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Spatial, temporal, and size-specific variation in mortality estimates of red abalone, *Haliotis rufescens*, from mark-recapture data in California

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Abstract

Estimates of size-specific mortality were made for red abalone, *Haliotis rufescens*, from mark-recapture data for three size classes at six sites in California. Instantaneous mortality for the smallest size class (≤100 mm) was 0.67 y^{-1} (0.52–0.84 y^{-1}, mean ± S.E.) to 1.02 y^{-1} (0.84–1.24 y^{-1}, mean ± S.E.) and decreased with increasing size in both northern and southern California. Mortality was spatially variable for legal size abalone (>178 mm), 0.05 y^{-1} (0.0–0.14 y^{-1}, mean ± S.E.) to 1.35 y^{-1} (1.17–1.56 y^{-1}, mean ± S.E.) in northern California and varied temporally in southern California, 0.27 y^{-1} (0.15–0.42 y^{-1}, mean ± S.E.) to 0.89 y^{-1} (0.73–1.08 y^{-1}, mean ± S.E.). Estimates of fishing mortality were 0.97 y^{-1} (±0.21S.E.) and 1.29 y^{-1} (±0.17S.E.) at two sites in northern California. Understanding the spatial and temporal dynamics of mortality estimates is critical for fishery management and conservation.

Keywords: *Haliotis rufescens*; Tag and recapture; Natural mortality; Fishing mortality; Recreational fishing; Red abalone; Program MARK

1. Introduction

Red abalone, *Haliotis rufescens*, is historically the most important commercial species of abalone in California and currently supports its only recreational abalone fishery (Cox, 1962; Karpov et al., 1998; Rogers-Bennett et al., 2002). *H. rufescens*, is the largest marine gastropod in California reaching sizes of 313 mm, maximum shell length (MSL) (Cox, 1962; Rogers-Bennett et al., in press) and is found in rocky intertidal and subtidal habitats on the west coast of the United States from Coos Bay, Oregon to Bahia Tortugas, Baja California Sur, Mexico (Cox, 1962). Demand for abalone meat and shells has resulted in declines of *Haliotis* species in California and lead to concern about the sustainability of the red abalone fishery in northern California (Karpov et al., 2000). This recreational fishery is an important resource for the north coast of California: in 2002 alone, more than 35,000 recreational fishers took >264,000 red abalone in 100,000 fishing days (Kalvass et al., in press). Concerns regarding the decline of red abalone stocks in California have led to a prohibition of commercial fishing throughout California, closure of the recreational fishery south of San Francisco Bay in 1997, and reductions in daily and annual limits in northern California in 2001 (California Senate Bill 463). The recreational fishery in northern California is currently regulated through the use of gear restrictions, a minimum legal size limit (178 mm, MSL), seasonal closures, and daily and annual bag limits (California Department of Fish and Game (CDFG), Marine Region, 2005).

Management of the red abalone fishery would benefit from accurate estimates of size-specific mortality rates. Natural mortality is a key population parameter used for a variety of predictive population models (Quinn and Deriso, 1999) and estimating this parameter with accuracy is essential for sound management (Clark, 1998). The importance of estimates of natural mortality has been shown empirically for conservation and fishery models of abalone. For example, the results of egg-per-recruit analyses of red and pink abalone (*H. corrugata*) populations are sensitive to changes in instantaneous natural mortality (Tegner

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et al., 1989). Furthermore, elasticity analyses of Lefkovitch matrix projection models of red and white abalone (*H. sorenseni*) revealed that model predictions are sensitive to changes in estimates of mortality (Rogers-Bennett and Leaf, 2006).

Few mortality estimates exist for red abalone populations in California. Tegner et al. (1989) used 5 years of length frequency distributions in southern California to estimate an instantaneous natural mortality, M, of 0.15 y^{-1}. Hines and Pearse (1982) found that in central California, where abalone are preyed upon by the California sea otter (*Enhydra lutris*), instantaneous mortality varied from 0.3 to 1.0 y^{-1}. Abalone mortality rates have been shown to vary with age, size, and habitat (Shepherd and Breen, 1992). At small sizes red abalone are found in cryptic crevice habitat and are preyed on by benthic invertebrates including octopuses (genus *Octopus*), crabs (genera *Loxorhynchus*, *Taliepus*, *Cancer*, and *Panulirus*), and sea-stars (genera *Pycnopodia* and *Astrometis*) (Tegner and Butler, 1985; Tegner et al., 1989). At larger sizes red abalone are found in cave or open habitat and are referred to as ‘emergent’ individuals because they are more visible by divers (Shepherd and Breen, 1992). Emergent red abalone are preyed on by fishes (genera *Scorpaenichthys*) and mammals (Hines and Pearse, 1982; Tegner and Butler, 1985; Tegner et al., 1989). Large emergent individuals may have a refuge from predation because of an increased ability to adhere to substrate, greater mobility, and the difficulty that predators have in handling them. Because of the differences in the intensity of predation throughout ontogeny, the use of survival rate estimates from one life stage, or size class, may not be sufficient for the population as a whole. Similarly, mortality rates may vary in time and space and knowledge of this variation is critical for management of the regional fishery.

In this study, we use Cormack–Jolly–Seber (Cormack, 1964; Jolly, 1965; Seber, 1965) algorithms to estimate size-specific apparent annual survival rates of red abalone using mark-recapture data from five sites in northern and one site in southern California. Estimates are made by specifying biologically relevant a priori models, using mark-recapture data, performing goodness-of-fit (GOF) testing to verify that mark-recapture data conform to model assumptions, estimating model parameters, and selecting the best fit model(s) (Lebreton et al., 1992). We use GOF and $\hat{c}$ dispersion criteria to censor data and construct a posteriori candidate models (Langtimm et al., 1998). We calculate instantaneous annual mortality from estimates of apparent survival of three size classes of abalone and compare mortality among the sites. We describe temporal patterns in mortality at one site in northern California over 5 years (1971–1976) and one site in southern California over 4 years (1978–1982). We then compare mortality at two fished and a reserve (unfished) site in northern California to estimate instantaneous annual fishing mortality, F.

2. Materials and methods

Red abalone tagging and census surveys in northern California were performed by personnel from the CDFG and Humboldt State University and in southern California by the CDFG and the Scripps Institute of Oceanography at the University of California at San Diego. Tagging and recapture surveys were conducted throughout the year in northern California at Point Cabrillo North Cove (NC) and Point Cabrillo South Cove (SC) (39.364°N, 123.830°W), Van Damme State Park (VD) (39.274°N, 123.791°W), Point Arena (PA) (39.269°N, 123.799°W), and Fort Ross State Park (FR) (38.512°N, 123.244°W) (Fig. 1) from 1971 to 1978. SC is inside the Point Cabrillo State Marine Conservation Area, an area where recreational and commercial fishing is prohibited and is monitored closely by personnel at the Point Cabrillo lighthouse. FR, PA, and VD are popular recreational fishing sites. NC may have experienced light fishing pressure from 1971 to 1974. Surveys in southern California were conducted annually in July from 1978 to 1984 (no sampling was performed in 1983) at a single location, Johnsons Lee (JL) (33.900°N, 120.110°W) (Fig. 1), which was open to recreational and commercial fishing (minimum legal size, 197 mm MSL) (Haaker et al., 1986, 1998). Each of these sites is characterized by rock reef and boulder habitat with kelp canopies of bull kelp (*Nereocystis luetkeana*) at the five northern California sites and giant kelp (*Macrocystis pyrifera*) in southern California.

During census occasions multiple teams of SCUBA divers surveyed each site using haphazard search swims. Red abalone were collected by SCUBA divers, brought to vessels, measured for maximum shell length, and tagged. Individually numbered stainless steel tags were attached with stainless steel wire threaded through fully formed respiratory pores. Tagged red abalone were returned to the locations and habitats where they were collected. Recapture history data from each site were partitioned into three size groups based on maximum shell length: those individuals ≤100 mm (MSL), those 100.1–178 mm (MSL), and those >178 mm (MSL). We use a break at 100 mm, as this is the size at first reproduction for females and all individuals >100 mm (MSL) are emergent (Rogers-Bennett et al., 2004). The break at 178 mm is used because this is the size that an individual enters the recreational fishery.

Recapture histories from individuals recovered between sampling periods were excluded from analysis because in many cases it was not possible to determine the fate of an individual after it was reported. Removal of these recapture histories from analysis minimized potential biases in survival and recapture probability associated with multiple handling of individuals between census periods. Data from individuals captured between census periods in southern California were not available. Annual tagging and recapture surveys were restricted to periods during March, April, and May in northern California and July at Johnsons Lee, in southern California.

The set of recapture histories of each size class at each site were examined to determine if data conformed to two of the model assumptions; homogeneity of recapture and apparent survival rates (Burnham et al., 1987). We used Release tests 2 and 3 which are a series of linked Chi-square contingency tables to test the assumptions of the equality of the probability of recapture (test 2) and survival (test 3) (Burnham et al., 1987). Recapture histories from each size class at every site that failed Release goodness-of-fit tests were not analyzed.

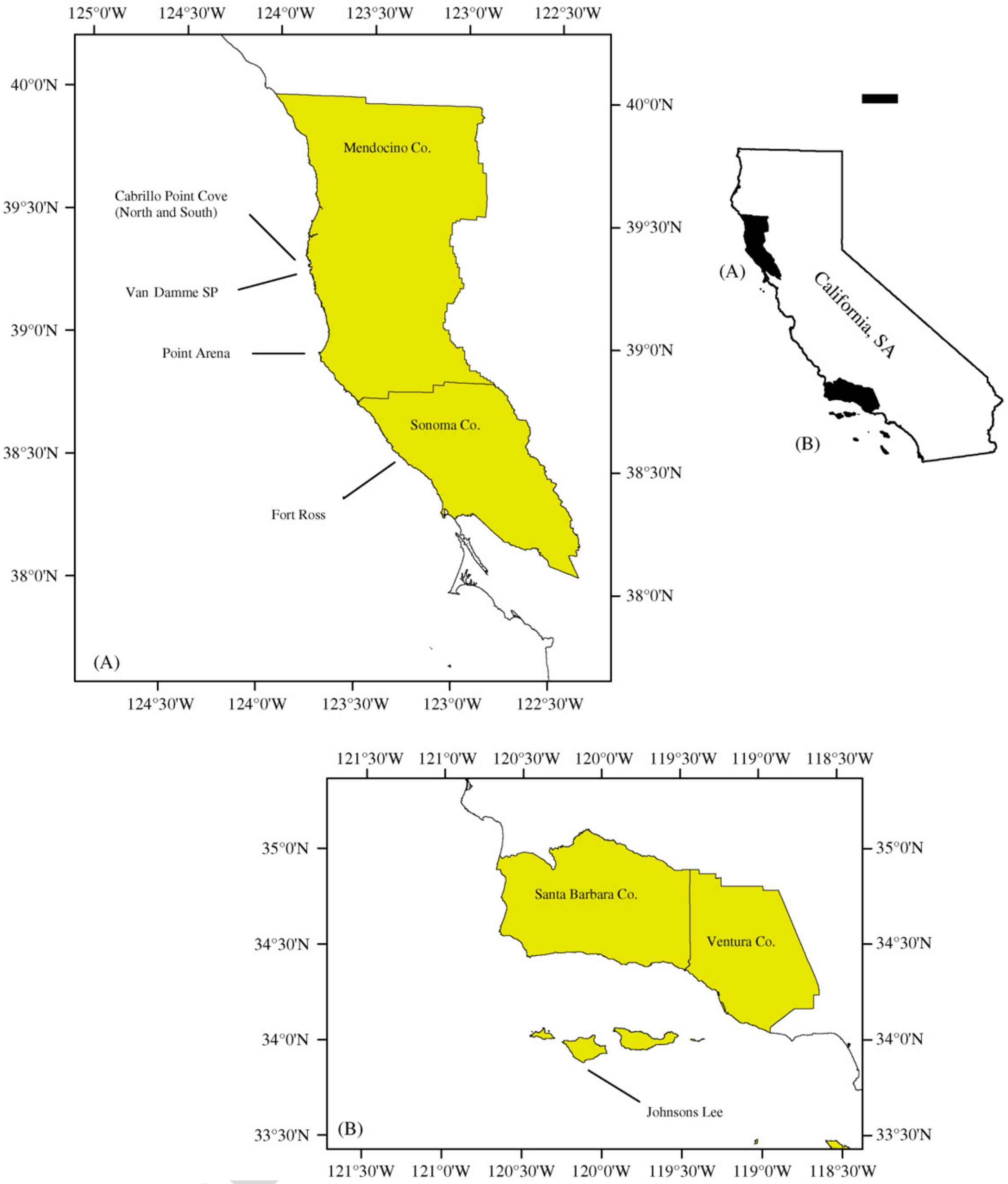

Fig. 1. Map of (A) northern and (B) southern California study sites where tag-recapture work was performed. See text for geographic coordinates of each site.

Following the notation of White and Burnham (1999), a ‘global model’ was specified in which apparent survivorship (φ) and recapture (p) probabilities were time dependent ($\varphi_t p_t$). Three additional models were specified for analysis of each size class at each site: both parameters constant in time ($\varphi.p.$), apparent survival probability variable with time and recapture probability constant ($\varphi_t p.$), and apparent survival probability constant and recapture probability variable in time ($\varphi.p_t$). Site-specific recapture history data were analyzed by parametric re-sampling to assess data dispersion, termed the quasi-likelihood parameter, $\hat{c}$, of the global model ($\varphi_t p_t$). Inflated values of $\hat{c}$ reveal a lack of fit to assumptions of Cormack (1964), Jolly (1965), and Seber (1965) model. Site-specific values of $\hat{c}$ for each size class ≥ 4.0 are considered over-dispersed (Burnham and Anderson, 1998) and were not analyzed.

Candidate models from size classes with satisfactory global models and $\hat{c} < 4.0$ were examined using the ‘recaptures only’ protocol in program MARK (White and Burnham, 1999). This algorithm estimates apparent survivorship and recapture probabilities of open populations by multi-model maximum likelihood estimation. Numerical iteration is used to estimate the values of φ and p that maximize the likelihood of the observed recapture frequencies. Variances of recapture and apparent survival parameters are derived from the shape of the curve at the maximum likelihood estimate, the profile likelihood confidence interval (White and Burnham, 1999).

The fit of candidate models to recapture history data were compared using their Akaike information criteria (AIC) values (Burnham and Anderson, 1998). AIC is an information index that is commonly used for model selection (Forster, 2000). It balances the fit of a particular candidate model to the data and the parsimony of the model, in terms of the number of model parameters, K; AIC = −2log Likelihood + 2K. Recent developments in model selection allow the data dispersion, evaluated as $\hat{c}$, to be incorporated into selection criteria. Each data set was evaluated using the four specified models with the adjusted $\hat{c}$ value of their respective global model. If the value of $\hat{c}$ (global model deviance/mean of re-sampled model deviance) is greater than 1.0, the recapture histories are over-dispersed. The resulting information values are referred to as the QAIC, the quasi-AIC, (White and Burnham, 1999):

$$\mathrm{QAIC} = -2\log \mathrm{Likelihood}/\hat{c} + 2K + 2K(K+1)/(n-K-1)$$

where n is the effective sample size. QAIC was used to rank candidate models (Burnham and Anderson, 1998). If competing models had QAIC values within 2.0 ($\Delta\mathrm{QAIC} \le 2.0$) the competing models were considered equivalent (Burnham and Anderson, 1998). Weighted parameter estimates were computed for those models whose information criteria values were similar. Parameter estimates were derived as weighted averages based on their QAIC values (Buckland et al., 1997). Annual apparent survivorship probabilities of each size class were converted to instantaneous mortality rates: instantaneous mortality is −ln (apparent survivorship, φ). Fishing mortality was determined by subtracting the natural mortality estimate obtained at the reserve site from the total mortality estimates obtained at each of the fished sites.

3. Results

3.1. Data and models

The size range of tagged red abalone varied at each site from 41.5 to 227 mm MSL (Fig. 2). The number of tags deployed, days of census, and number of census occasions varied at the sites in northern California (Table 1). SC had the fewest days between census occasions and the shortest census periods for each sampling occasion (Table 1). VD had the fewest number of tagged individuals, less than half of any other site. NC, VD, PA, and FR had approximately annual tagging occasions although the number of census occasions varied for each site. Recapture history data were eliminated from analysis of some size classes at some sites by goodness-of-fit and $\hat{c}$ criteria (Table 2; Fig. 2).

No single candidate model fit the recapture histories of all size classes at all sites (Table 3). In most cases, QAIC values ($\Delta\mathrm{QAIC} < 2$) indicated that two or more models described the observed data equally well (Table 3).

3.2. Mortality estimates

QAIC weighted annual mortality estimates varied among size classes and sites (Fig. 3a and b). A pattern of size-specific mortality, with smaller abalone having greater mean mortality, was evident in both northern and southern California. Individuals in the ≤100 mm size class in southern California had estimated annual instantaneous mortality rates of 0.67 y^{-1} (0.52–0.84 y^{-1}, mean ± S.E.) to 1.02 y^{-1} (0.84–1.24 y^{-1}, mean ± S.E.). In northern California, small abalone (≤100 mm) had similar instantaneous annual mortality rates of 0.65 y^{-1} (0.56–0.75 y^{-1},

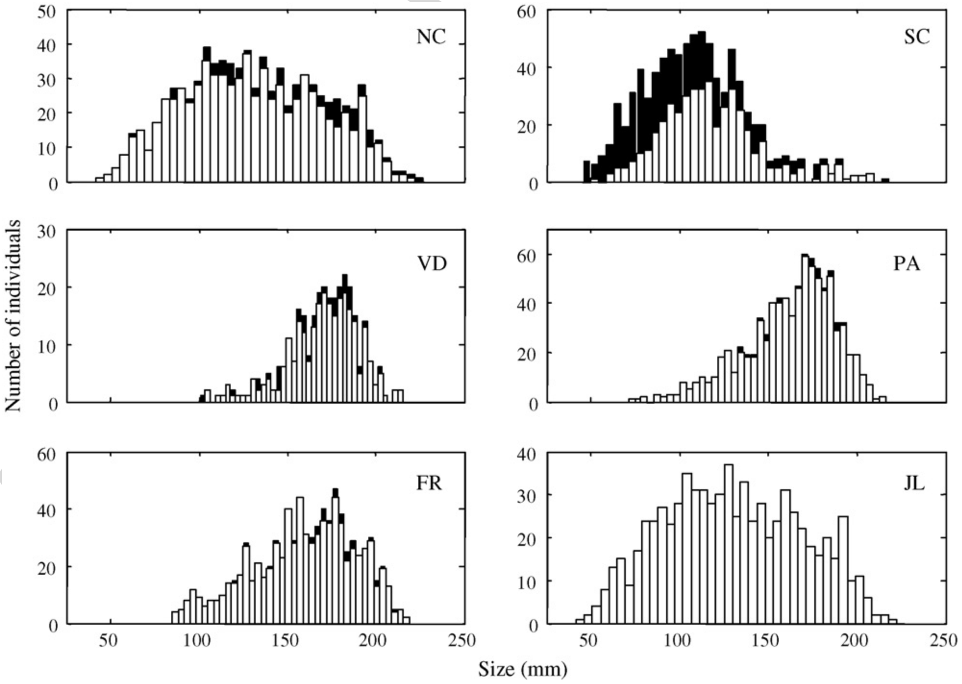

Fig. 2. Size frequency distributions of tagged red abalone, retained (white) or removed (black), from analysis at each site in northern California, Point Cabrillo Cove North (NC), Point Cabrillo Cove South (SC), Van Damme State Park (VD), Point Arena (PA), and Fort Ross State Park (FR) and southern California, Johnsons Lee (JL).

Table 1
Characteristics of red abalone study populations for the five northern California sites; Point Cabrillo Reserve North (NC), Point Cabrillo Reserve South (SC), Van Damme State Park (VD), Point Arena (PA), and Fort Ross State Park (FR), and one southern California site, Johnsons Lee (JL)

Site	Minimum size (mm)	Maximum size (mm)	Number of census occasions	Number of days for each census	Number of days between census occasions	Number of individuals tagged	Number of individuals for capture-mark-recapture analysis	Duration of tagging and recapture
NC	41.5	227	7	2–38	350–398	831	746	1971–1977
SC	53.5	208	5	1–13	135–237	836	453	1975–1977
VD	100.5	217	4	10–100	332–394	308	273	1974–1977
PA	71	217	3	3–40	354	811	786	1975–1977
FR	85	221	3	12–68	321–362	831	799	1975–1977
JL	55.5	222	5	1–30	364–350	2145	2145	1978–1984

mean ± S.E.). For the southern California population, models predicted greater temporal variation in mortality for the smallest size class, while in the north mean mortality estimates were relatively constant over the time examined (Fig. 3a and b).

Recapture history data for the 100.1–178 mm size class from the four sites (NC, VD, PA, and FR) in the north permitted determinations of annual mortality estimates (Fig. 3a). Mean mortality of individuals in this intermediate size class in northern California was less than that estimated for the smallest size class and ranged from 0.34 y^{-1} (0.28–0.40 y^{-1}, mean ± S.E.) to 0.75 y^{-1} (0.65–0.87 y^{-1}, mean ± S.E.). Models predicted similar but temporally variable mortality in southern California for the intermediate size class, 0.19 y^{-1} (0.07–0.31 y^{-1}, mean ± S.E.) to 0.59 y^{-1} (0.45–0.62 y^{-1}, mean ± S.E.).

The largest size class had the greatest variation in mean annual mortality for both northern and southern California populations consistent with site-specific fishing history. Red abalone at SC, the fishing reserve site, had the lowest annual mortality, 0.05 y^{-1} (0.0–0.14 y^{-1}, mean ± S.E.). Mortality of this size class at NC was 0.34 y^{-1} (0.29–0.40 y^{-1}, mean ± S.E.) where there was light fishing pressure. Populations of red abalone at PA and FR, popular fishing sites, had the greatest mortality estimates; 1.35 y^{-1} (1.17–1.56 y^{-1}, mean ± S.E.) and 1.02 y^{-1} (0.89–1.17 y^{-1}, mean ± S.E.), respectively. In southern California individuals in the largest size class had mortality estimates ranging from 0.27 y^{-1} (0.15–0.42 y^{-1}, mean ± S.E.) to 0.89 y^{-1} (0.73–1.08 y^{-1}, mean ± S.E.) (Fig. 3b). Both the legal and the 100.1–178 mm size classes in southern California had increased mortality from the July 1979 census to the July 1981 census compared with the rest of the time examined.

Estimates of fishing mortality were made for two heavily fished sites in northern California. The mean instantaneous total mortality rate ($F+M$) at FR and PA was 1.02 and 1.34 y^{-1}, respectively. Instantaneous mean mortality of legal sized individuals at the reserve site SC was 0.05 and is due to natural mortality. The differences in the mean total annual instantaneous mortality rate ($F+M$) between the two fished sites (FR and PA) and reserve site (SC) were 0.97 y^{-1} (±0.21S.E.) and 1.29 y^{-1} (±0.17S.E.), respectively.

Table 2
Summary of goodness-of-fit (GOF) tests and binomial dipersion ($\hat{c}$) values of recapture history data for size partitioned recapture history data at each site

Site	Size class (mm)	Test 2			Test 3			Test 2 + Test 3			$\hat{c}$
		χ^2	d.f.	P-value	χ^2	d.f.	P-value	χ^2	d.f.	P-value	
NC	<100	3.405	4	0.493	–	–	–	–	–	–	1.05
	100–178	14.136	8	0.078	25.929	8	0.001	40.066	16	0.001	1.17
	>178	1.968	4	0.742	4.233	7	0.753	6.202	11	0.860	1.04
SC	<100	6.779	2	0.034	–	–	–	–	–	–	4.07
	100–178	1.283	3	0.733	–	–	–	–	–	–	5.61
	>178	0.263	2	0.877	–	–	–	–	–	–	1.22
VD	100–178	2.708	1	0.100	0.979	3	0.806	3.686	4	0.450	1.06
	>178	0	1	1.000	–	–	–	–	–	–	1.51
PA	100–178	–	–	–	–	–	–	–	–	–	1.00
	>178	–	–	–	–	–	–	–	–	–	1.00
FR	100–178	–	–	–	–	–	–	–	–	–	1.13
	>178	–	–	–	–	–	–	–	–	–	1.00
JL	<100	0.872	3	0.832	1.647	5	0.863	2.774	8	0.948	1.52
	100–178	9.876	5	0.079	21.195	7	0.004	31.071	12	0.002	1.41
	>178	0.415	3	0.937	2.698	7	0.912	3.113	10	0.979	1.45

Tests 2 and 3 are those of Program Release (Burnham et al., 1987). $\hat{c}$ values are calculated as (global model deviance/mean of resampled model deviance).

Table 3
Model selection table of recapture history data from each site with $\hat{c}$ values less than 4.0 and non-significant Release goodness-of-fit values

Site	Size class (mm)	Number of individuals	Model	Number of parameters	QAIC	ΔQAIC	QAIC weight
NC	<100	179	$\varphi.p.$	2	355.55	0	1.00
NC	100 to 178	470	$\varphi.p.$	2	1131.51	0	0.33
			$\varphi.p_t$	7	1131.57	0.06	0.33
			$\varphi_t p.$	7	1133.35	1.83	0.33
NC	>178	97	$\varphi.p.$	2	261.13	0	1.00
SC	>178	24	$\varphi.p_t$	5	97.83	0	1.00
VD	100 to 178	166	$\varphi.p_t$	4	307.79	0	0.50
			$\varphi_t p.$	4	307.90	0.11	0.50
PA	100 to 178	558	$\varphi.p.$	2	927.62	0	0.25
			$\varphi.p_t$	3	929.34	1.72	0.25
			$\varphi_t p.$	3	929.34	1.72	0.25
			$\varphi_t p_t$	3	929.34	1.72	0.25
PA	>178	238	$\varphi_t p.$	3	415.13	0	0.33
			$\varphi_t p_t$	3	415.13	0	0.32
			$\varphi.p_t$	3	415.14	0.01	0.32
FR	100 to 178	545	$\varphi.p.$	2	1017.65	0	0.25
			$\varphi.p_t$	3	1019.58	1.93	0.25
			$\varphi_t p.$	3	1019.58	1.93	0.25
			$\varphi_t p_t$	3	1019.58	1.93	0.25
FR	>178	221	$\varphi.p.$	2	279.05	0	0.25
			$\varphi.p_t$	3	279.66	0.61	0.25
			$\varphi_t p.$	3	279.66	0.61	0.25
			$\varphi_t p_t$	3	279.66	0.61	0.25
JL	<100	336	$\varphi_t p.$	6	347.16	0	0.33
			$\varphi.p.$	2	347.36	0.21	0.33
			$\varphi.p_t$	6	348.05	0.89	0.33
JL	100 to 178	1390	$\varphi_t p_t$	9	2596.37	0	1.00
JL	>178	419	$\varphi_t p.$	6	638.38	0	1.00

Recapture history data from NC (100 to 178 mm) and JL (100 to 178 mm) failed Test 3 but were included in capture-mark-recapture analysis. Candidate models for each size class in each site are in order of descending QAIC value.

3.3. Recapture estimates

Mean recapture rates for each size class at each site were variable and ranged from 0.31 y^{-1} (±0.13S.E.) to 0.71 y^{-1} (±0.05S.E.). In northern California mean recapture rates were greatest for larger size classes Fig. 4a. Recapture rates at VD for the 100.1–178 mm size class were the greatest for this size class, 0.58 (±0.12S.E.) to 0.61 y^{-1} (±0.10S.E.). Recapture estimates for the 100.1–178 mm size classes at PA and FR were lower than those at the reserve site NC; 0.29 y^{-1} (±0.05S.E.) to 0.51 y^{-1} (±0.13S.E.). Estimates of recapture rates for individuals >178 mm at FR and PA were similar: 0.51 y^{-1} (±0.13S.E.) to 0.52 y^{-1} (±0.08S.E.). In southern California, recapture rates for the 100.1–178 mm size class at JL varied little throughout the study period, ranging from 0.46 y^{-1} (±0.05S.E.) to 0.56 y^{-1} (±0.04S.E.) Fig. 4b.

4. Discussion

Natural and fishing mortality rates are poorly understood for red abalone but are critical for understanding the population dynamics and ecology of this species. We present a number of temporal and spatial patterns in mortality rates using mark-recapture analysis: (1) mean annual mortality estimates decrease with increasing size in both northern and southern California, (2) total mortality estimates for the largest size class (>178 mm) was generally high and varied spatially across sites in northern California as well as between northern and southern California, (3) natural mortality of large adults inside a reserve in the north was low, 0.05 y^{-1} (0.0–0.14 y^{-1}, mean ± S.E.), and (4) mortality estimates changed little over 5 years in one site (NC) in northern California, but varied over 4 years at one site (JL) in southern California across all size classes.

Spatial variation in mortality estimates is apparent for the >178 mm size class but not for the sub-legal sizes at four sites in the northern California suggesting heterogeneous fishing pressure may be responsible for the observed variation. Sites FR and PA are easily accessible to fishing because they are protected from northwest swell and are close to the populated San Francisco Bay area. Red abalone populations in southern Sonoma County are more heavily fished than in northern as indicated by punch card records of the catch submitted by fishers (2000–2005) to CDFG (J. Kashiwada, personal communication). It is likely that differences in mortality at FR and PA reflect the intensity of recreational fishing. Spatial differences in mortality, as a result of site characteristics, may also be con-

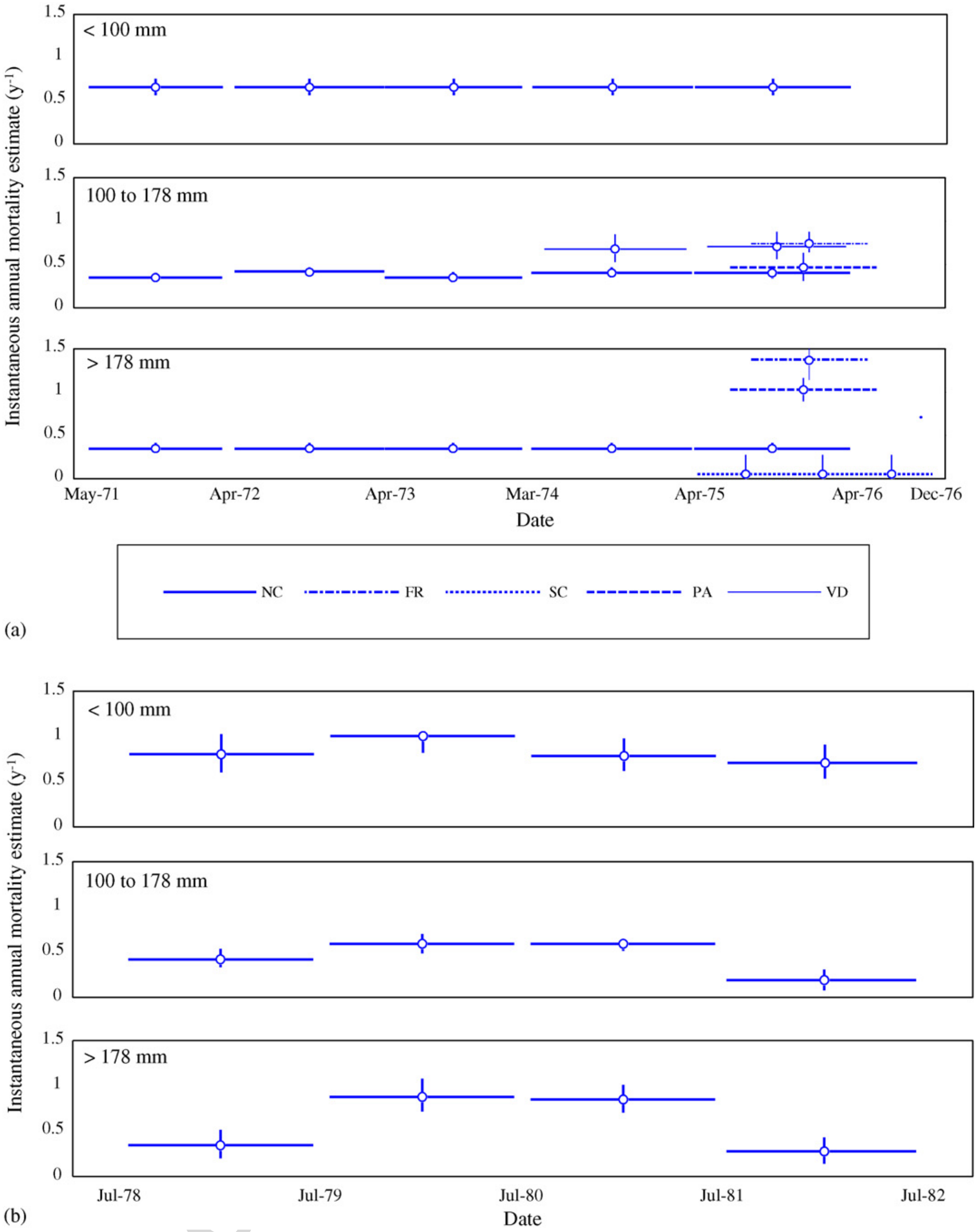

Fig. 3. (a) Instantaneous annual mortality estimates from individuals in each size class (<100, 100–178, and >178 mm) from tag and recapture data from northern California sites Point Cabrillo Cove North (NC), Point Cabrillo Cove South (SC), Van Damme State Park (VD), Point Arena (PA), and Fort Ross State Park (FR). (◯) Indicates median date of period for which tagged individuals were at large. (b) Instantaneous annual mortality estimates from individuals in each size class (<100, 100–178, and >178 mm) from southern California tag and recapture data from site Johnsons Lee (JL). (◯) Indicates median date of period for which tagged individuals were at large. Error bars are standard error (S.E.).

tributing to produce the observed patterns. Red abalone in the 100.1–178 mm size class are susceptible to incidental fishing mortality, but estimates suggest this may be low (on the order of 3%) of the more than 264,000 abalone taken annually in the 2002 fishing year (CDFG, 2005). We found little variation among the mean mortality rates of the sub-legal sized abalone between the reserve and the fished sites.

Temporal changes in mortality estimates were observed in southern California but not in the north, suggesting that there were major changes impacting mortality during 1979–1981 in the south. These temporal changes may reflect changes in fishing pressure over the 4-year period observed, but because these changes were mirrored in all three size classes (including sub-legal abalone) this implies that environmental factors were important. There was a strong El Niño in the eastern Pacific in 1981–1982 resulting in unusually rough seas, large waves, and increased water temperatures which may have decreased food availability (Vilchis et al., 2005). The factors responsible for the temporal variation observed in the mortality estimates in southern California remain unknown.

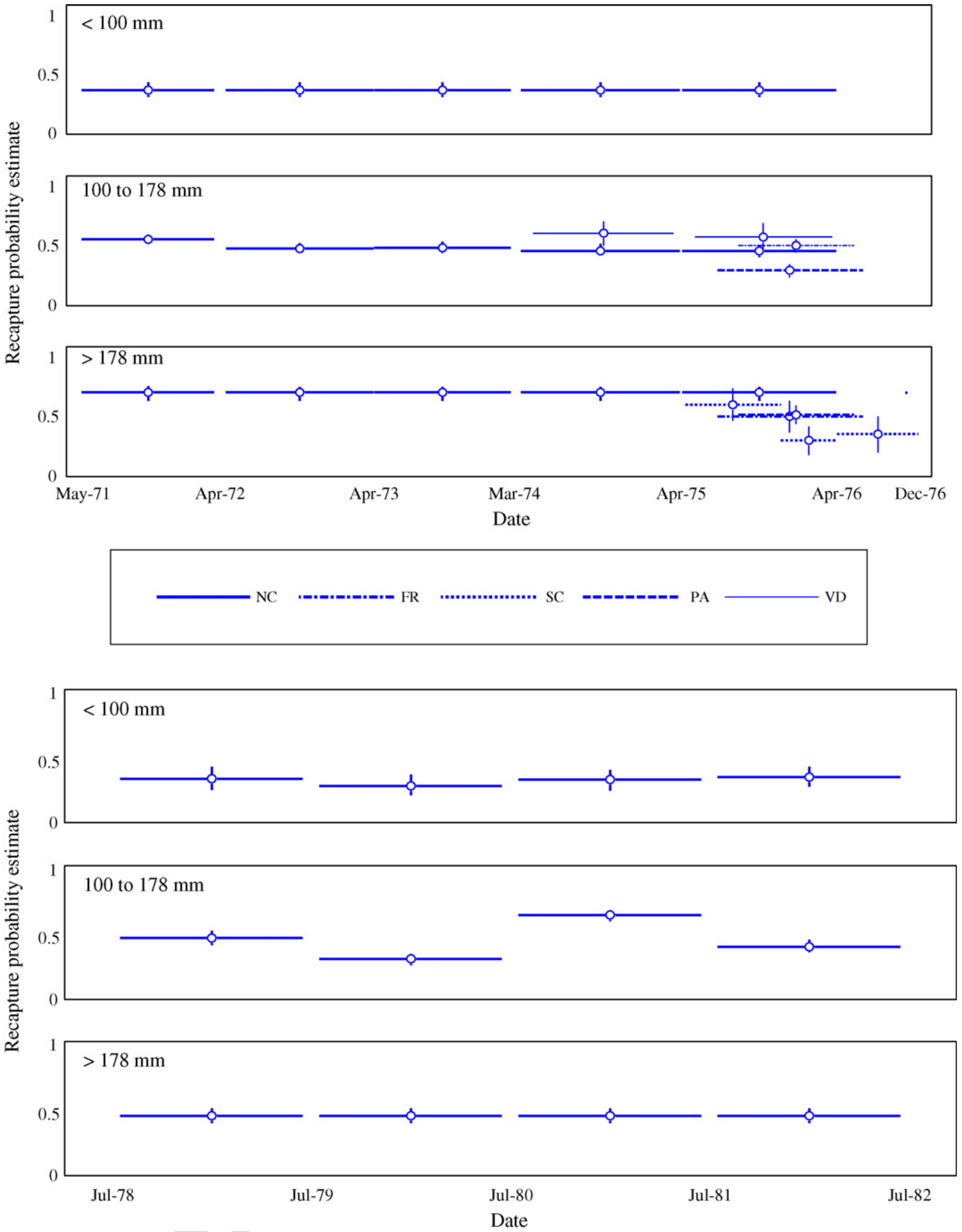

Fig. 4. (a) Annual recapture probability estimates from individuals in each size class (<100, 100–178, and >178 mm) from tag and recapture data from northern California sites Point Cabrillo Cove North (NC), Point Cabrillo Cove South (SC), Van Damme State Park (VD), Point Arena (PA), and Fort Ross State Park (FR). (○) Indicates median date of period for which tagged individuals were at large. (b) Annual recapture estimates from individuals in each size class (<100, 100–178, and >178 mm) from southern California tag and recapture data from site Johnsons Lee (JL). (○) Indicates median date of period for which tagged individuals were at large. Error bars are standard error (S.E.).

Of the three size classes used in this study, the smallest size class had the greatest mortality in both northern and southern California. This observation is consistent with the hypothesis that abalone are susceptible to predation at smaller sizes. Estimates of mortality for the smallest size class were available for one site in northern California (NC) and one site in southern California (JL). Red abalone in this size class are cryptic and difficult to detect by SCUBA survey so it is not surprising that recapture rates for this size class were lower than those estimated for larger size classes. Recapture rates of the larger size classes at VD, SC, FR, and PA are variable and are presumably influenced by abalone movement as well as site-specific characteristics, such as substrate rugosity. In northern California, recapture rates for NC and SC are consistent within each site over time.

The heterogeneity of recapture rates is indicative of the difficulty of detecting small individuals and these heterogeneities can result in failure to meet an assumption of the mark-recapture models. Although the 100.1–178 mm size classes at NC and JL each failed Release test 2 and 3, $\hat{c}$ values were sufficiently small to justify the inclusion of these data in the analysis. Burnham et al. (1987) have noted that failures of Release tests are frequent in studies with releases of initially marked and previously marked individuals. In some studies researchers do not perform or present Release test results (Koenig and Coleman, 1998; Tucker et al., 2001; Mills et al., 2002; Doherty et al., 2004). This may be because candidate models contain parameters that are associated with individual covariates, and cannot be evaluated for goodness-of-fit, or because the inclusion of the quasi-likelihood parameter, $\hat{c}$, into candidate models is considered sufficient to enhance the model's robustness if the recapture history data fails Release goodness-of-fit (Connolly and Miller, 2001; Dinsmore and Collazo, 2003).

Annual mortality estimates reported here are similar to those found for adult red abalone by Hines and Pearse (1982) in central California but are less than those estimated by Tegner et al. (1989) in southern California. These data are consistent with Tegner et al. (1992) suggestion that there are a large number of abalone predators in southern California and that natural mortality rates may be greater in the south than the north. Similarly, greater mortality in southern California has been observed in a study of red sea urchins, *Strongylocentrotus franciscanus*, along a geographical gradient (Ebert et al., 1999). The mean mortality estimates from NC are slightly less than those obtained by indirect methods such as those described by Beverton and Holt (1956), Ssentongo and Larkin (1973), and Alverson and Carney (1975).

Estimates of capture probabilities and mortality estimates, based on apparent survival, will be affected by survey technique, tag loss, and heterogeneity of movement during ontogeny (Williams et al., 2001). Although each site was different in its size and habitat characteristics, the number of divers employed to census each area was assumed to be adequate for complete area coverage. No data regarding the effort allocated for each survey were available. These data would be desirable to incorporate as a parameter in the JCS model as a covariate of the recapture probability. Tag loss during a study can result in bias and lack of precision in Jolly–Seber derived parameter estimates (Arnason and Mills, 1981). Double tagging and the use of different tag types during a study allow experimenters to estimate rates of tag loss to correct biased estimates. The use of a single tag type in this study did not allow an estimate of tag loss. Although red abalone are generally considered sedentary, they are capable of >1 km movement (Ault and DeMartini, 1987). Temporary emigration of individuals from a study site will result in bias and lack of precision in model estimates.

Studies such as this one and others that use mark and recapture data originally intended for the determination of age and growth relationships, movement, and stage transition probabilities (Ault and DeMartini, 1987; Haaker et al., 1998; Rogers-Bennett and Leaf, 2006) have the potential to be useful in the estimation of vital rates. Langtimm et al. (1998) have shown that unbiased retrospective analysis can be performed given consistent data collection and conservative criteria to censor data. In this study we used goodness-of-fit and $\hat{c}$ criteria to censor data and were conservative in the construction of a posteriori candidate models.

Understanding the scale and magnitude of variation of size-specific mortality rates is necessary for management and conservation of red abalone. The patterns in mortality reported here suggest that spatial, temporal, and size-specific differences in mortality exist for red abalone in California. Temporal variation in mortality estimates was pronounced in southern California but size-specific patterns in mortality were observed in both northern and southern California populations. This information can be incorporated into population models to better predict the effects of fishery management efforts for red abalone in California.

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