**0.957**

Table 9. Evaluation of the overall level of extinction risk for black abalone (*Haliotis cracherodii*) using the “likelihood point” method (FEMAT, 1993). These evaluations do not consider protective efforts, and therefore are not recommendations regarding Endangered Species Act listing status. Each SRT member distributed 10 likelihood points among the three overall extinction risk categories. Placement of all 10 points in a given risk category reflect 100% certainty that level of risk reflects the true level of extinction risk for the species. Distributing points between risk categories reflects uncertainty in whether a given category reflects the true species status. Reported below are the mean overall level of extinction risk points (standard deviation) for each category.

	Overall Risk Category [1]		
	“In Danger of Extinction”	“Likely to become endangered in the foreseeable future”	“Neither ‘in danger of extinction’ or ‘likely to become endangered in the foreseeable future’”
Number of likelihood points	8.4(0.92)	1.6(0.91)	0(0)

Comments: All SRT members placed the vast majority of their likelihood points in the “in danger of extinction” category, and a minority of points in the “likely to become endangered in the foreseeable future.” One SRT member placed all their likelihood points in the “in danger of extinction” category. High to very high risks to the species’ abundance, growth/productivity, spatial structure/connectivity, and diversity contributed to the SRT’s assessment that the species’ is at high risk of extinction in the long and short terms. Other threats posed by disease (i.e. withering syndrome), suboptimal water temperatures; and illegal take exacerbate the risk of extinction faced by the species. The SRT estimated that there is approximately a 95% probability that black abalone will be effectively extinct in 30 years due to the progression of withering syndrome and the limited prospects for disease resistance becoming established. The threat posed by withering syndrome is worsened for local populations by thermal effluents, and throughout the species range by El Niño events and increasing sea surface temperatures with global climate change. Illegal take, and the limited resources afforded enforcement agencies, likely will intensify demographic risks already facing populations with critically low densities, and further aggravate the species’ risk of extinction.

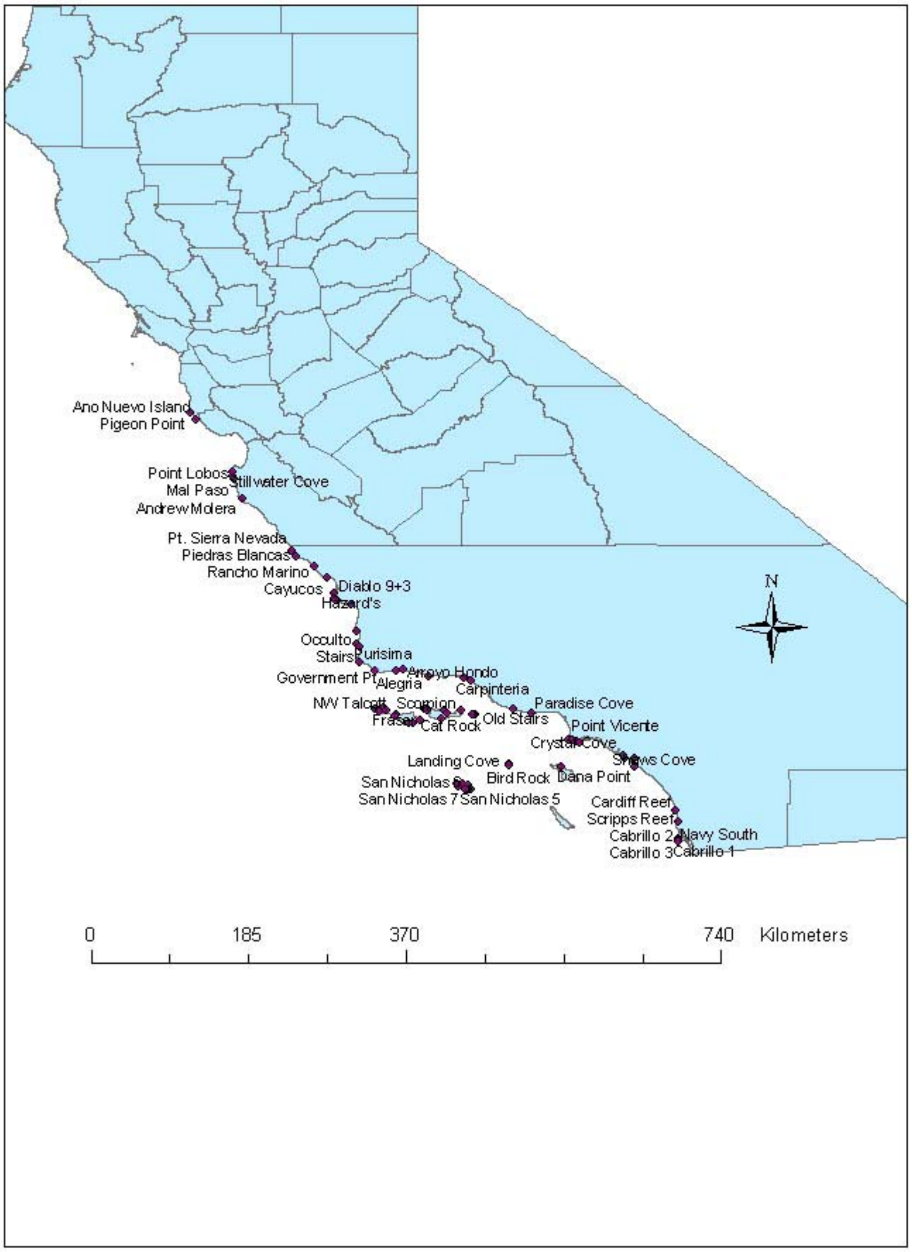

Figure 1. Study sites examined for long-term monitoring data and the presence of black abalone.

Figure 2. Several black abalone within a crevice on San Nicolas Island. Photo taken by Dave Witting (NOAA Restoration Center).

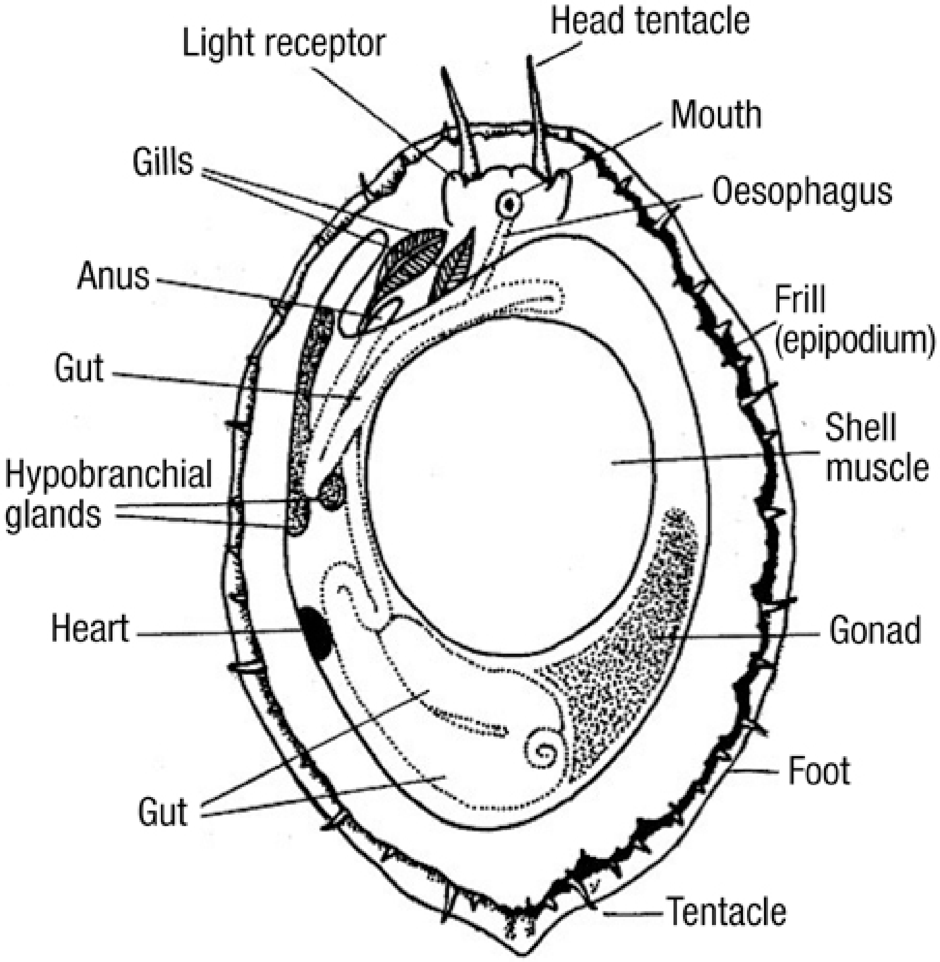

Figure 3. Anatomy of an abalone with shell removed. From Cox, 1962.

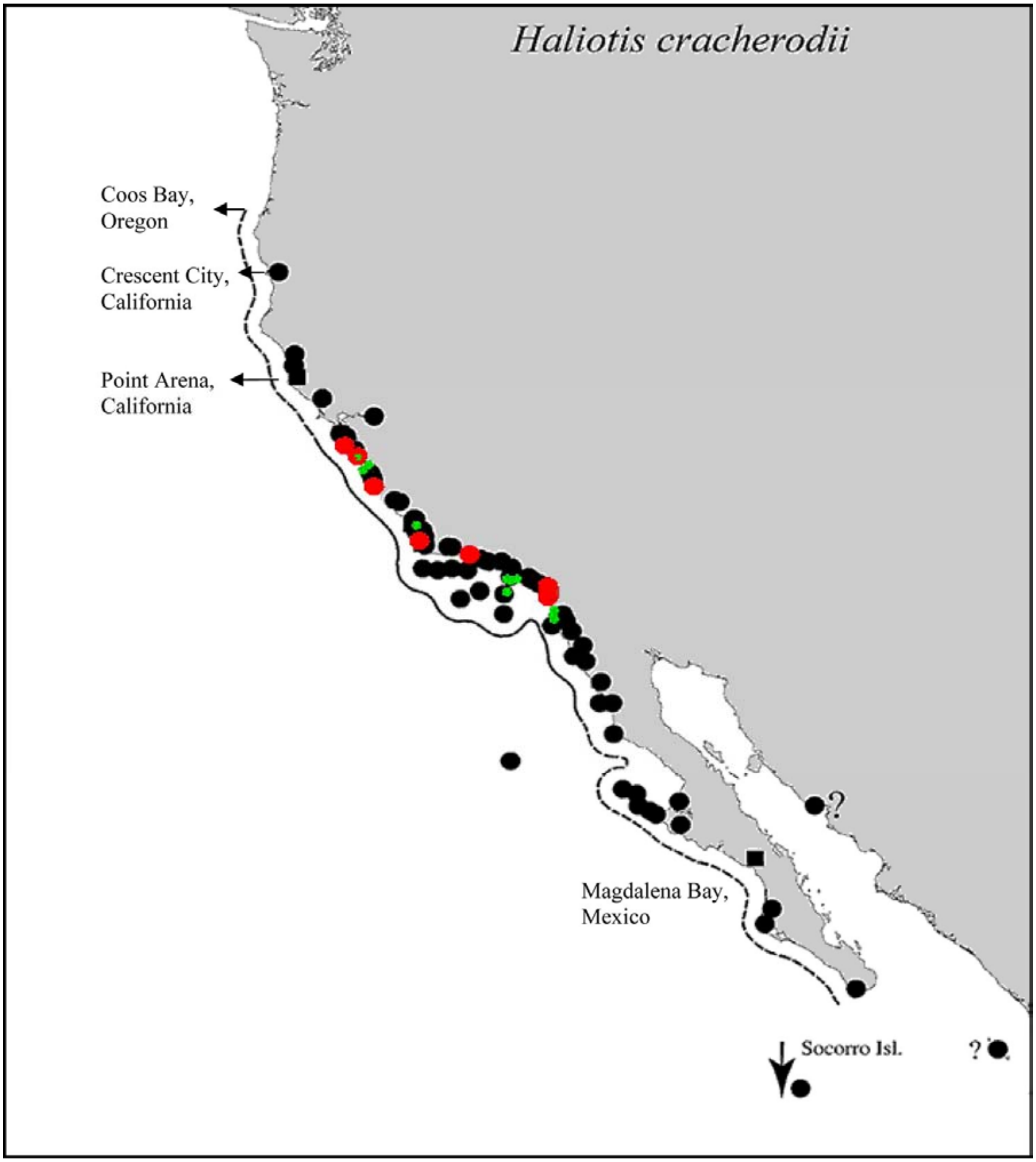

Figure 4. Geographic distribution of black abalone based on specimen records (after Geiger, 2004). A continuous line shows the range on which most experts agree, broken lines show the range that some authors mention, others do not. Circles indicate specimen records, squares indicate literature record, question marks show a dubious record. Dots in red are new records not published in Geiger (2000), dots in green are from the Australian Museum, Sydney. Map adapted from: http://www.vetigastropoda.com/ABMAP/crac-map.html

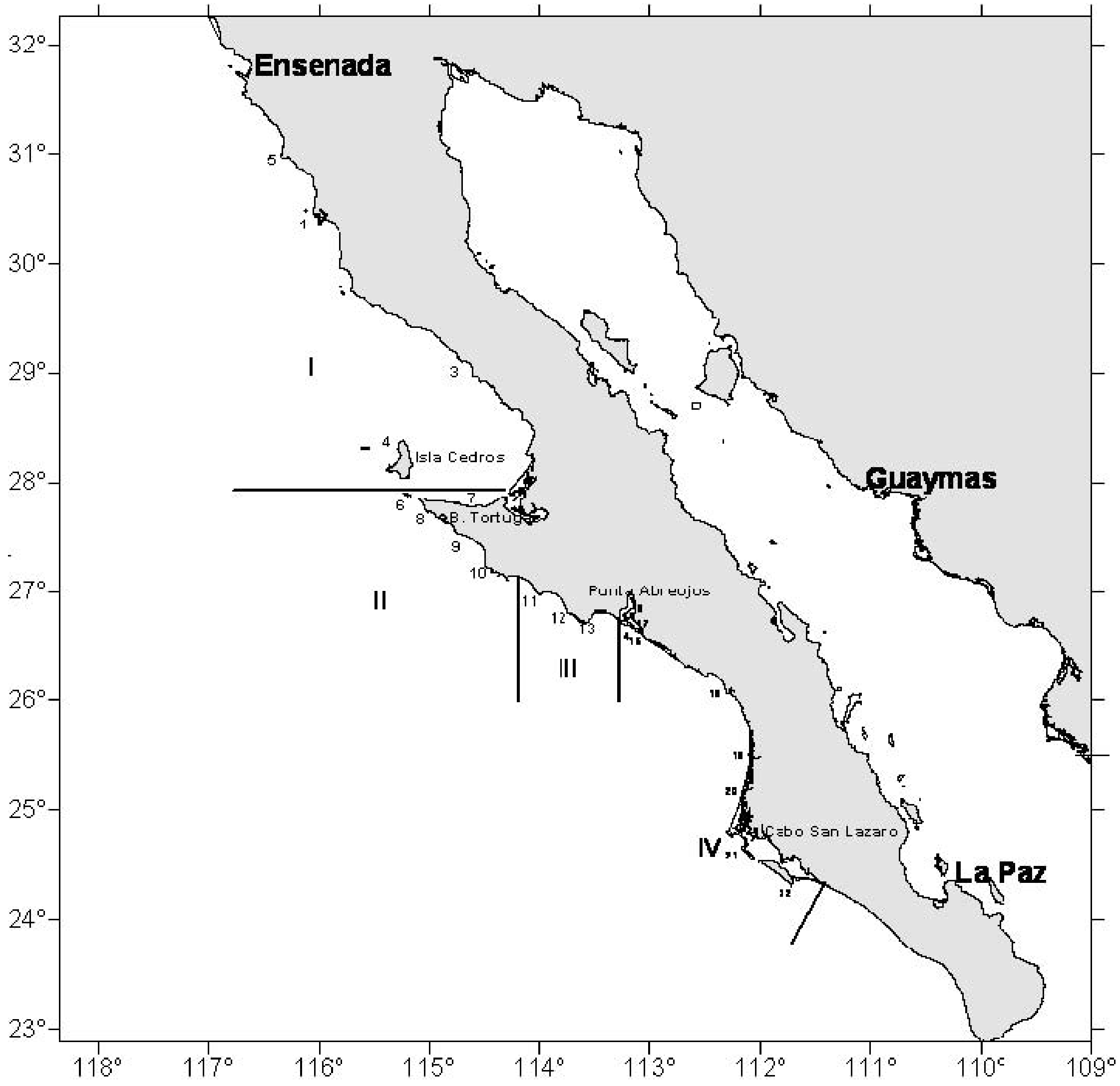

Figure 5. Four abalone fishery management zones (I-IV), encompassing 22 fishing cooperatives (1-22), along the Pacific coast of the Baja California Peninsula, Mexico. Adapted from Sierra-Rodriguez et al. 2006.

Figure 6. Three of the four National Marine Sanctuaries in California contain black abalone: the Gulf of the Farallones, Monterey Bay, and Channel Islands.

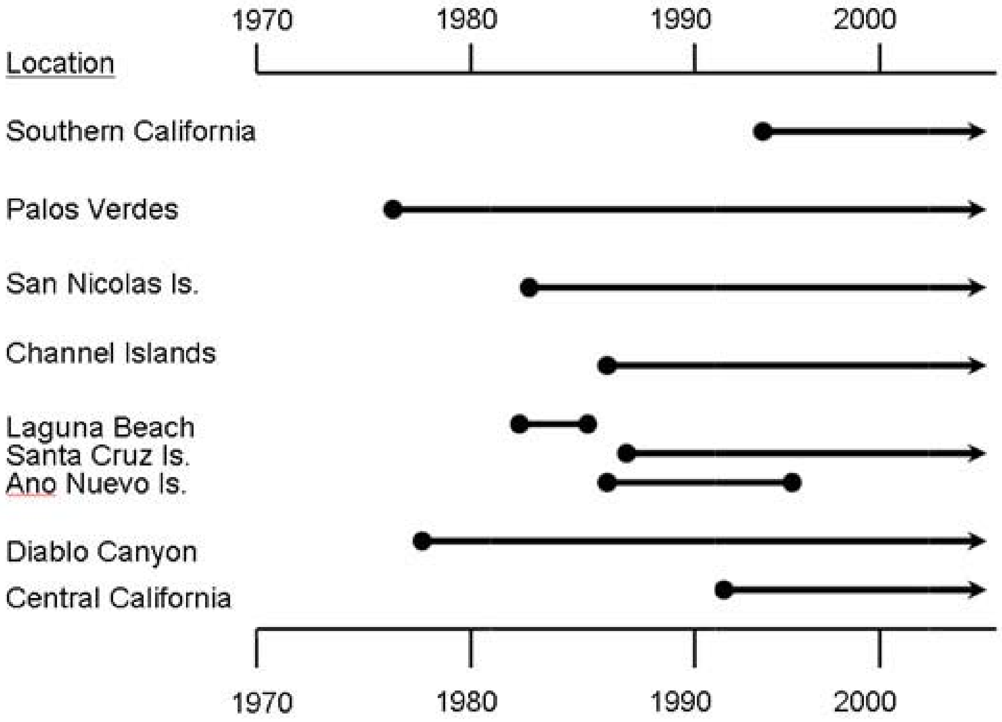

Figure 7. Time-series of long-term data sets on black abalone in California.

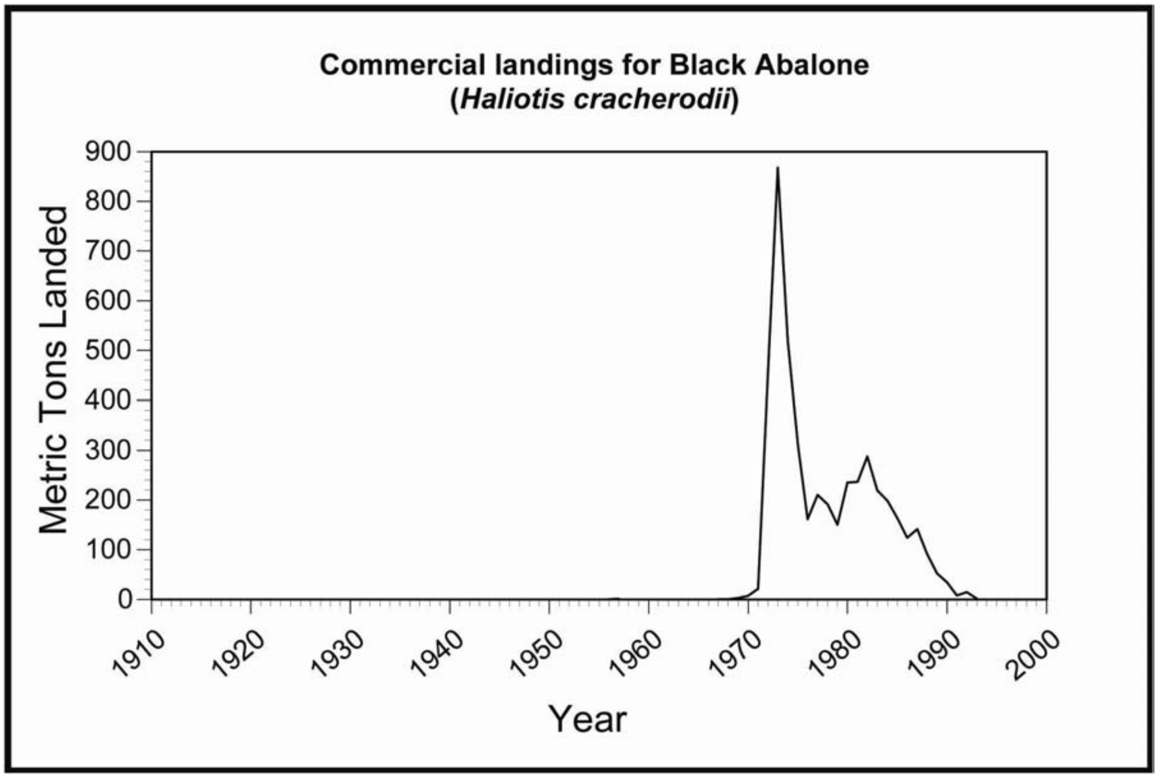

Figure 8. Abalone landings data recorded by the California Department of Fish and Game 1956-1993.

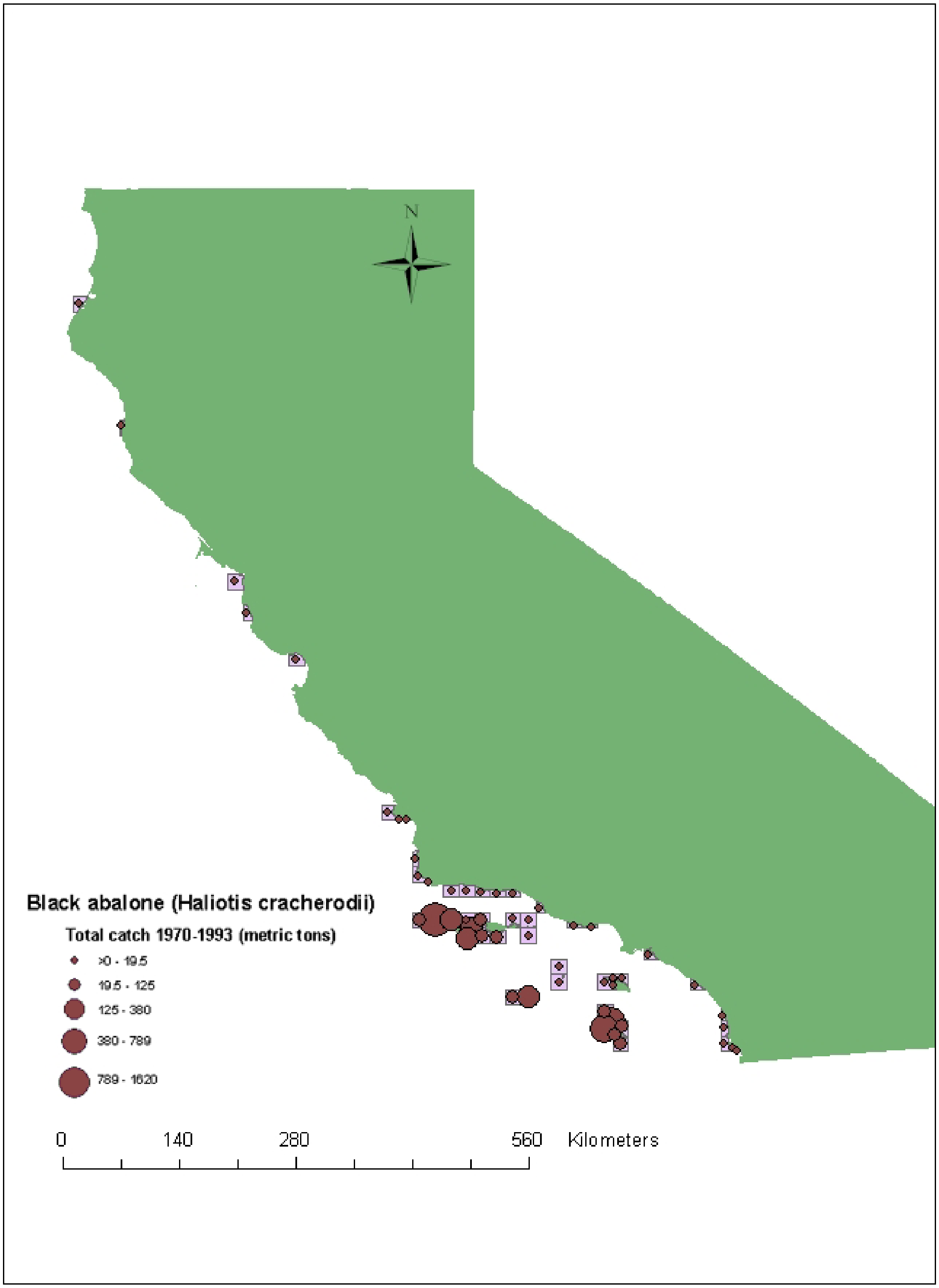

Figure 9. Total commercial catch of black abalone by fishery block in California, 1970-1993.

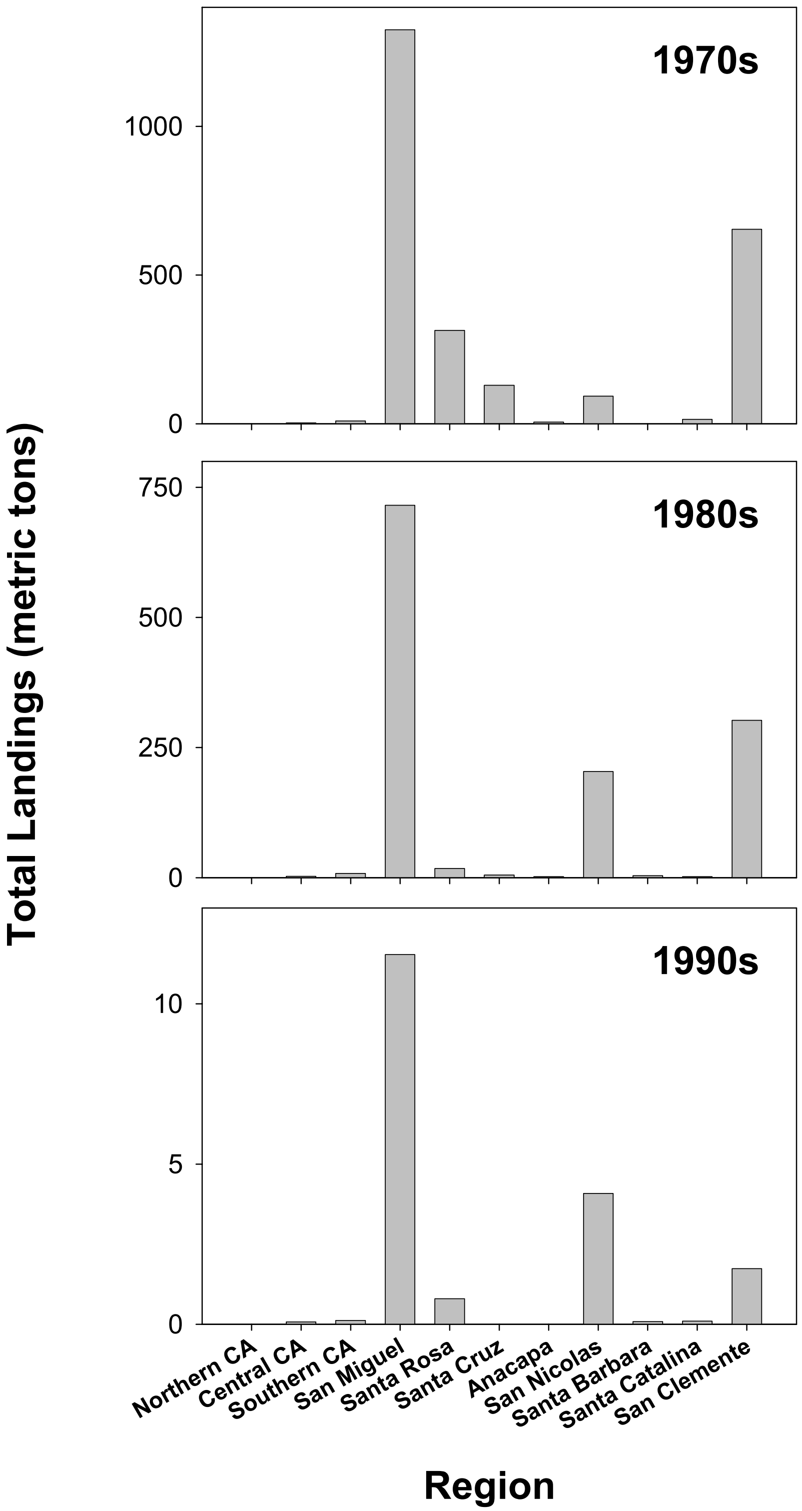

Figure 10. Commercial fishery landings by regions and decades in California.

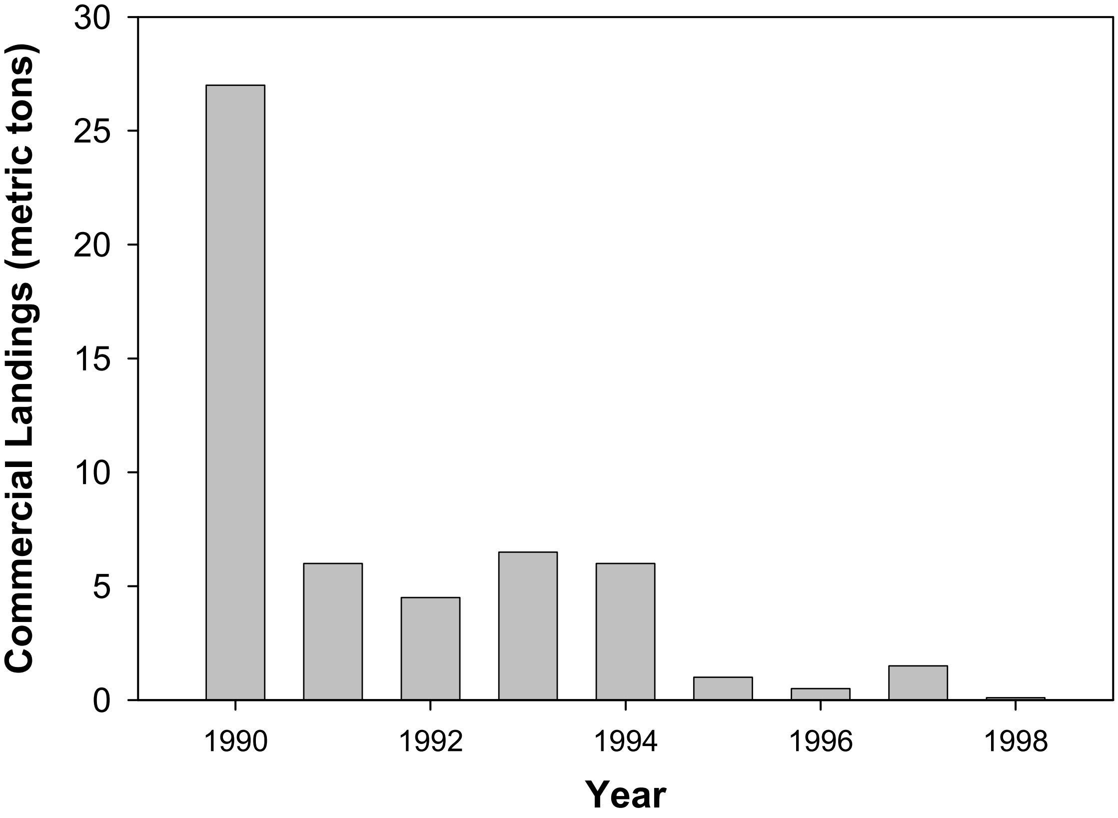

Figure 11. Commercial fishery landings of black abalone (weight of meat) in Baja California, Fishery Cooperative Zone 1, from 1990-1998. (data from Palleiro, cited in Hobday and Tegner, 2000). From Tissot 2007.

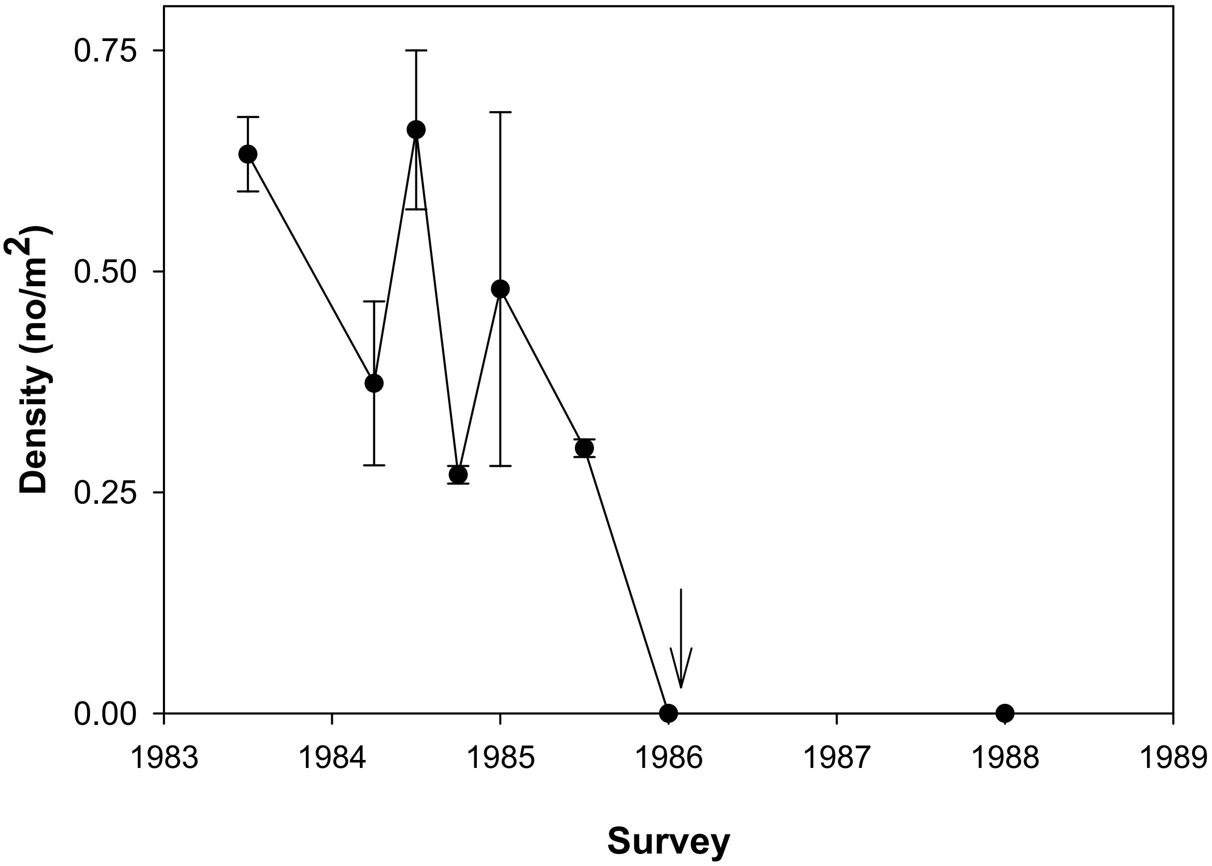

Figure 12. Trends in abundance of black abalone at Laguna Beach, 1983-1986 (Tissot, 1988). The arrow indicates the time at which the population went locally extinct.

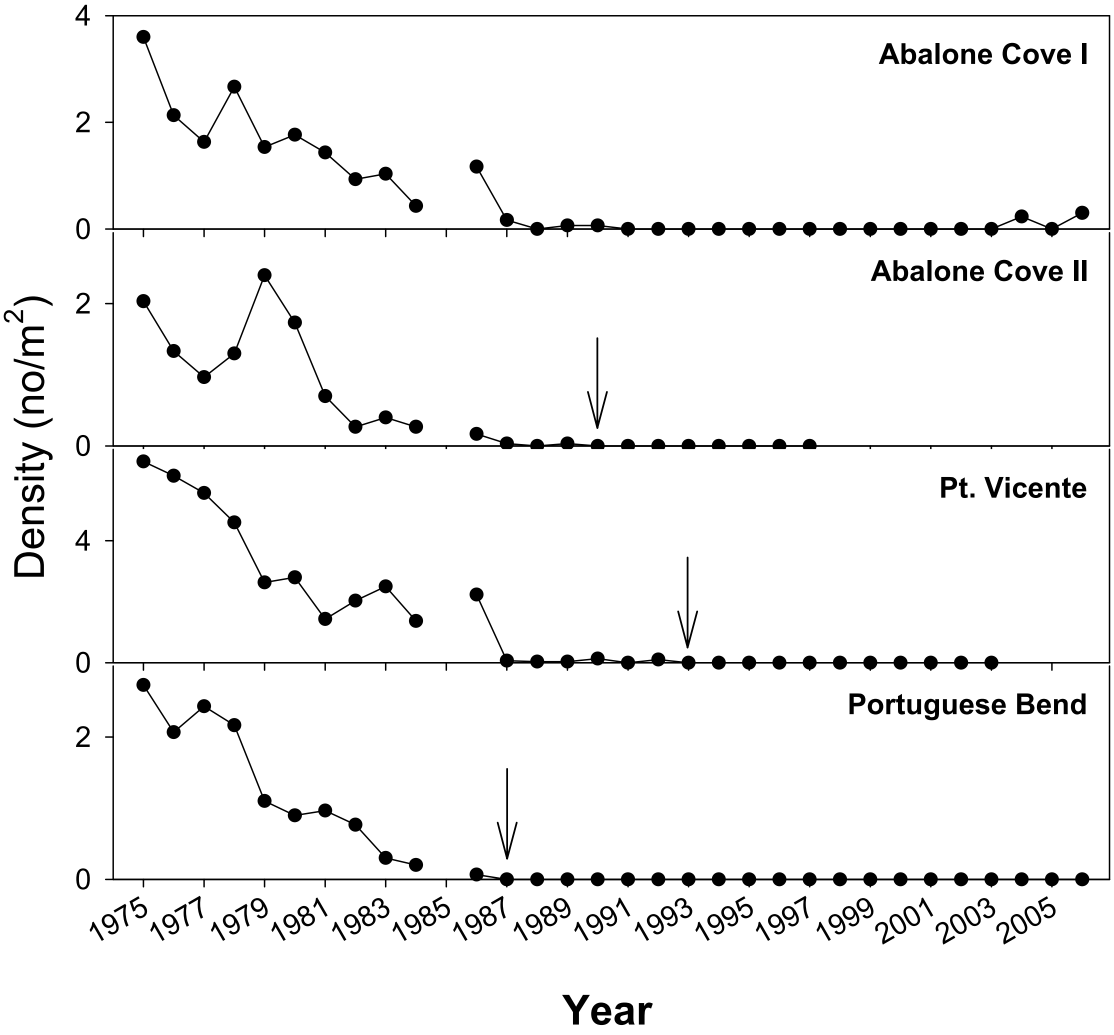

Figure 13. Trends in abundance of black abalone at four sites at Palos Verdes, 1975-2006. Arrows indicates times at which the populations went locally extinct.

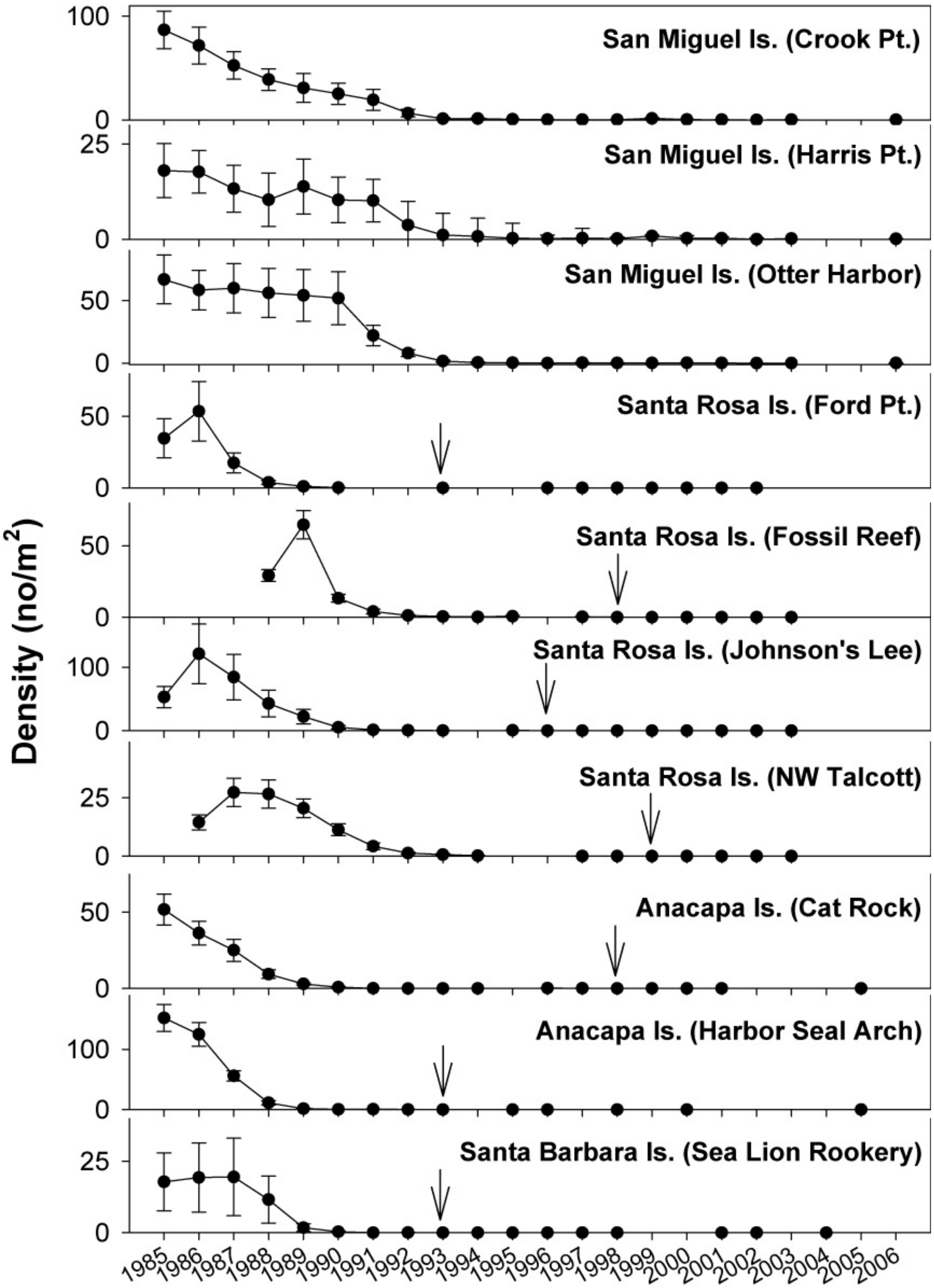

Figure 14. Trends in abundance of black abalone in the Channel Islands, 1985-2006. Arrows indicates times at which the populations went locally extinct.

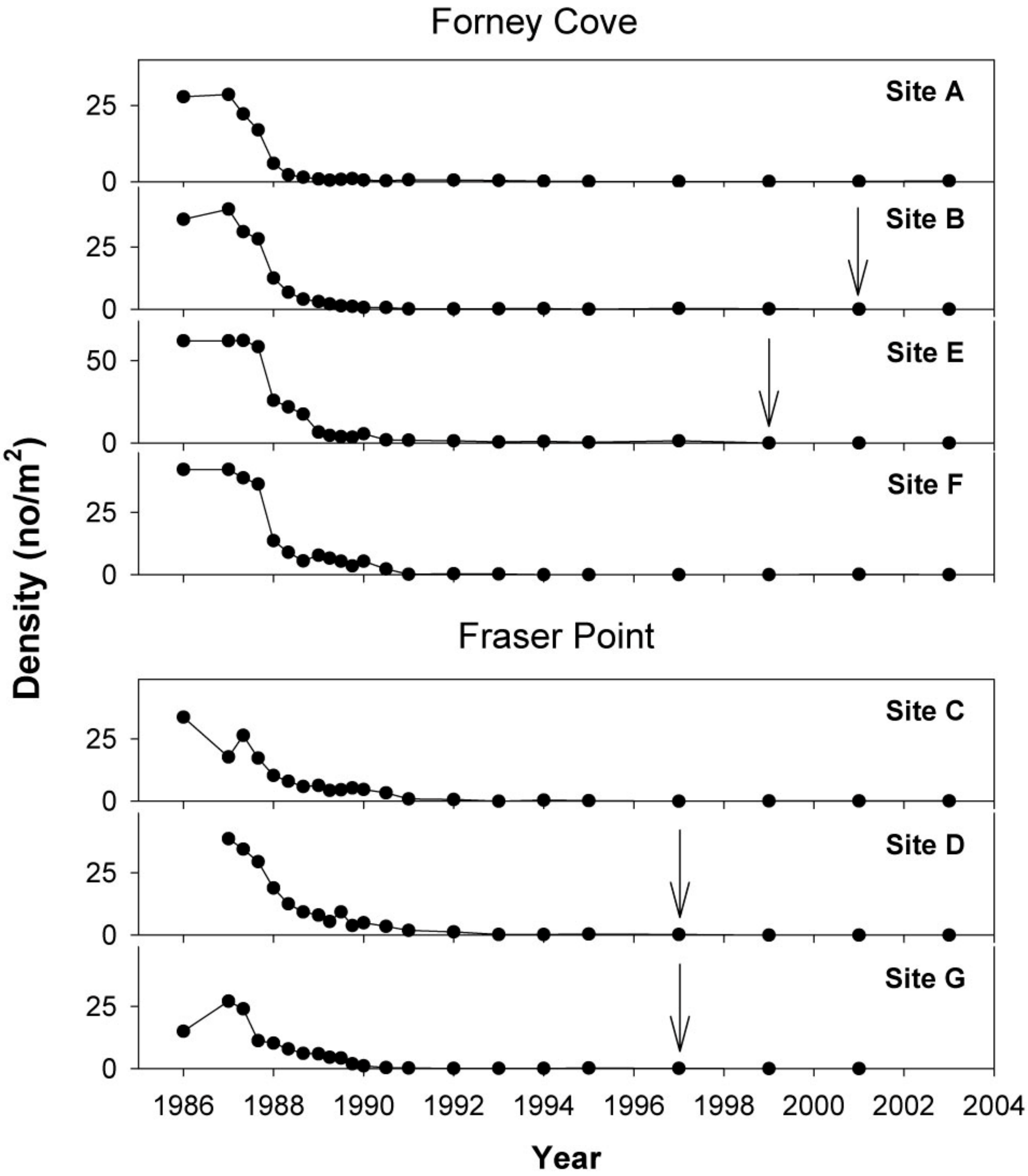

Figure 15. Trends in abundance of black abalone at seven sites at the west end of Santa Cruz Island, 1986-2003. Arrows indicates times at which the populations went locally extinct.

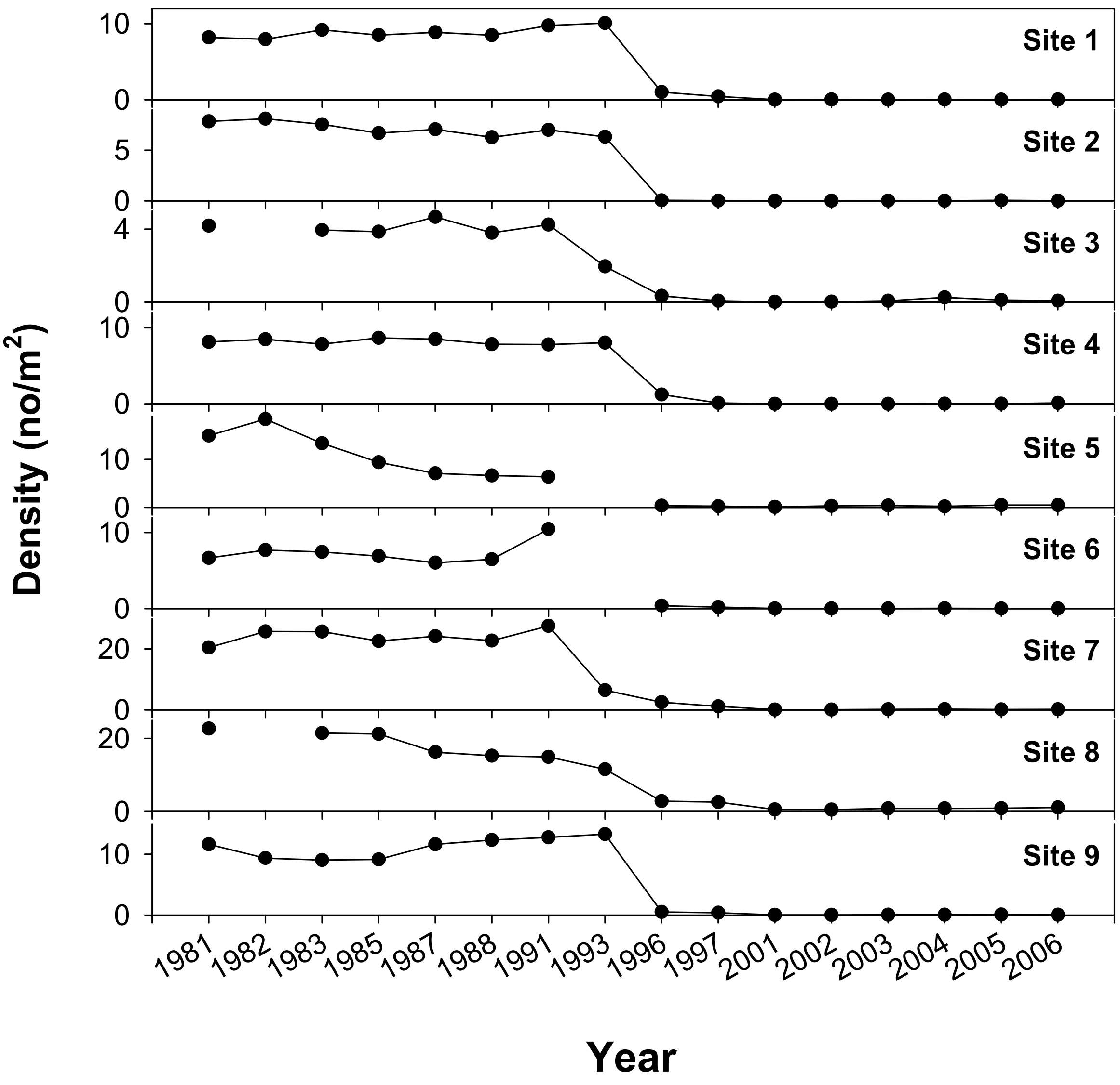

Figure 16. Trends in abundance of black abalone at nine sites at San Nicolas island, 1981-2006. No populations have gone locally extinct.

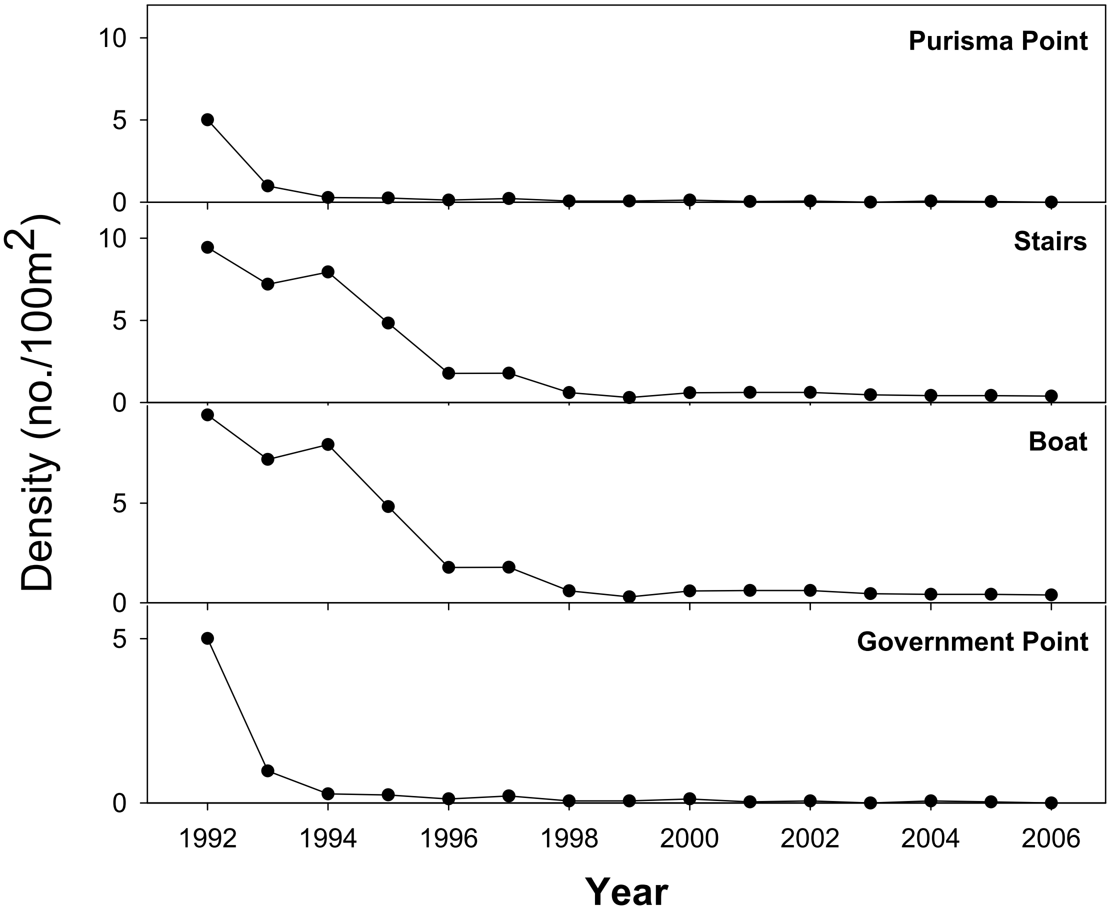

Figure 17. Trends in abundance of black abalone at 4 sites in central California, 1992-2006.

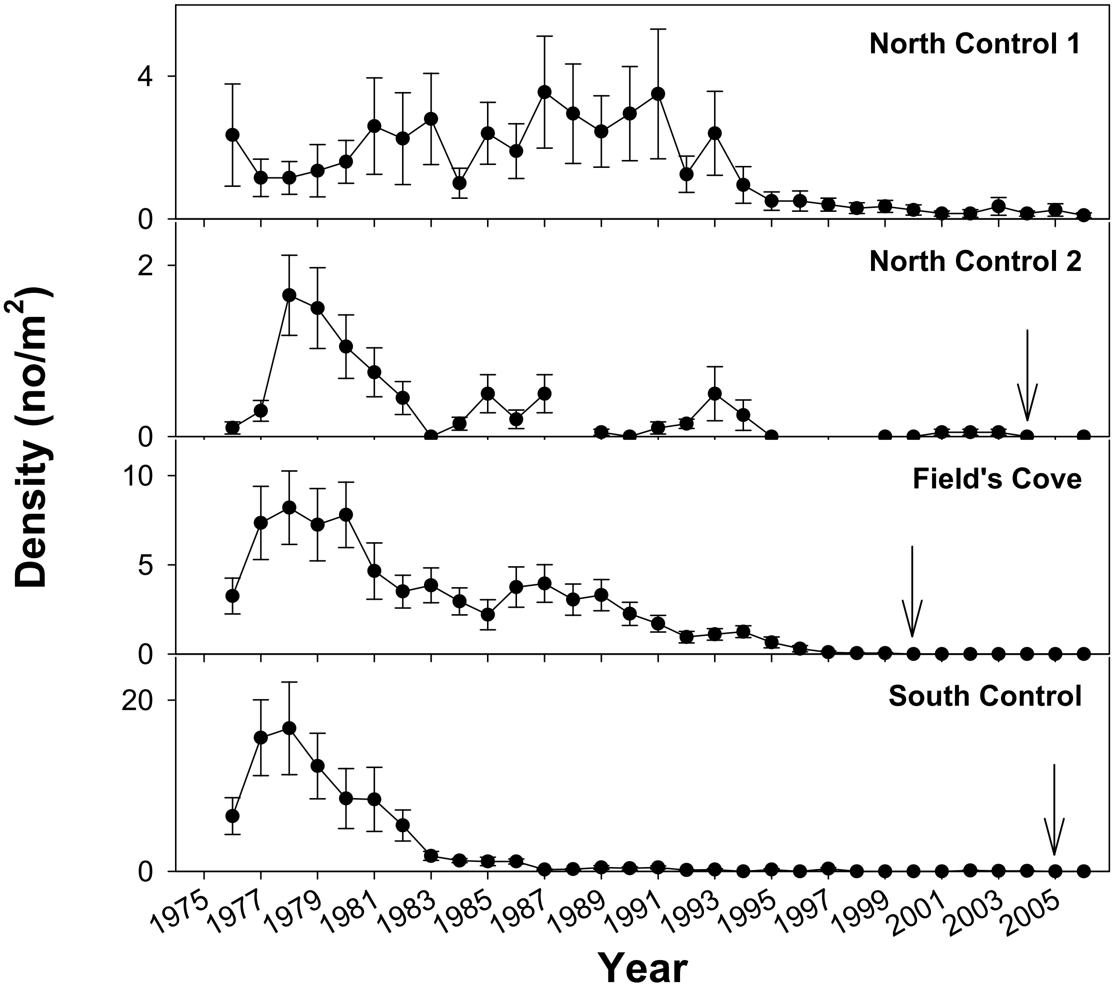

Figure 18. Trends in abundance of black abalone at four sites near Diablo Canyon, 1976-2006. Arrows indicate times at which populations went locally extinct.

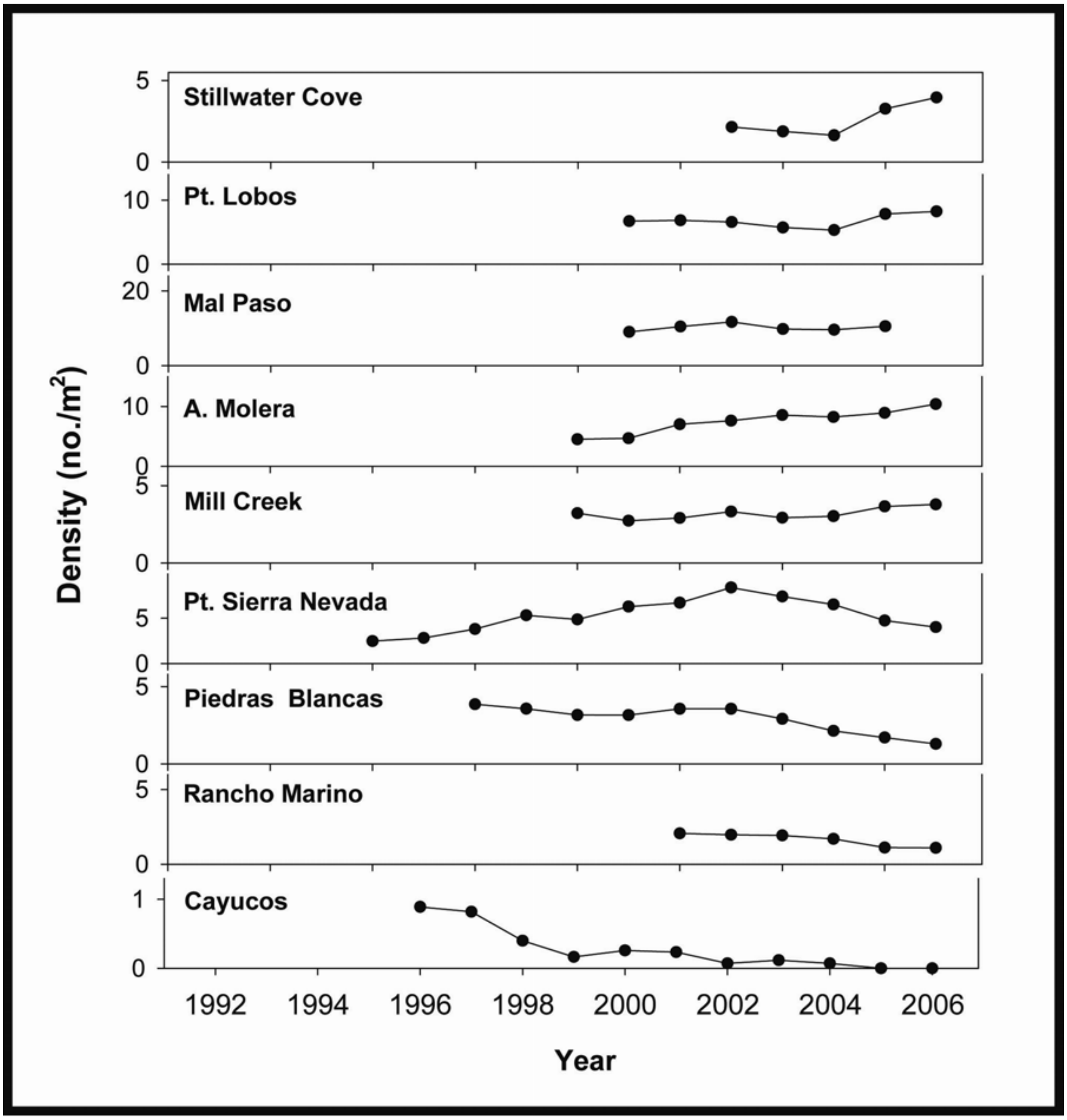

Figure 19. Trends in abundance of black abalone at six sites in central California, 1992-2006. The arrow indicates the time at which the population went locally extinct.

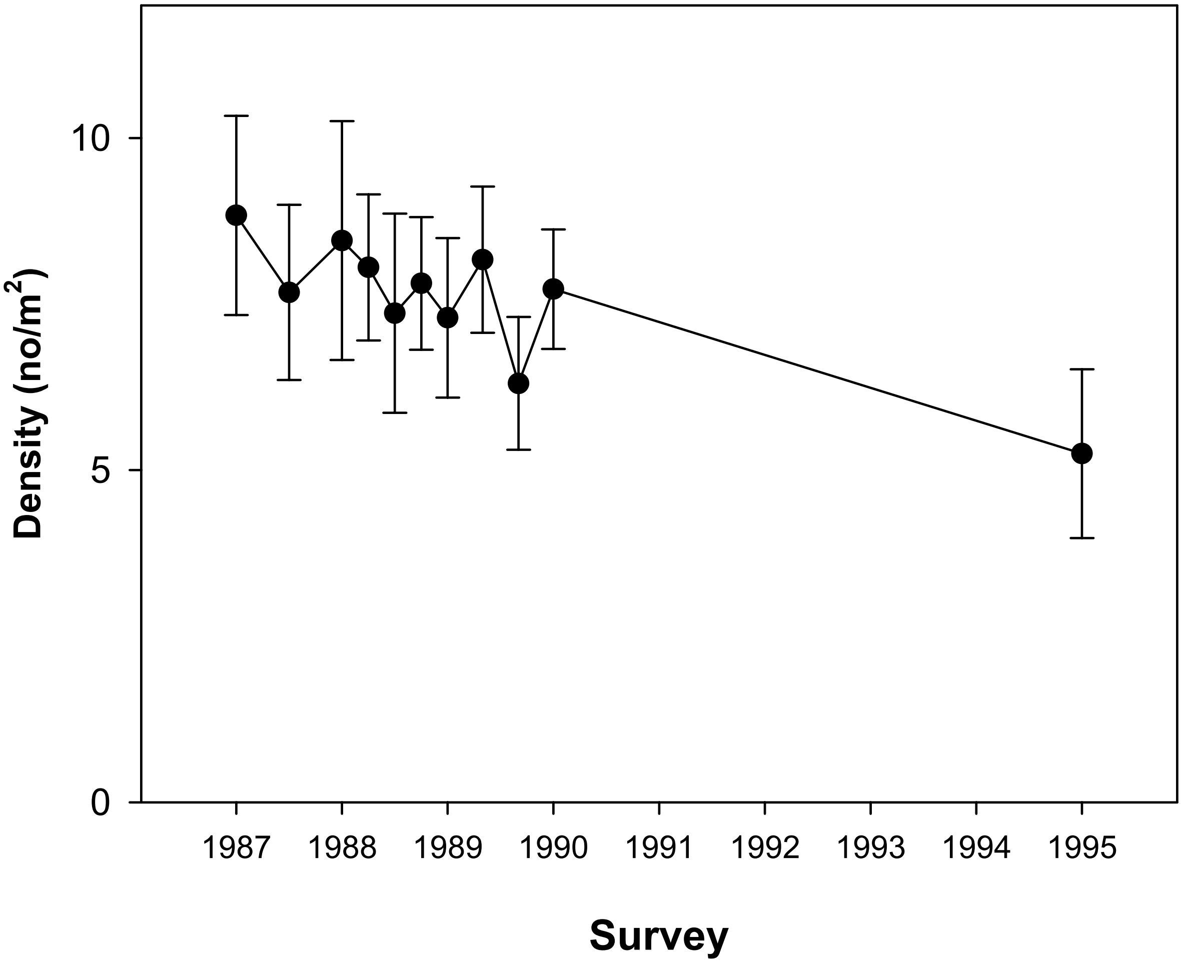

Figure 20. Trends in abundance of black abalone at Año Nuevo Island, 1986-1995.

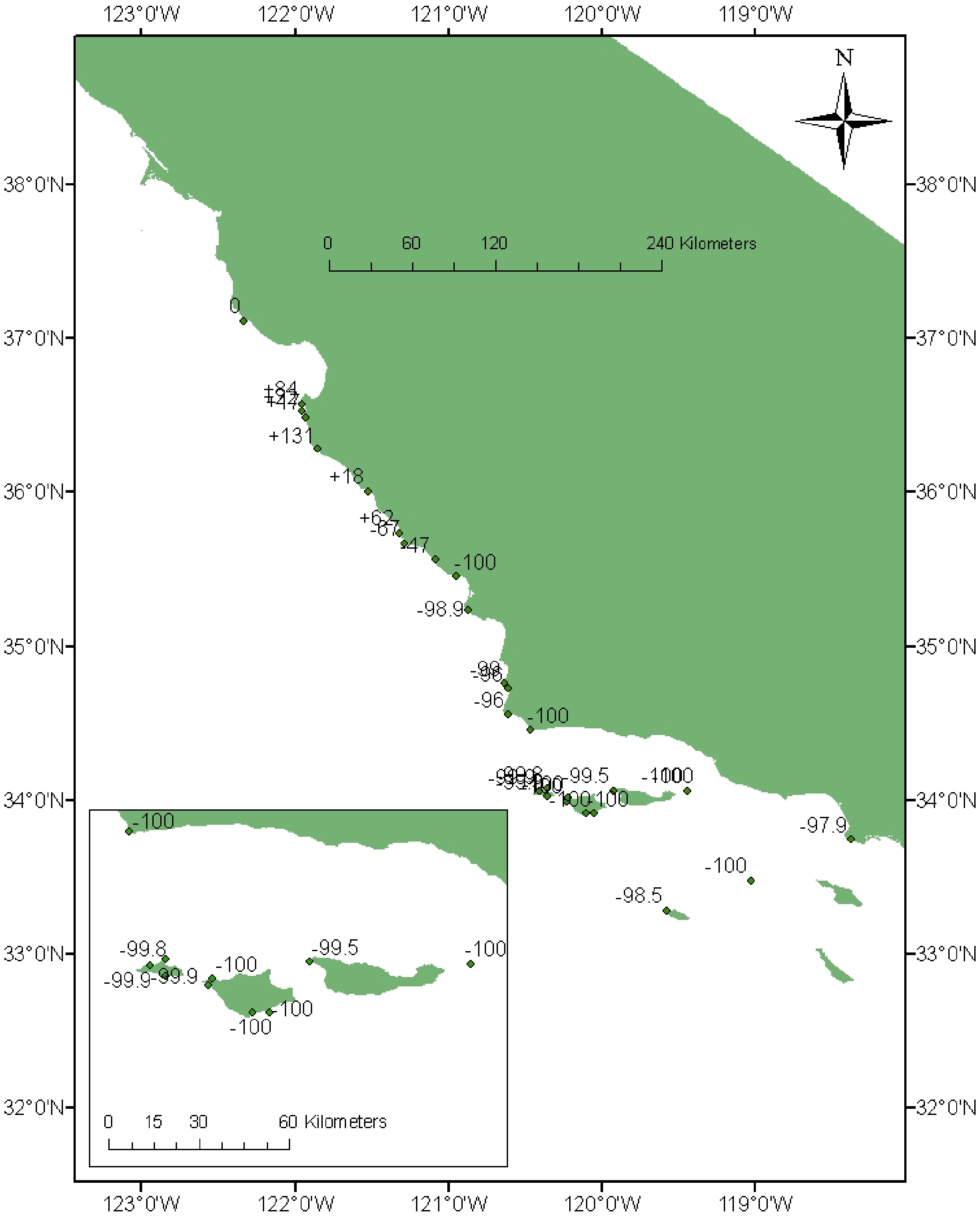

Figure 21. Percent declines in abundance at long-term monitoring sites in California due to withering syndrome. Declines were estimated by comparing pre-withering syndrome densities to post-withering syndrome densities in 2006 (see text).

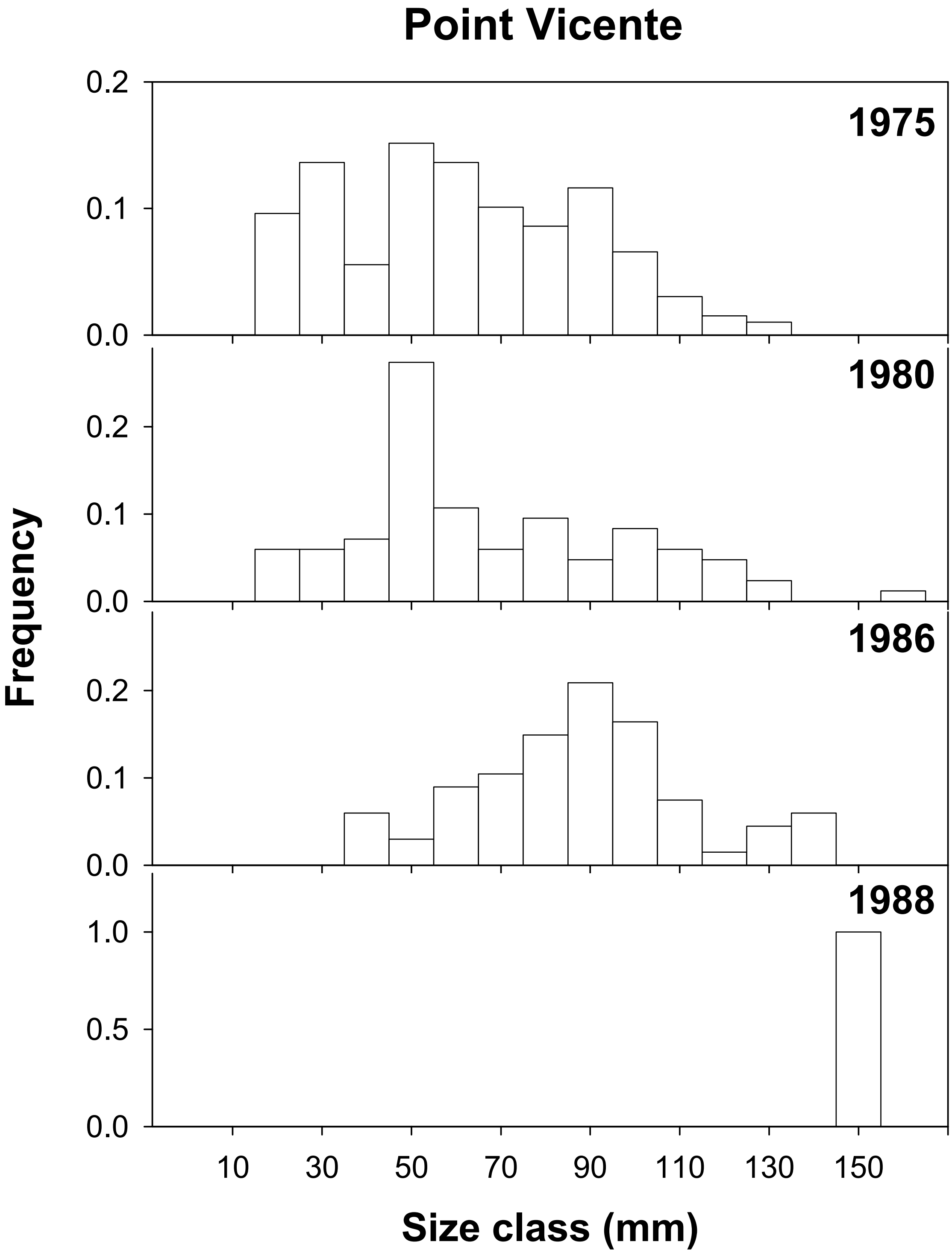

Figure 22. Shifts in abalone size distributions at Point Vicente from 1975-1988.

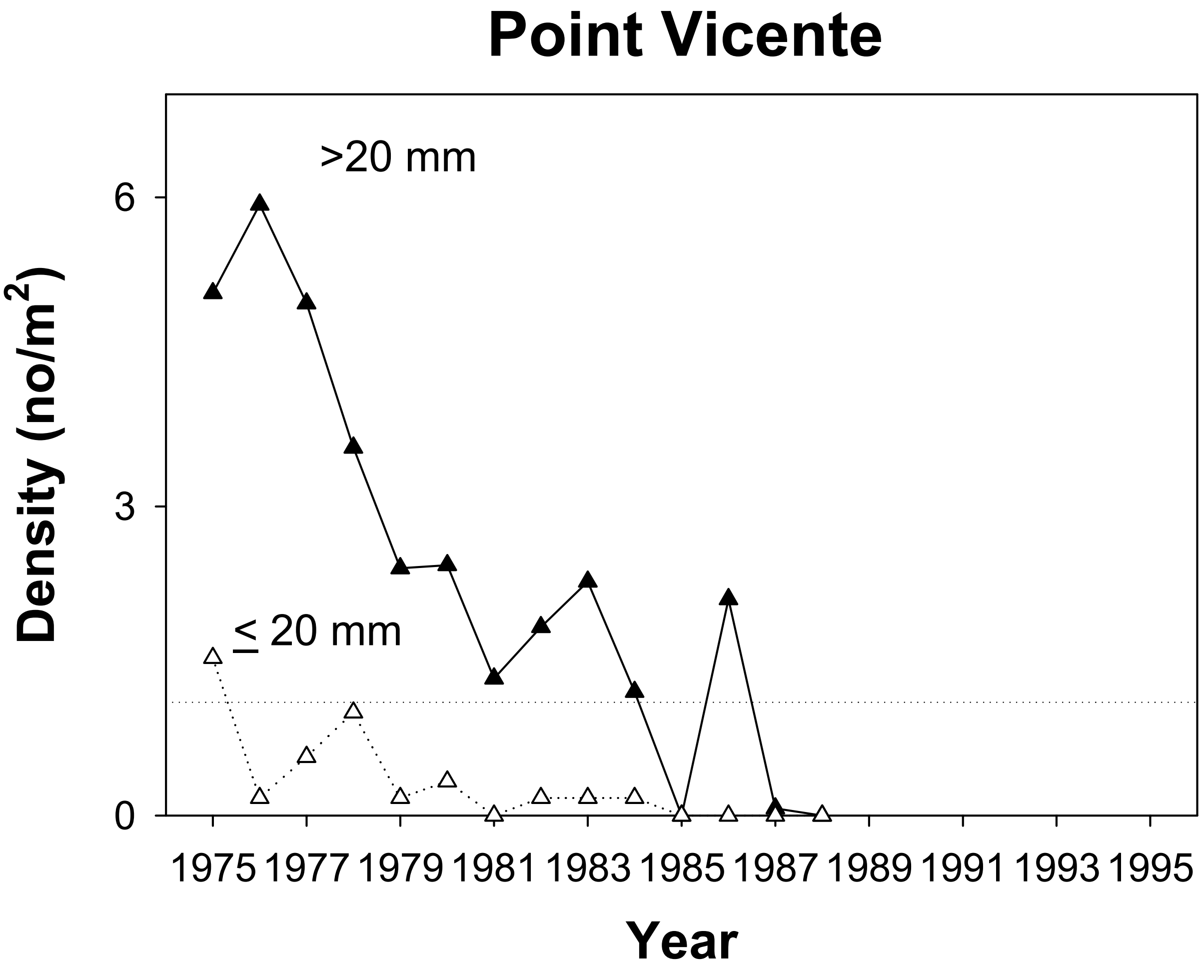

Figure 23. Relationship between the density of new abalone recruits (≤20mm) and adult density (>20mm) at Point Vicente. The dotted horizontal line indicates the estimated adult density below which recruitment failure occurred in 1985.

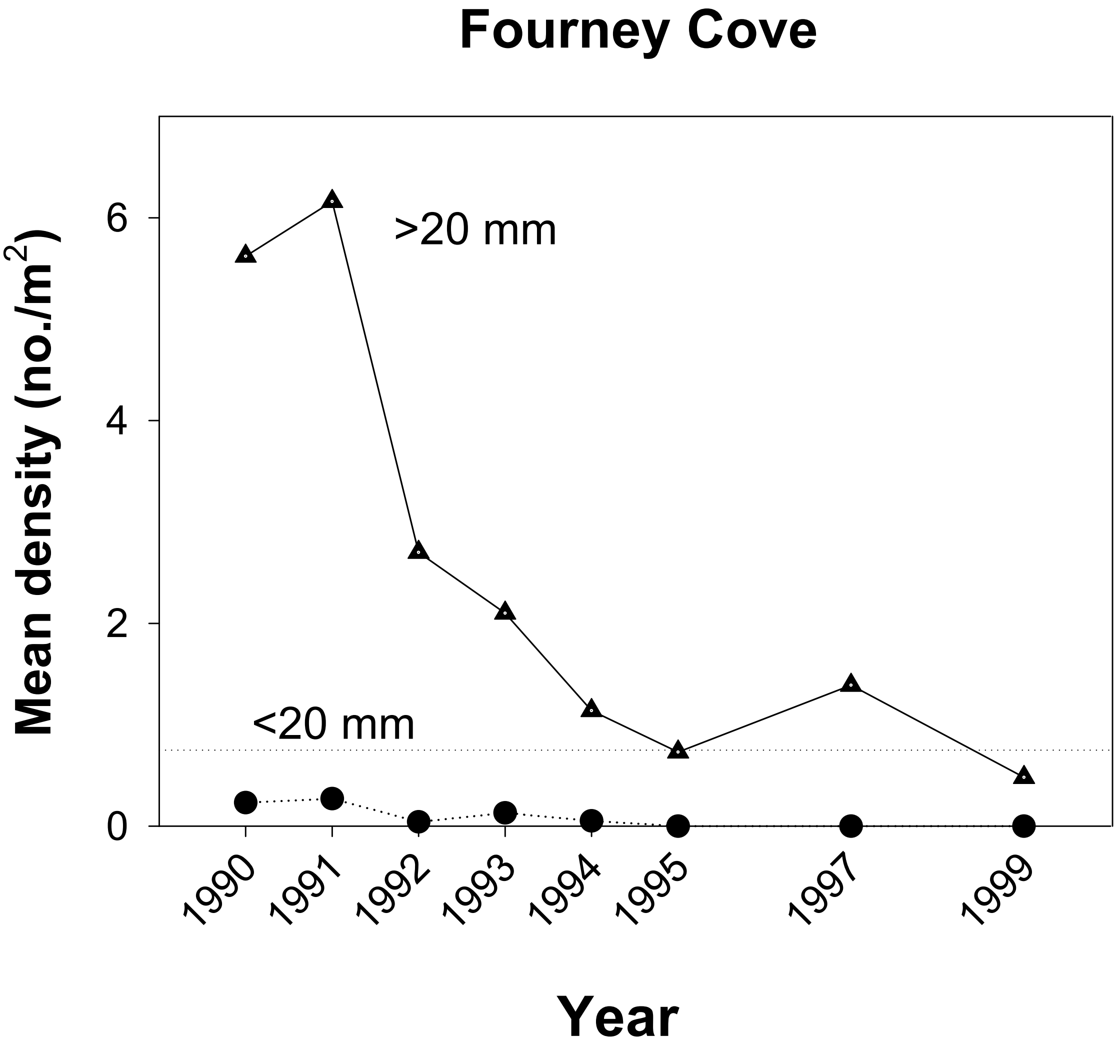

Figure 24. Relationship between the density of new abalone recruits (≤20mm) and adult density (>20mm) at Forney Cove, Santa Cruz Island. The dotted horizontal line indicates the estimated adult density below which recruitment failure occurred in 1995.

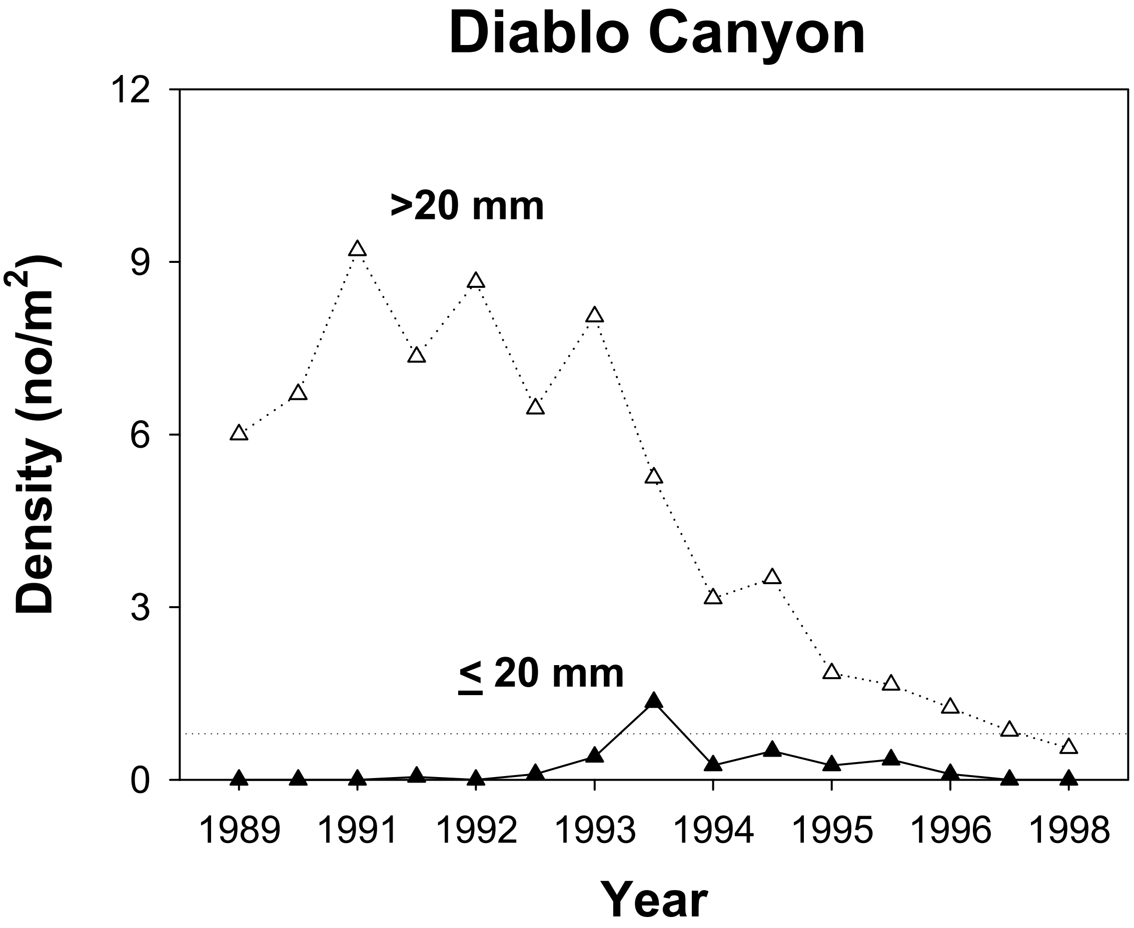

Figure 25. Relationship between the density of new abalone recruits (≤20mm) and adult density (>20mm) at Diablo Canyon. The dotted horizontal line indicates the estimated adult density below which recruitment failure occurred in 1997.

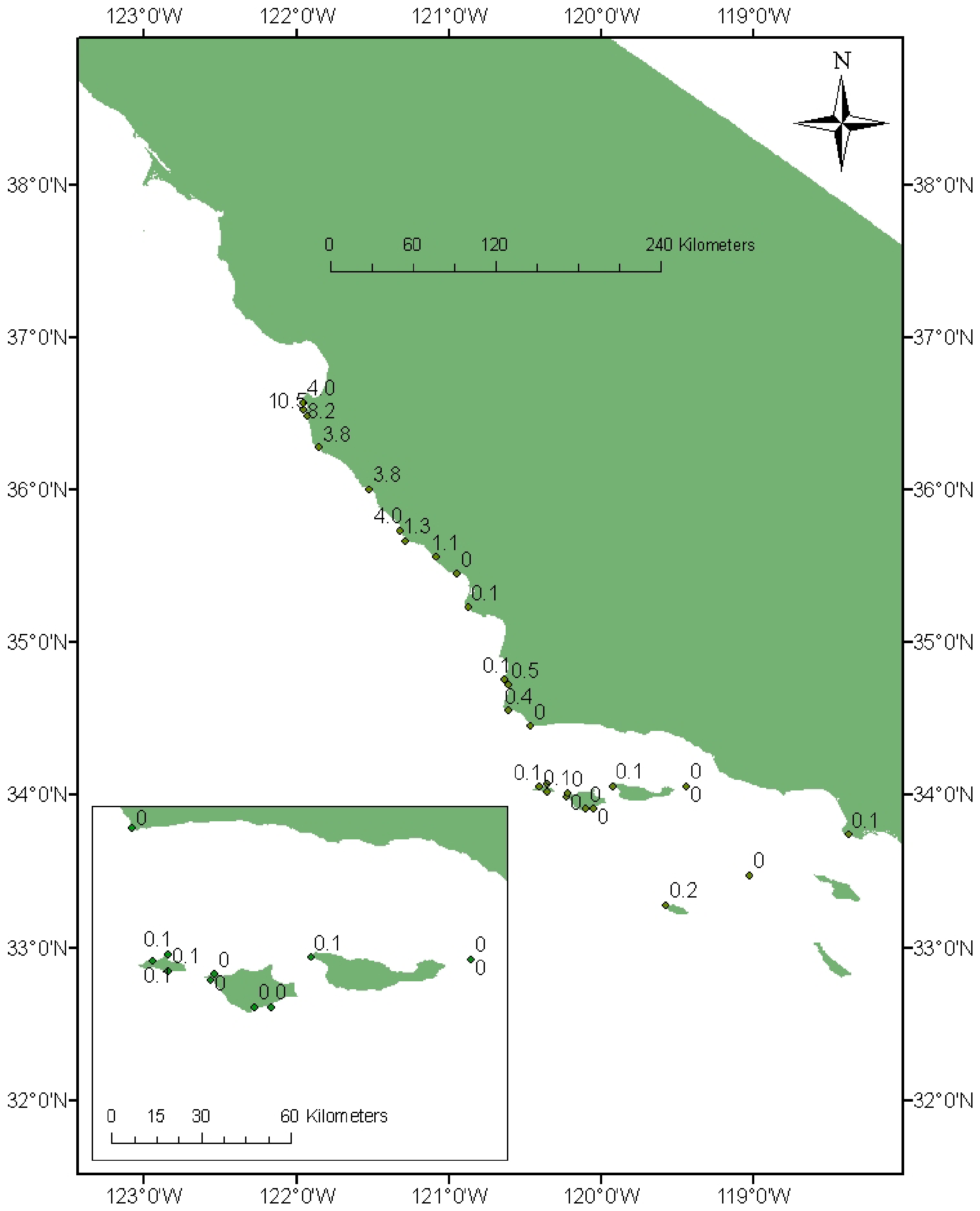

Figure 26. Mean density (no./m^2) of black abalone at long-term monitoring sites in California in 2002-2006.

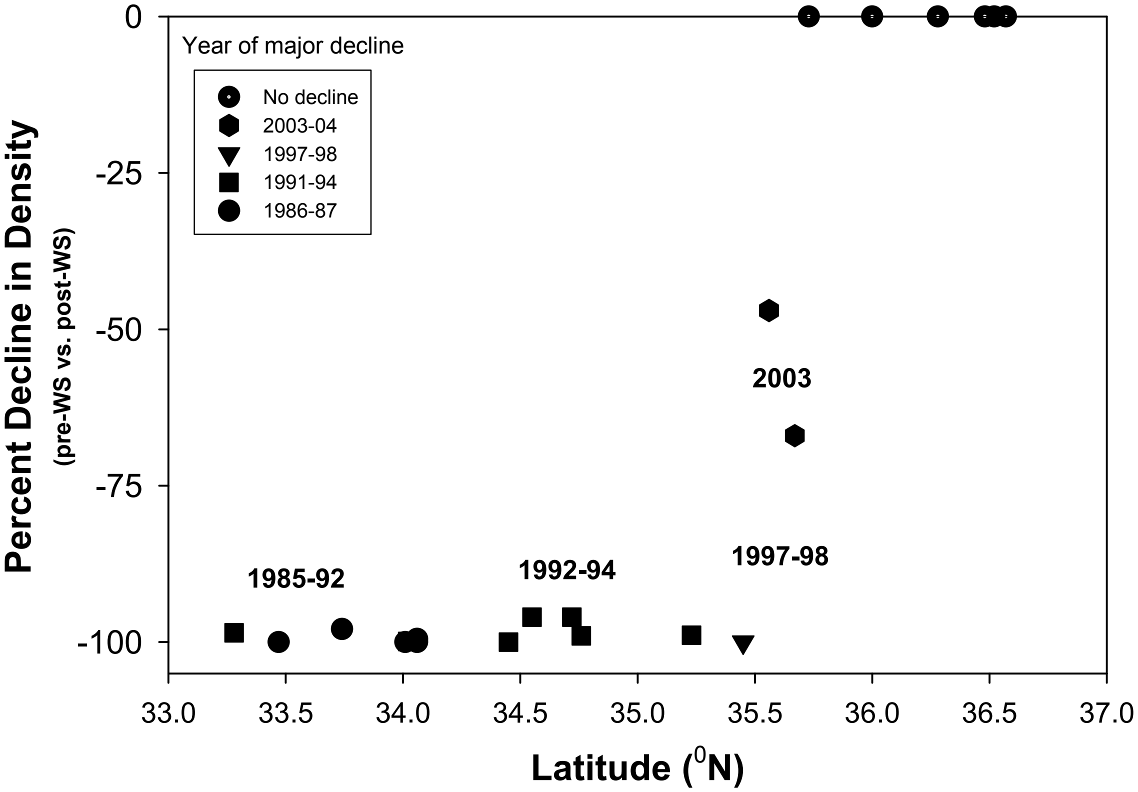

Figure 27. Geographic trends in the spread of withering syndrome and associated declines in black abalone populations in California. An anomaly to the trend of increasing northern expansion with time is San Nicolas Island at 33.2° N in 1991-94 (probably due to isolation, VanBlaricom et al., 1993).