THE WARM AND THE COLD: INFLUENCE OF TEMPERATURE AND FISHING ON LOCAL POPULATION DYNAMICS OF RED ABALONE

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ABSTRACT

We developed an individual-based, spatially explicit population-dynamics model to explore the effects of temperature, fishing pressure, and reserve size on red abalone (*Haliotis rufescens*) populations at two of the northern Channel Islands off the coast of California. The model locations represent the "warm" Santa Cruz Island, which has a fishing history of declining abalone stocks, and the "cold" San Miguel Island, which has a history of stable catches. We investigated the effects of three temperature scenarios for 100-year periods on the behavior of each population. In the first scenario we used the real temperature environment (sea surface temperature, SST) from the last 100 years; results showed a decline in both model populations over the last 20 years, with and without fishing. In the second scenario model runs using an SST time series generated from current conditions at the islands showed that in the absence of larval connectivity the warm population would go extinct within 75 years regardless of fishing level. The final SST scenario involved a range of constant, potential SSTs that could occur in the future; abalone populations persisted when the SST was between 11°C and 16°C.

The influence of temperature on the model populations and the latitudinal range of suitable SST suggest a northward migration of the real red abalone range as SST increases over the next 100 years. Efforts to rebuild or protect populations for the future should consider which West Coast regions would provide suitable red abalone habitat given rising ocean temperatures.

INTRODUCTION

Abalone are long-lived, broadcast-spawning coastal gastropods that live in relatively predictable and accessible locations (reviewed by Tegner 1989). They are a valuable fishery resource, yet overexploitation has been a problem in every producing country in the world (e.g., Breen 1986; Tegner 1989). California once supported fisheries for five species of abalones, but all commercial harvesting was halted in 1997 (Tegner 2000). One of these over-exploited species, white abalone (*Haliotis sorenseni*), recently became the first marine invertebrate in the United States to be listed as an endangered species under the federal Endangered Species Act (Hobday et al. 2001). Recovery efforts for this and other abalone species are underway in California.

Abalone fisheries have typically been managed by regulating a minimum size for capture, although quotas now exist in regions where harvesting continues (e.g., Tasmania, South Africa, New Zealand). The size-limit approach was intended to allow several years of reproduction before capture was possible. This approach may succeed if recruitment is frequent, but the combination of abalone life-history characters—specifically, long life span and broadcast spawning—indicate that high recruitment does not occur every year (Hobday et al. 2001). Successful reproduction in broadcast spawning invertebrates also depends on proximity between spawning individuals and their gametes (e.g., Pennington 1985; Babcock and Keesing 1998; Levitan 1998; Claereboudt 1999). Intense fishing can increase the distance between neighbors such that fertilization cannot occur, leading to recruitment failure (e.g., Shepherd and Brown 1993; Hughes and Tanner 1998). Recruitment failure over a period of time is likely to lead to dramatic population decline and loss of the fishery resource (Shepherd et al. 1998). Fishing has often borne the sole blame for stock collapse in many regions.

It is important to note that recruitment failure can occur in the absence of fishing, and some investigators suggest that variation in the environment may be a causative factor in irregular recruitment of abalone (e.g., Shepherd et al. 1998). Indeed, the life history characteristics that allow abalone to persist evolved well before human exploitation began, and so irregular recruitment may be a natural process, offset by long-lived adults. The role of the environment has not been clearly demonstrated in the population dynamics of these marine invertebrates, in part because manipulating and monitoring subtidal populations is difficult. Population models are one tool that may improve our understanding of these complex natural patterns (e.g., Claereboudt 1999).

Our goal in this study was to develop a model that incorporated abalone population dynamics, environmental variation, and level of fishing to explore production characteristics of abalone populations. The

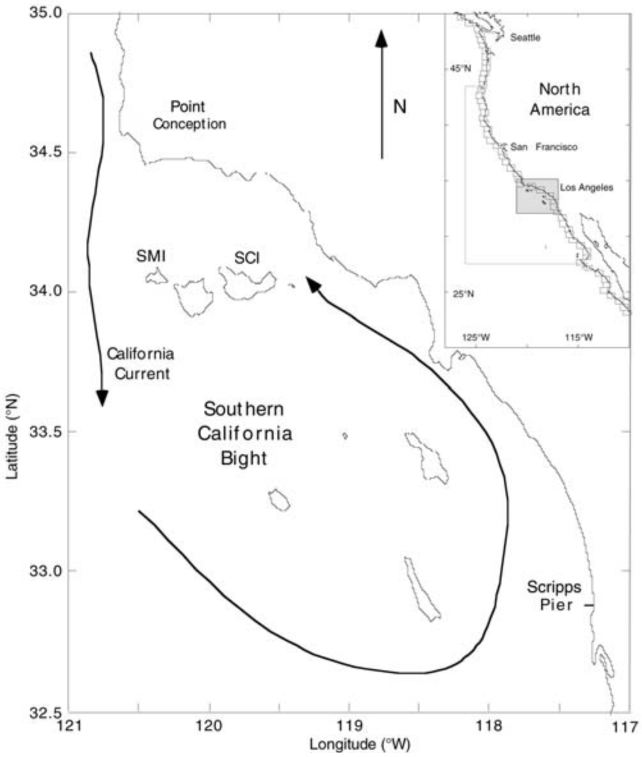

Figure 1. Model abalone populations were located at San Miguel Island (SMI) and Santa Cruz Island (SCI). Shown are the location of the Scripps Pier SST time series and two currents within the southern California Bight (California Current and Southern California Eddy). Inset map shows range of red abalone (*Haliotis rufescens*), from Sunset Bay, Oregon, in the north to Punta Banda, Mexico, in the south; shaded box is area expanded in main panel. Mean monthly SST was extracted from Pathfinder satellite images in each 0.5° latitude box along the West Coast.

model was intended to represent two populations of red abalone (*H. rufescens*)—one at San Miguel Island and the other at Santa Cruz Island, both off southern California (fig. 1). Red abalone have been exploited at these islands since at least 1950 (Karpov et al. 2000). Despite exposure to similar levels of fishing (Karpov et al. 2000), each location has a different catch history. By 1996, commercial catches of red abalone at Santa Cruz Island declined to less than 1% of the peak catch; at San Miguel Island catches were maintained at higher levels and were 23% of the peak catch when the fishery was closed in 1997 (Karpov et al. 2000). San Miguel Island is under the influence of the cold, southward flowing California Current, whereas Santa Cruz Island experiences the warmer waters circulating in the Southern California Bight (Haaker 1994; Harms and Winant 1998) (fig. 1). The difference in water temperature (approximately 1°C) has been suggested as a factor influencing the differences in abalone productivity and harvest sustainability at these two locations (Tegner et al. 1989). Abalone recovery and future management efforts will benefit from a more complete understanding of the influence of fishing and the environment on population dynamics.

MODEL FRAMEWORK AND GOALS

To create an individual-based, spatially explicit population-dynamics model we used MATLAB (from MathWorks). We took this approach because it was important to incorporate fertilization processes at the scale of the individual, and we needed to track the position and size of each individual while it persisted in the population. The model was designed to explore the following scenarios:

1. Given the sea surface temperature (SST) environment at the “warm” and “cold” islands over the last 100 years, what can be observed about red abalone population dynamics? What would have happened to these populations in the absence of fishing?
2. Given recent SST conditions at the islands, and assuming these conditions continue, what would happen to the abalone populations with and without fishing? What would be the effect of a marine reserve on these populations if fishing occurs?
3. If, as seems likely, SST continues to rise for the next 100 years, what is the potential fate of the “warm” and “cold” abalone populations with and without fishing? This scenario will allow “critical SST” to be identified; this has implications for management responses, such as setting SST trigger points for short-term closure if there is a fishery. Results from this scenario may provide guidance for selecting regions where red abalone restoration and reserve efforts should be concentrated, namely, where the SST environment is likely to remain suitable for red abalone into the future.

MODEL PARAMETERS AND ASSUMPTIONS

Model Area and Reserve Proportion

The model domain for each population was a continuous plane 100 m by 100 m ($10,000 \text{ m}^2 = 1 \text{ ha}$) (tab. 1) and was uniformly suitable for abalone. This area represents between 1% and 10% of the red abalone habitat at each island and is the size within which recruitment is driven by local abundance (Prince et al. 1987). The model was initiated by randomly allocating 1,000 abalone of random size and sex to each area. A portion of each area could be protected from fishing (tab. 1). Abalone larger than the legal harvest size could only be removed by fishing from the nonreserve portion.

Abalone Size

Settlement size of abalone was set at 1 mm (Shepherd and Daume 1986). First-year growth was not calculated; abalone were assumed to recruit throughout the year

TABLE 1
Parameters and Values Used in the Abalone Model

Parameter	Value	Reference
General		
Fishing mortality	Range: 0–70% per year	
Larval connectivity	0 or 5%	Tegner and Butler 1985; Hobday 2000
Reserve fraction	0 or 25%	
Habitat quality	Uniform	Tegner et al. 1989
Model area	10,000 m^2	
Maximum adult density	0.1 m^{-2}	Davis 1995; Guzman del Proo 1992; Tegner et al. 1989; Karpov et al. 1998; Karpov et al. 2001
Maximum adult population	Area x max. adult density	
Initial population size	1,000	
Size and growth		
Settlement size	1 mm	Shepherd and Daume 1996
Maximum first-year size	30 mm	Davis 1995; Tegner et al. 1989
Emergent size	80 mm	Tegner et al. 1989; Karpov et al. 1998
Adult size	90 mm	Owen et al. 1984
Harvest size (commercial)	197 mm	Haaker et al. 1998; Tegner et al. 1989.
Maximum size, $L\infty$	225 mm	Haaker et al. 1998; Tegner 1989
K (von Bertalanffy)	0.27	Tegner et al. 1989
± SE (in K)	0.03	Haaker et al. 1998
Fecundity	$F = aL^b$	
a	0.0004650	Tegner et al. 1989
b	4.518	Tegner et al. 1989
Fertilization		
Lowest rate	0	
Highest rate	90%	*Haliotis laevigata*; Shepherd and Partington 1995; Babcock and Keesing, 1999
Fertilization radius	4 m	*Haliotis laevigata*; Babcock and Keesing 1999
Survival		
Larval survival	0.0001	unknown
Juvenile survival	50%	Davis, 1995; Tegner and Butler 1985
Adult survival	85%	Tegner et al. 1989
Density-dependence settlement	0.5 max. adult density	unknown
Environmental effects		
Optimum adult SST for growth and survival	12°C	Haaker et al. 1998; Tegner et al. unpubl.
Optimum larval SST	15°C	Leighton 1974; Ebert and Hamilton 1983
Optimum fecundity SST	12°C	Owen et al. 1984
Larval period	Year-round	Boolootian et al. 1962; Davis 1995
Fecundity period	Year-round	Leighton 1974; Boolootian et al. 1962

Note: Values, discussed further in the text, are for red abalone, *Haliotis rufescens*, unless otherwise noted.

(Leighton 1974; Davis 1995), and initial size at the end of the year was a random size between settlement size and the maximum observed size after 1 year, 30 mm (Leighton 1972; Davis 1995) (tab. 1). Sex was randomly assigned to each settled abalone, mimicking a 1:1 sex ratio, as is the case for most large abalone populations (e.g., Tegner et al. 1989; Shepherd et al. 1995).

Abalones initially occupy cryptic habitats when they settle and later emerge to a more exposed position (Cox 1962). Red abalone become emergent at 70–80 mm (Tegner et al. 1989; Karpov et al. 1998); an emergent size of 80 mm was used here to represent the size when survival changed from the juvenile to the adult level (tab. 1).

Adult size, when sexual maturity occurs, is reached at approximately 60–90 mm for red abalone (Owen et al. 1984). A size of 90 mm was used in this model. In the 1980s and 1990s, when the California abalone fishery was still operating, commercial size for red abalone harvest was 197 mm (Haaker et al. 1998). The legal size for recreational harvest was smaller, but the catch by noncommercial fishers was minor (Karpov et al. 2000) and not considered in this model.

The maximum size of red abalone has been reported to be 300 mm (Cox 1962); however, growth models for red abalone in southern California typically report maximum size as about 200 mm (e.g., Tegner et al. 1989; Haaker et al. 1998). A maximum size of 225 mm was used in this model, as it allowed abalone to grow large enough for legal harvest.

Growth

The Von Bertalanffy growth equation is commonly used to describe abalone growth (e.g., Day and Fleming

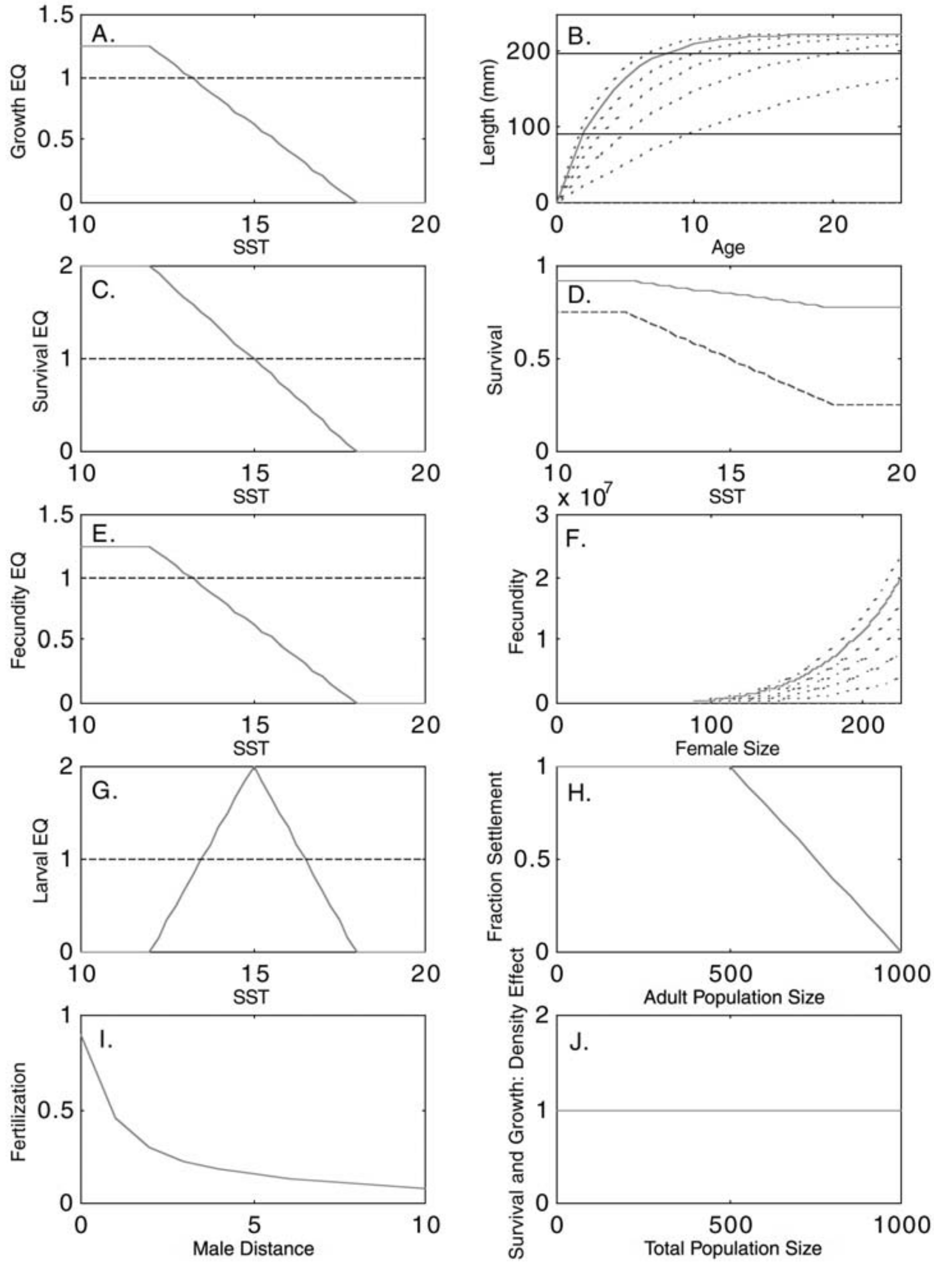

Figure 2. Influence of SST on model parameters: *A*, growth rate multiplier as a function of SST. *B*, growth relationships for a range of environmental qualities, with the lowest dashed line indicating lowest quality, and the solid line representing the base condition. *C*, survival multiplier as a function of SST. *D*, actual survival for juveniles (*solid line*) and adults (*dashed line*) as a function of SST. *E*, fecundity multiplier as a function of SST. *F*, size-fecundity relationships for a range of environmental qualities; dashed lines represent a range of environmental qualities, and the solid line represents the base condition. *G*, larval survival multiplier as a function of SST. *H*, proportion of recruit settlement as a function of adult density; the proportion of recruits that settle declines linearly from 1 to 0 between half and the maximum adult density. *I*, proportion of eggs fertilized by a single male as a function of distance from the female. *J*, juvenile and adult survival rates are independent of adult density.

1992) and was used in this model. Variation in the growth rate constant, K, was selected randomly for each individual each year from a normal distribution with mean of 0 and a maximum value of 0.06, after considering the range of values in Haaker et al. (1998).

The SST influenced *K*, increasing it in "good" years and decreasing it in "bad" years, according to a year-quality scaling factor ranging from 0 to 1.25 (fig. 2a). Thus, the minimum value for *K* was 0 at high SST, and the maximum value was 1.25 times the "normal *K*" at low SST (fig. 2b). Optimum growth for red abalone has been reported at high SST (15–18°C) (Leighton 1974), but a value of 12°C was used here based on recent work by Haaker et al. (1998) and Tegner et. al.[1]

Survival

Postsettlement juvenile and adult survival were set at an annual baseline value of 50% (Tegner and Butler 1985; Davis 1995) and 85% (Tegner et al. 1989), respectively (tab. 1). The SST environment influenced both survival values in the model, linearly increasing or decreasing baseline mortality (1-survival) by up to 50% for good and bad years, respectively (fig. 2c,d). Each year, each abalone was randomly allocated a survival probability from a uniform distribution (value 0–1). Individuals that had a survival probability greater than the mortality level were retained.

Fishing and Catch

We investigated a range of fishing levels (0–70% of all surviving legal abalone caught per year) and used the survival probabilities for each abalone to "catch" animals if fishing was included in the model. Abalone larger than legal harvest size (and not in the reserve portion, if it existed) were removed from the population if the individual survival value was less than the sum of the fishing level and the population survival value (i.e., fishing occurred after natural mortality). Exploitation was thus randomly distributed over the model area, which is reasonable given the scale of this model. Fishing began at year 50 in each model run to allow extinction to occur in the absence of exploitation. There was no poaching or mortality of undersized (sublegal) abalone due to fishing in the model, although the model could be adjusted to include this variation if such information existed.

Fecundity

Abalone fecundity is related to female size and in the model is described by the commonly used relationship

$$E = aL^b \tag{1}$$

where E is individual fecundity (number of eggs), L is female length, and a and b are constants fit to data (e.g., Shepherd et al. 1992). These constants were available for red abalone (tab. 1). Red abalone are fecund year-round off southern California (Boolootian et al. 1962; Leighton 1974) except in warm years (Cox 1962). Fecundity was influenced by SST in the model; individual female fecundity was multiplied by a scaling factor of 0–1.25, according to the fecundity year quality, Q_F (fig. 2e,f).

Fertilization Success

Fertilization success in broadcast spawning marine invertebrates is influenced by a number of factors, including the local density of each sex, water movement, degree of synchrony, and sperm and egg densities (e.g., Levitan and Sewell 1998; Levitan 1998; Claereboudt 1999). In population models, fertilization success has most often been calculated using the overall density of adults or the distribution of cluster sizes (e.g., Shepherd and Partington 1995). If a more biologically realistic local distribution is used, the number and distance of males surrounding each female is required, and this local distribution needs to be translated into a proportion of eggs fertilized during spawning. Most information exists for echinoderms (e.g., Pennington 1985; Levitan et al. 1992), but there are a few abalone studies (e.g., Levitan and Sewell 1998; Babcock and Keesing 1999) though none specific to red abalone. Declining fertilization success with increasing male-female separation has been generally observed. For example, fertilization success in *H. laevigata* dropped rapidly with increasing distance from the sperm source, from a high of 80–97% at 0 m to a low of 3% at 16 m (Babcock and Keesing 1999). The effect of increased male abundance (aggregation) close to the spawning female is less well understood. The closest male that spawns will likely have the highest fertilization rate, but males farther away may also contribute to fertilization of the remaining unfertilized eggs.

In this model we used the local abundance of male abalone to estimate female fertilization success. The fertilization relationship was based on a number of studies, though none specific to red abalone (Pennington 1985; Shepherd and Partington 1995; Babcock and Keesing 1999). The distance of all males within the fertilization radius of each female (tab. 1) was determined and these female-male distances ranked. The contribution of the closest male to fertilization of the eggs declined with distance according to the relationship

$$F = [1/(d_m + 1)] \cdot F_m \tag{2}$$

where F is the proportion of eggs fertilized, d_m is the distance to that male, and F_m is the maximum fertilization rate (fig. 2i). Subsequent males were evaluated individually by distance from the female, and the remaining portion of unfertilized eggs was fertilized according to equation 2. The total fertilization was obtained by summing the contribution of each male. The model assumed that each female spawned annually, and spawning synchrony between each female and the males within the fertilization distance was 100%.

Abalone aggregation may occur during the spawning season (e.g., *H. laevigata*; Shepherd 1986), although evidence is inconclusive for this behavior in red abalone.

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[1] M. Tegner., K. Riser, and L. Vilchis, unpubl. data.

In the model there was no movement or aggregation after abalone settlement.

Larval Survival, Duration, Connectivity, and Settlement

Larval survival is unknown, and values of 0.01–0.0001% were tested in this model to allow some population persistence in the absence of fishing before a single base value was selected (tab. 1). This base larval survival was influenced by the year quality (Q_L) in the model; it was highest at 15°C and declined linearly to zero at 15°C ± 3°C (fig. 2g). This is the SST range within which red abalone larvae survive (Leighton 1974).

Larval connectivity between the two islands is unknown. Studies by Tegner and Butler (1985) using drift cards, and Hobday (2000) using satellite-tracked drifters, indicate less than 5% of larvae at the surface would disperse between populations on San Miguel and Santa Cruz Islands within the larval duration. Larvae may be benthic, which would further restrict dispersal. There is evidence for local, but not delayed, settlement in abalone (Prince et al. 1987). The likely scale of dispersal is less than 100 m for larvae that are close to the bottom with a larval duration of 4–7 days (Prince et al. 1987; but see Shepherd et al. 1992), which is the lifetime for red abalone (Leighton 1974; Jaeckle and Mananhan 1989). In this study, connectivity (C) between populations was fixed in each run at either 0 or 5% (tab. 1).

Recruitment of red abalone has been reported as occurring throughout the year (Boolootian et al. 1962; Davis 1995). Settlement of red abalone at small scales does not seem to be influenced by the presence of adults, but given dispersal patterns it is likely to be from local sources. In this model, larvae settled at random locations in each model area, were randomly designated male or female, and were given a size between settlement size and maximum first-year size (tab. 1), which simulates continuous settlement. Overall, the number of recruits produced by each population was

$$R_{\text{local}} = \sum(E \cdot F) \cdot S_L \cdot Q_L \qquad (3)$$

where E is the individual fecundity, F the fertilization success of individual females, S_L the larval survival, and Q_L the scaling factor for the larval environment quality. The total number of recruits to each population is the sum of the local recruits plus the proportion due to larval connectivity (C) between the populations:

$$R_{\text{total}} = R_{\text{local}} + C \cdot R_{\text{other}} \qquad (4)$$

Maximum Density

The maximum density of red abalone under natural conditions is highly variable (e.g., Karpov et al. 2000) and is complicated by surveying problems, predators, fishing or poaching, and regional or local variation (e.g., Karpov et al. 1998). The overall density of abalone in the model was constrained at adult densities greater than 0.1 adults per square meter (Tegner et al. 1989; Guzman del Proo 1992; Davis 1995; Karpov et al. 1998), with settlement not allowed (tab. 1). Density dependence in settlement also occurred below this maximum adult density, with recruitment declining linearly from a factor of one at half the maximum adult density to zero at the maximum adult density (fig. 2h). Density did not influence growth or survival (fig. 2j). Biologically, this model condition represents lack of space and bulldozing by adults, either at settlement or when juvenile abalone become emergent.

Environmental Data

The current SST scenario data for the islands represented in the model was monthly SST from National Weather Service SST analyses between 1982 and 1999[2] averaged to create an annual time series. Because this SST dataset was only 18 years long, 8-year segments were randomly selected and appended to simulate 100-year time series. This preserved some of the structure of interannual variation in the SST signal. New SST time series were generated for each run of the model.

The longest historical SST time series available for southern California is from the Scripps Institution of Oceanography Pier (1920–98). We increased the length of this time series to 100 years by adding the first 22 years to the beginning of the time series. We then used this time series to simulate the last 100 years of SST conditions at the islands by adding the mean difference between each island and the Scripps Pier time series for the overlapping period (1982–98) to the whole Scripps Pier time series. Finally, future SST scenarios were evaluated using 100-year constant-value SST time series between 11°C and 18°C, in 0.5°C increments.

For each scenario we calculated the year quality factor for juvenile and adult growth and survival using the annual SST for each population. For fecundity and larval survival we used the mean SST value for the fecundity and spawning months (Jan.–Dec. for red abalone) to determine the year quality factor (tab. 1 and fig. 2). Year quality values greater or less than 1 adjusted the base parameter values explained earlier and represented "good" and "bad" conditions, respectively.

Using satellite SST data for the west coast of North America we explored the potential latitudinal ranges for red abalone under future SST conditions. The data were extracted from the NOAA Pathfinder monthly data set for the period 1987–99 (http://podaac.jpl.nasa.gov). The

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[2] J. Engle, unpubl. data.

median SST for 0.5° latitude boxes extending 0.5° offshore (fig. 1) was found each month and averaged to provide annual values by latitude.

Model Experiments and Runs

Each model run was for 100 years with the population characteristics updated each year. Ten replications of each run were undertaken for each set of parameter values. The parameter values we investigated in detail were fishing level, larval connectivity, and reserve size. Simulation experiments were chosen that would represent the range of choices that might be possible through management decisions, such as creating a reserve area, and to show the impact of fishing.

We conducted three experiments for the past 100 years and for current SST environment scenarios:

1. Range of fishing levels (0–70%), no larval connectivity, no reserve area
2. Range of fishing levels (0–70%), 5% larval connectivity, no reserve area
3. Range of fishing levels (0–70%), 5% larval connectivity, 25% reserve area

For future SST scenarios, we conducted four experiments:

1. No fishing, no larval connectivity, no reserve area
2. No fishing, 5% larval connectivity, no reserve area
3. 30% fishing level, 5% larval connectivity, no reserve area
4. 30% fishing level, 5% larval connectivity, 25% reserve area

Model Output

Output from the model simulations for each population included the mean and final total adult and legal abalone population sizes, proportion of recruits from the local population, mean year quality, frequency of and mean time to extinction, proportion of females with eggs fertilized, number of years with fertilization and recruitment, and total catch. Population sizes are reported as numbers of individuals; these can be converted to densities (individuals per square meter) by dividing by the model area (10,000 m^2).

RESULTS

Differences in the SST Environment

The mean annual SST using the in situ time series between 1982 and 1998 was 14.8°C at San Miguel Island and 15.8°C at Santa Cruz Island. During this period, the Scripps Pier SST was 2.04°C warmer than Santa Cruz Island ($r = 0.72$) and 3.02°C warmer then San Miguel Island ($r = 0.71$) (fig. 3). The difference for each island was subtracted from the Scripps Pier SST to create the past 100-year time series for each island population.

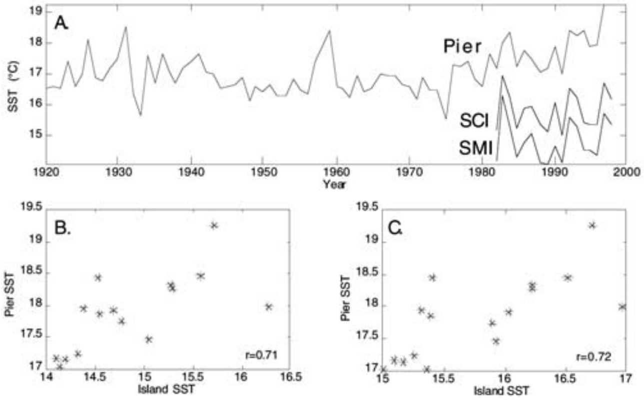

Figure 3. Real SST time series: *A*, annual Scripps Pier SST and island SST; *B*, relationship between San Miguel Island and Scripps Pier SST (1982–98); *C*, relationship between Santa Cruz Island and Scripps Pier SST (1982–98).

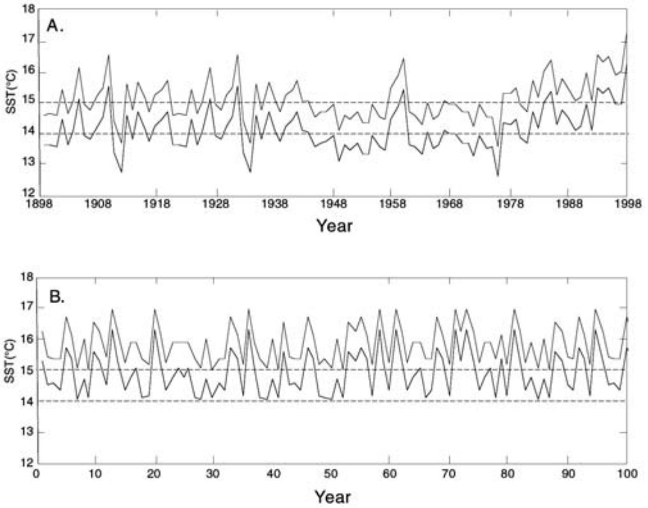

Figure 4. SST time series: *A*, scenario 1. *B*, scenario 2; the upper (lower) time series in each panel is SST at the warm (cold) location. The upper dashed line on each panel represents the SST optimal for larval survival; the lower dashed line represents the SST that divides good and bad conditions for postsettlement survival, growth, and fecundity.

Scenario 1: Last 100 Years

The SST time series for the last 100 years had warm and cold events but the temperature was reasonably stationary until about 1976, when it began to increase steadily (fig. 4a). The mean year quality during this period for the warm Santa Cruz Island was 1.15, and 1.47 for the cold San Miguel Island (fig. 5o). Appendix 1 shows a representative model run, with fishing removing 30% of the surviving legal animals each year and 5% larval connectivity. The decline in the size of the "warm" population occurred as the SST increased over the last 20 years and was also observed in the absence of fishing. ***Range of fishing levels, no larval connectivity, no reserve.*** The level of fishing exploitation ranged from 0 to 70% of surviving legal abalone removed each year. The cold population size was larger than the warm population at

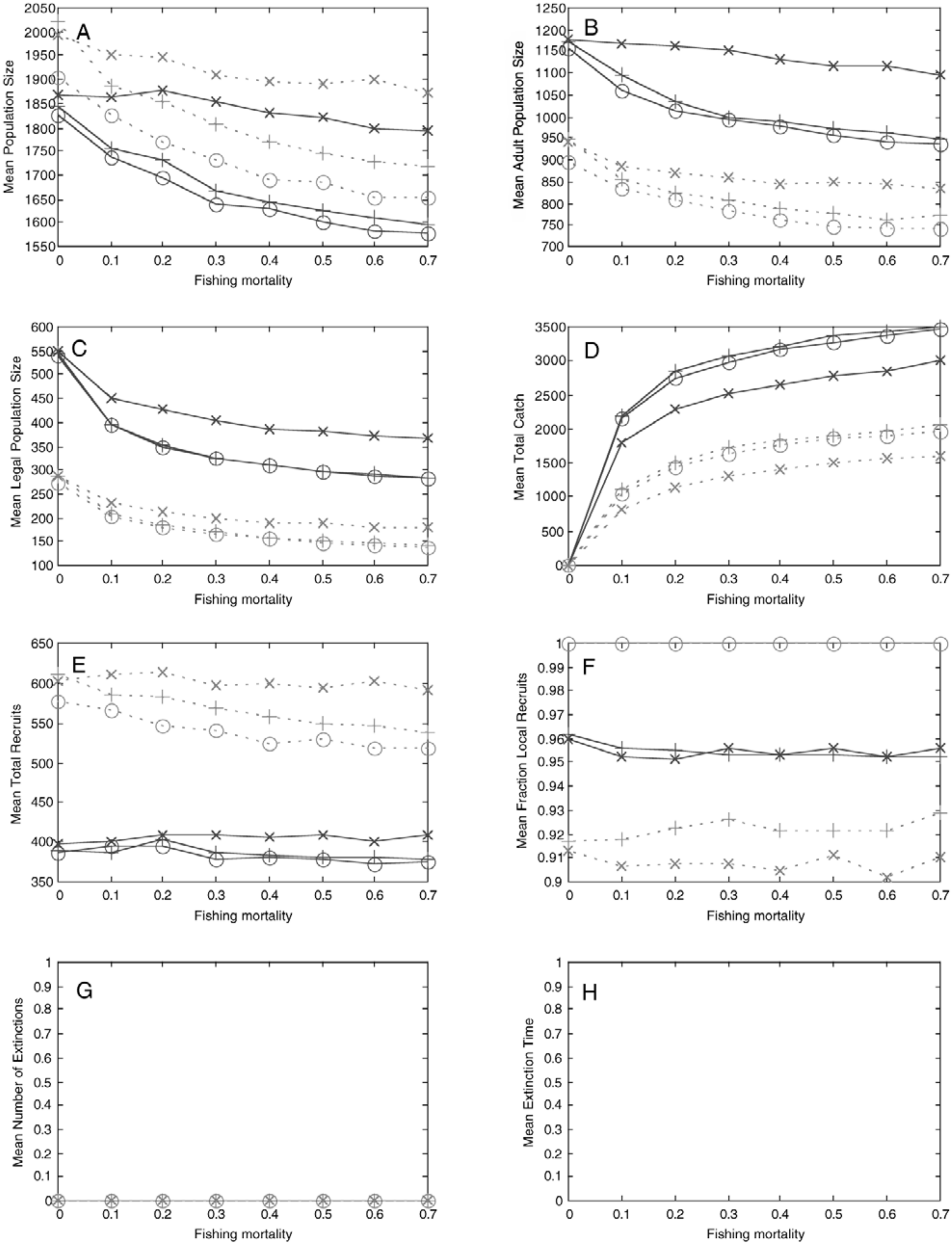

Figure 5. Scenario 1. Population dynamics based on the last 100 years of SST at the warm (*dotted*) and cold (*solid*) islands for a range of fishing levels. Symbols on each line refer to the version of the scenario. (o) no larval connectivity, (+) 5% larval connectivity, and (x) 5% larval connectivity and 25% reserve area.

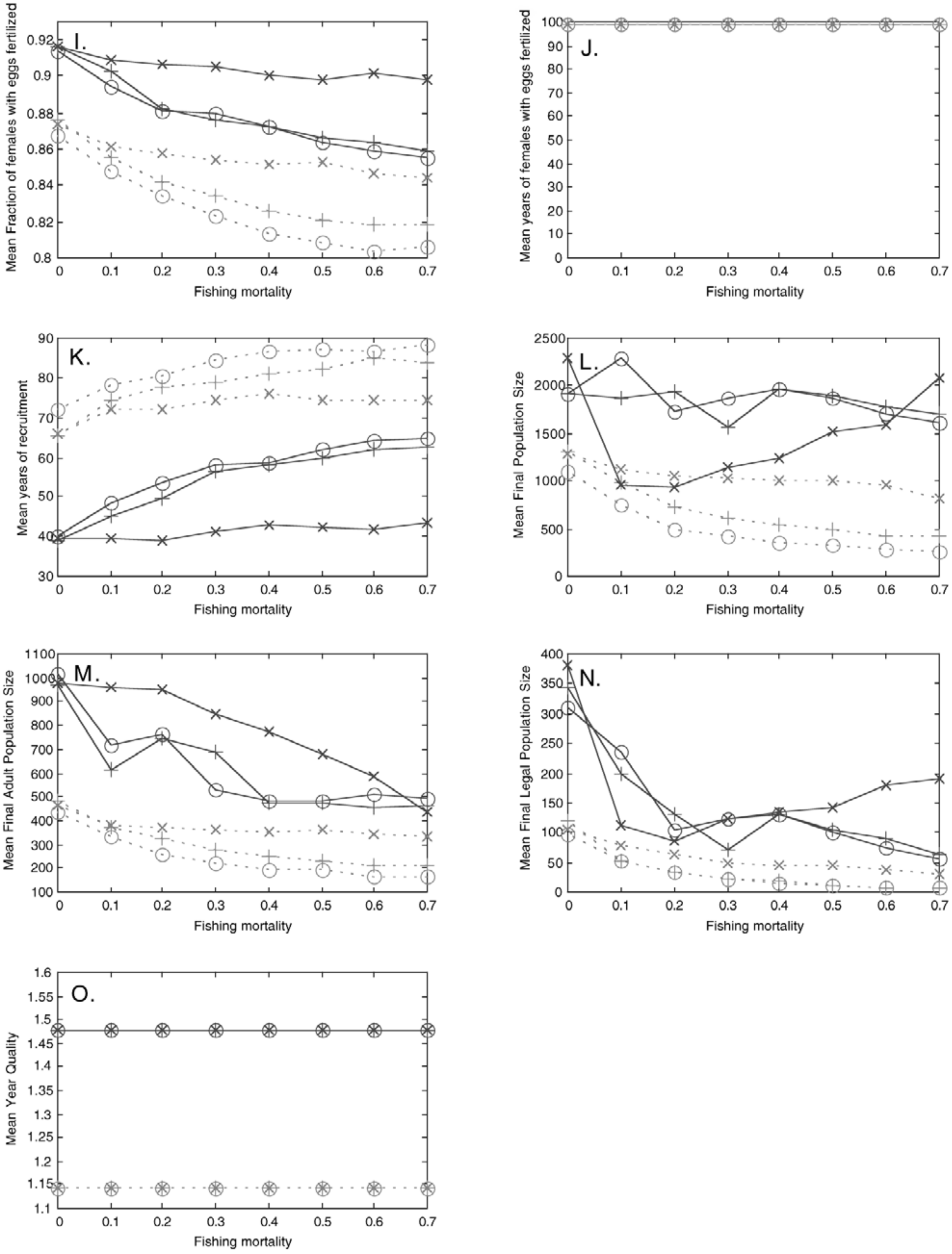

Figure 5. *Scenario 1, continued.*

all levels of fishing exploitation. Mean total, adult, and legal population sizes decreased with increasing fishing level, and the decline in adult and legal population size was lower at fishing levels above 30% removal (fig. 5a–c). Total catch increased with fishing level, although the increase was small above the 20% fishing level (fig. 5d). The warm population had a higher average number of recruits (fig. 5e), because the smaller size of the adult population allowed more density-dependent settlement. The average number of warm recruits declined with increasing fishing level but for the cold population remained similar at all fishing levels. All recruits were from the local population because there was no larval exchange in this experiment (fig. 5f) and there were no extinctions in either population (fig. 5g,h). The proportion of females with eggs fertilized was higher in the cold population (fig. 5i) with a larger adult population size, and this proportion decreased in both populations as fishing level increased. Eggs from at least some females were fertilized in all years (fig. 5j). The number of years in which recruitment occurred actually increased with increasing fishing pressure (fig. 5k) because the reduction in population size allowed settlement to occur more often. The final total, adult, and legal population sizes were higher for the cold population, and the size of both populations declined with fishing pressure (fig. 5l–n). Little further decline occurred at fishing levels above 30%. In the warm population, the final population size of legal animals was very low above this fishing level.

Range of fishing levels, 5% larval connectivity, no reserve. With the inclusion of larval exchange in the models using the last 100 years of SST data, there was a reduction in the decline of the warm population representing Santa Cruz Island. At all levels of fishing the size of the cold population was still larger than the size of the warm population; however, the population size patterns were very similar to those observed when there was no larval exchange (fig. 5a–e). With no fishing the cold and warm populations supplied about 96% and 92%, respectively, of their own recruits; this remained constant across the range of fishing levels (fig. 5f). There were no extinctions in either population (fig. 5g,h). The proportion of females with eggs fertilized was higher in the cold population, although the proportion decreased with increased fishing level as for the models without larval exchange (fig. 5i), and eggs from at least some females were fertilized in all years for both populations (fig. 5 j). The number of years in which recruitment occurred increased with increasing fishing pressure (fig. 5k). The final total, adult, and legal population sizes were larger in the cold population and declined in both populations when fishing level increased (fig. 5l–n). The final population sizes were slightly larger in this experiment than in the one without larval exchange.

Range of fishing levels, 5% larval connectivity, 25% reserve area. For both populations, including larval exchange and reserving part of the model area from fishing did not prevent declines in the mean total, adult, and final population sizes as fishing level increased. The adult and legal population sizes were still larger in the cold population than in the warm population at all levels of fishing; however, both populations were larger than when there was no reserve (fig. 5a–c). The total catch was less than it was in cases without a reserve across the range of fishing levels (fig. 5d). Patterns of total recruits and proportion of local recruits were similar to the preceding case, although the proportion of local recruitment was slightly lower at all fishing levels (fig. 5f), indicating that each population was less self-dependent. As for the two previous cases, extinction did not occur in either population (fig. 5g,h). The proportion of females with eggs fertilized was higher in the cold population than in the warm (fig. 5i); however, both populations had a higher proportion of females with eggs fertilized compared with the nonreserve cases. As before, eggs from at least some females were fertilized in all years for both populations (fig. 5j). The number of years in which recruitment occurred increased with increasing fishing pressure (fig. 5k) but was lower than the nonreserve cases because of the larger adult population and density-dependent settlement. The final total, adult, and legal population sizes were larger in the cold population, and the size of both populations declined with increasing fishing level (fig. 5l–n). These final population sizes were larger than observed in cases without a reserve.

Scenario 2: Current Conditions

The SST time series for the current island conditions was stationary because it was formed from appending random portions of the same 20-year time series (fig. 4b). The mean year quality differed slightly for each run because the exact composition of the SST time series changed; for all experimental combinations the warm Santa Cruz Island population was ≈ 0.9, whereas for the cold San Miguel Island population year quality was ≈ 1.22 (fig. 6o).

Range of fishing levels, no larval connectivity, no reserve. Using the current SST conditions, the cold population had larger mean total, adult, and legal population sizes than the warm population at all fishing levels (fig. 6a–c). Only the cold population declined with increasing fishing level; the size of the warm population was small at all levels. The total catch increased with increasing fishing level for the cold population, though the increase was small when the fishing level was above 30% (fig. 6d). The catch was low at all levels for the warm population. The average number of recruits was higher for the cold population than for the warm population, and in both

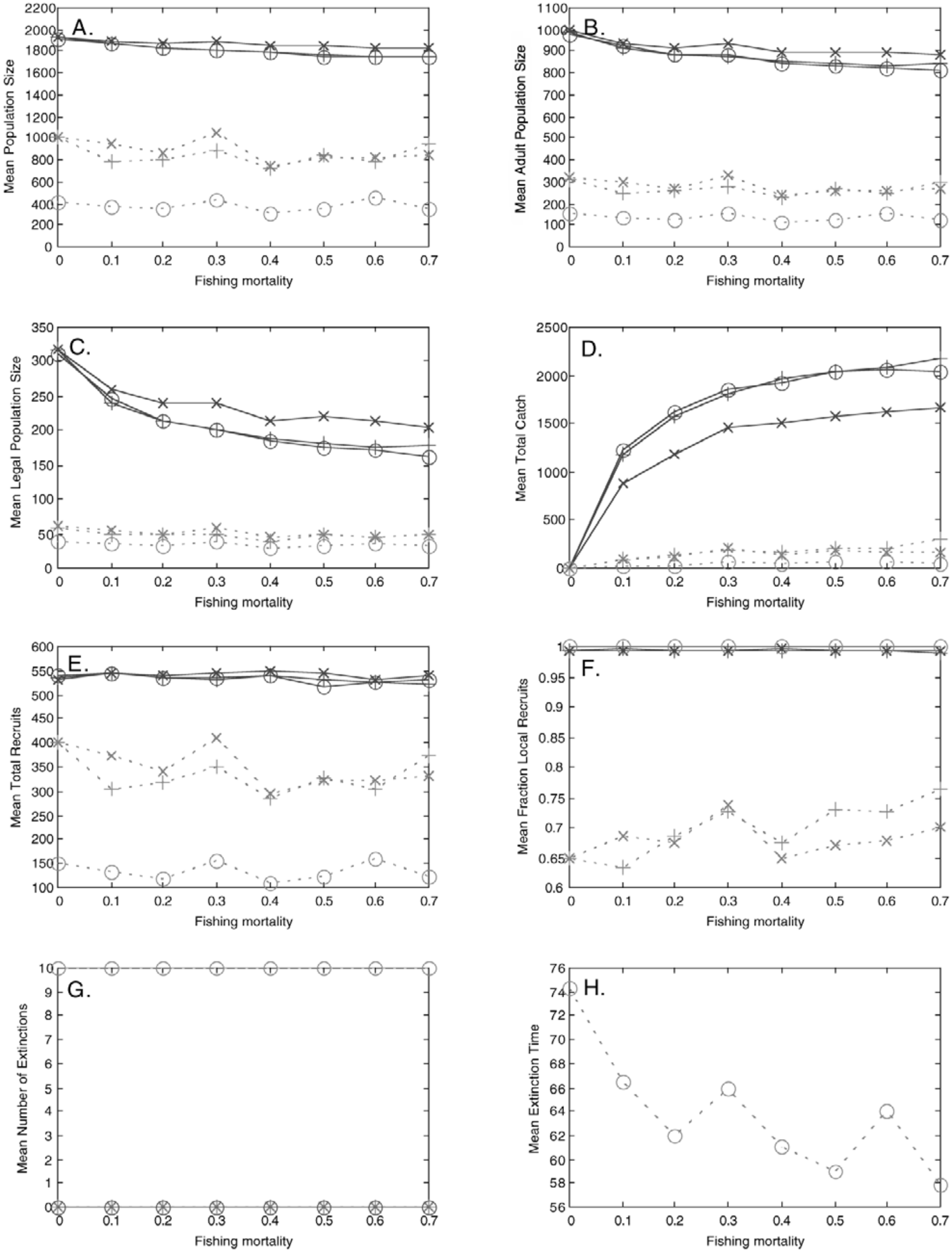

Figure 6. Scenario 2. Population dynamics based on 100 years of current SST conditions at the warm (*dotted*) and cold (*solid*) islands for a range of fishing levels. Symbols on each line refer to the version of the scenario. (o) no larval connectivity, (+) 5% larval connectivity, and (x) 5% larval connectivity and 25% reserve area.

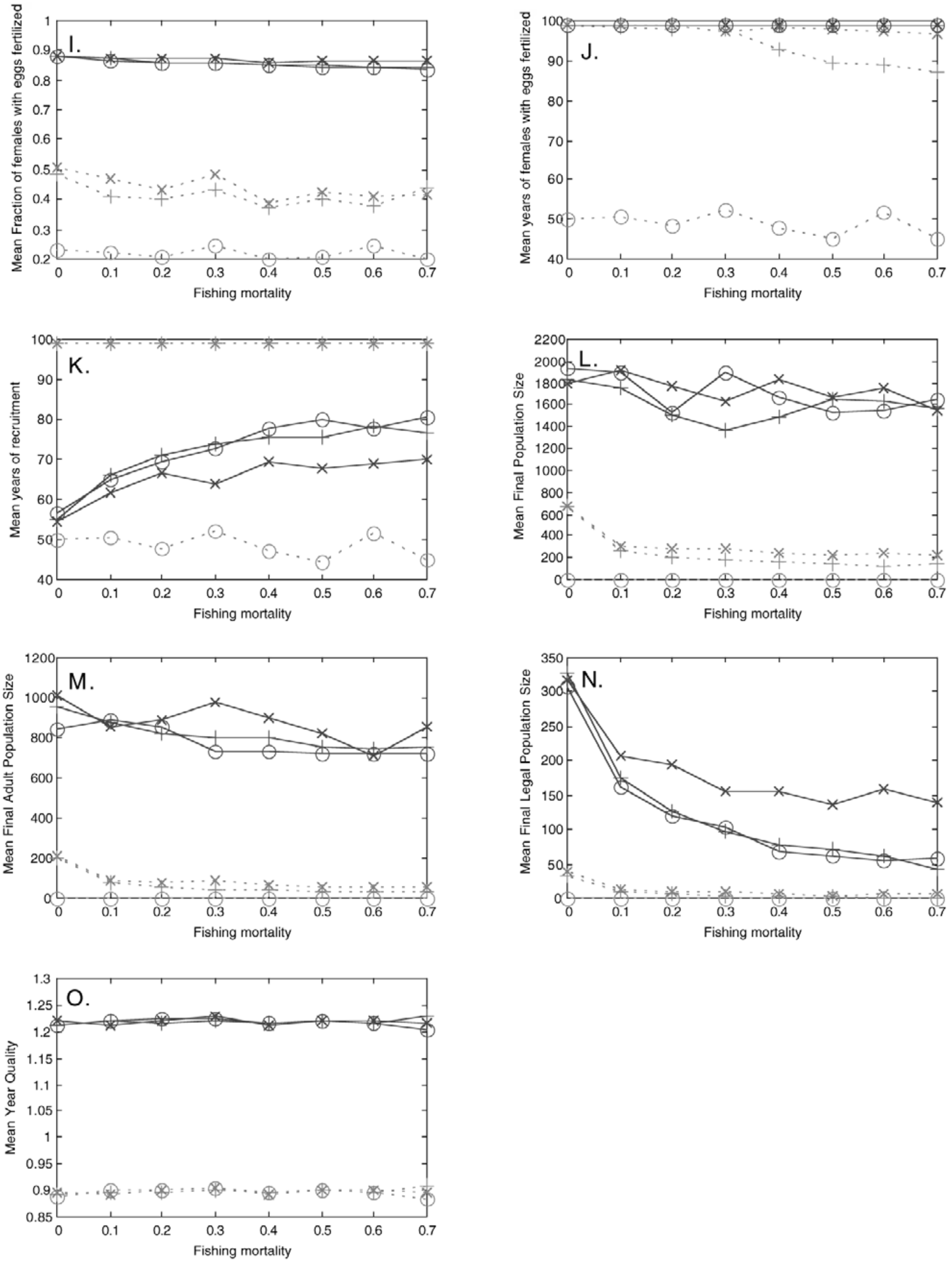

Figure 6. *Scenario 2, continued.*

populations the number was constant across the range of fishing levels (fig. 6e). All recruits were from the local population as there was no larval exchange in this simulation (fig. 6f). The cold population never went extinct, whereas the warm population became extinct in every run regardless of fishing pressure (fig. 6g), though the time to extinction decreased as fishing pressure increased (fig. 6h). At the highest level of fishing, the warm population was extinct within ten years of fishing activity. The proportion of females with eggs fertilized was higher in the cold population than in the warm, and in both populations the proportion changed little with changes in fishing level (fig. 6i). Eggs from at least some females were fertilized in all years for the cold population, whereas in the warm population the number of years in which eggs were fertilized was much lower (fig. 6j) due to the reduced persistence of this population. The number of years in which recruitment occurred increased with increasing fishing level for the cold population (fig. 6k) as a consequence of reduced population size, which allowed increased settlement; in the warm population it was again low and similar to the persistence time of the population. The final total, adult, and legal population sizes were zero for the warm population since it went extinct in all cases, whereas for the cold population the total and adult population sizes remained similar with increased fishing level (fig. 6l,m). As might be expected, the final legal population size declined as fishing level increased, with the minimum population size reached at a fishing level of about 40% (fig. 6 N).

Range of fishing levels, 5% larval connectivity, no reserve. Including larval connectivity in the model simulations did not change the outcome for the cold population for any of the variables considered because the warm population was unable to supply sufficient recruits to make an impact (fig. 6a–n). Larval connectivity did make a difference for the warm Santa Cruz Island population, increasing the mean total, adult, and legal population sizes threefold at all levels of fishing (fig. 6a–c). Even with larval connectivity, total catch was still low for the warm population (fig. 6d). The average number of recruits in the warm population increased to 80% of the cold population at low levels of fishing pressure, and declined to about 50% at high levels (fig. 6e). Over 99% of the recruits in the cold population were local compared with about 70% in the warm population (fig. 6f). Larval connectivity with the cold population prevented the warm population from extinction regardless of fishing level (fig. 6g). The proportion of females with eggs fertilized was higher in the cold population (90%) than in the warm one (about 50%), and both changed little with changes in the fishing level (fig. 6i). Eggs from at least some females were fertilized in all years for the cold population and in all years of the warm population at low fishing levels (fig. 6j). Recruitment to the warm population occurred in all years at all fishing levels (fig. 6k) because of the larval contribution from the cold population. The final total, adult, and legal warm population sizes were low compared with the cold population and were sharply reduced with any fishing (fig. 6l–n).

Range of fishing levels, 5% larval connectivity, 25% reserve area. Including both a reserve area and larval connectivity in the simulations did not change the outcome compared with including only larval connectivity for the cold San Miguel Island population for most of the variables considered (fig. 6a–n). The exceptions were a 25% decrease in the total catch (fig. 6d) and a greater than 50% increase in the final legal population size (fig. 6n) as fishing level increased. There was also little effect on the warm Santa Cruz Island population, apart from a slight increase in the final legal population size compared with the case without a reserve (fig. 6n).

Scenario 3: Future Conditions

The SST time series for the future scenario were constant for each set of ten runs and ranged from 11°C to 18°C in 0.5°C increments within each experiment, for a total of 150 runs per experiment. The two-population case can be understood by recalling the 1°C difference in SST between them; that is, when SST is 15°C at the cold population, it is 16°C at the warm population. At low SST the mean year quality was 2, whereas at the highest SST considered it was zero (fig. 7o).

No fishing, no larval connectivity, no reserve. In the absence of any fishing, larval connectivity, and reserve area the mean total population size was greatest at 15°C (fig. 7a), just below the temperature at which larval recruitment was greatest (15.5°C, fig. 7e). Adult population size was greatest at 14°C (fig. 7b), whereas the legal population size was greatest at 13°C (fig. 7c). Recruitment was constrained to be entirely local (fig. 7f). At temperatures below 12.5°C, approximately half the model's population runs ended in extinction (fig. 7g) in 80–90 years (fig. 7h). At SST above 15.5°C all the population runs ended in extinction, with the time to extinction decreasing with increasing SST. The populations all persisted when the SST was between these values. At the temperatures where the population persisted ≈ 90% of females had eggs fertilized (fig. 7i) in all years (fig. 7j). The number of years in which recruitment occurred was highest at the best SST for maximum recruitment (fig. 7k). The number of years of recruitment was actually reduced in the middle of the SST range due to the increase in population size, which reduced settlement. The final total, adult, and legal population sizes were largest at 14°C, 13.5°C, and 13°C, respectively (fig. 7l–n).

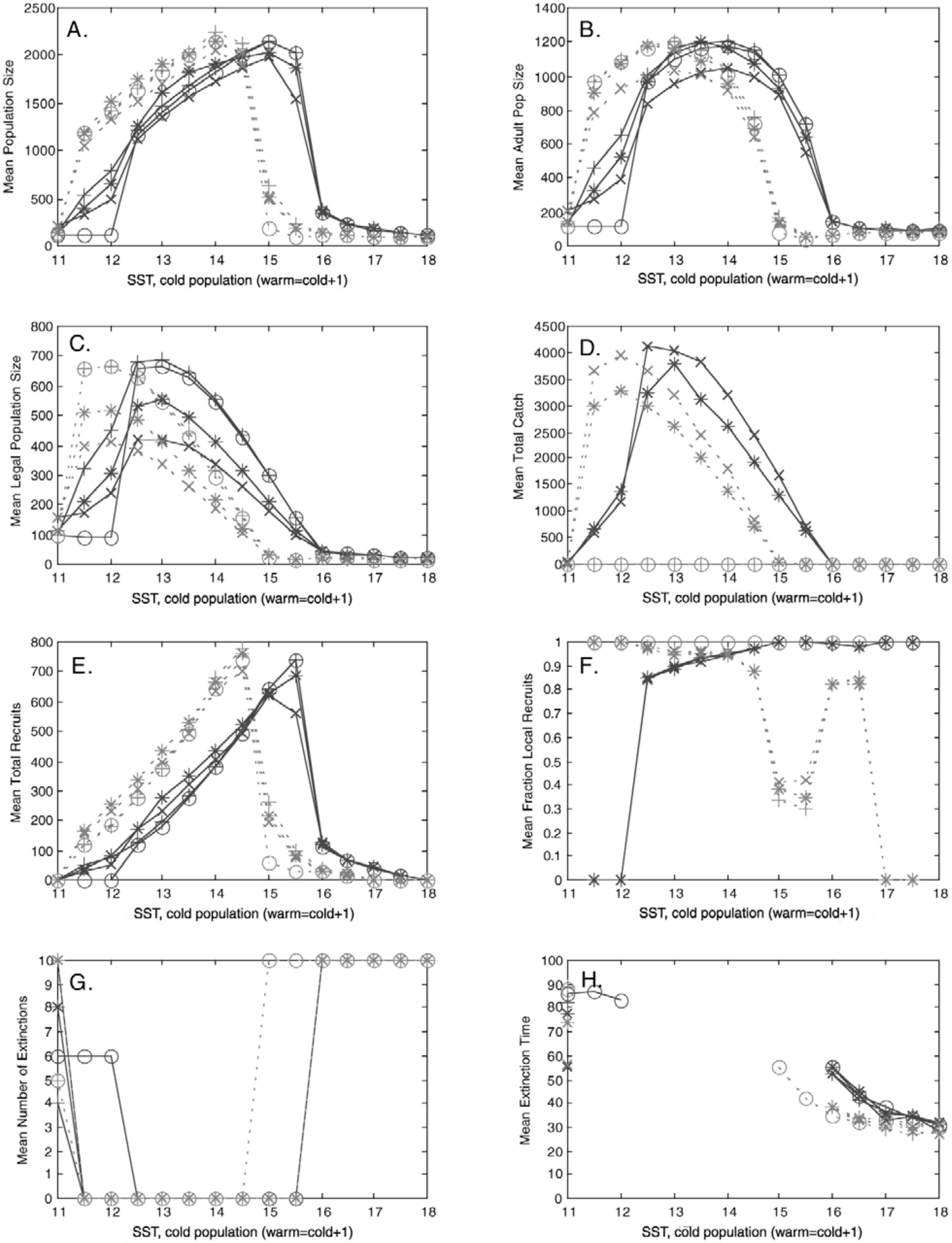

Figure 7. Scenario 3. Population dynamics based on 100 years of future SST conditions at the warm (*dotted*) and cold (*solid*) islands for a range of SST. Symbols on each line refer to the version of the scenario. (o) no fishing, no larval connectivity; (+) no fishing, 5% larval connectivity; (x) 30% fishing, 5% larval connectivity; and (*) 30% fishing, 5% larval connectivity, and 25% reserve area.

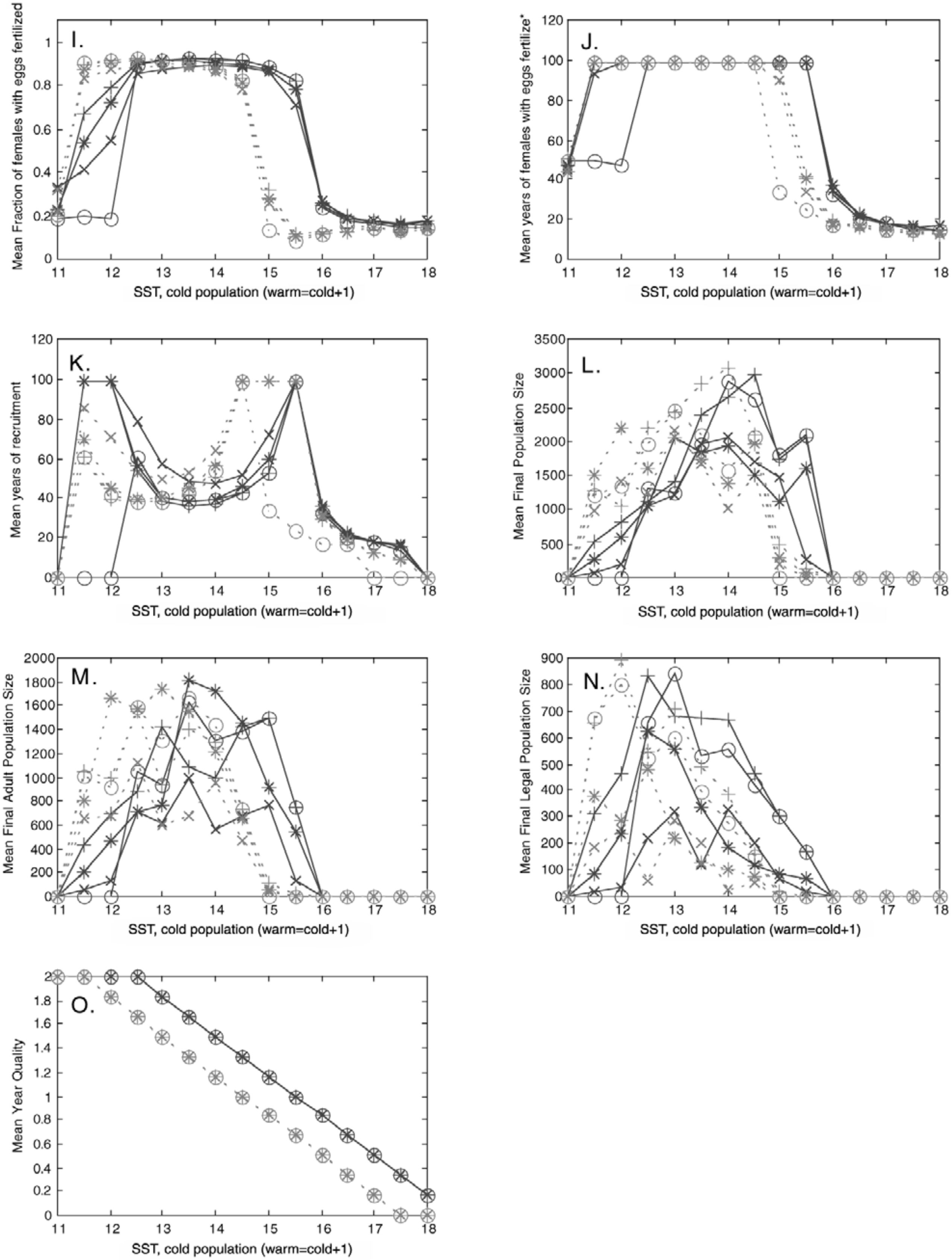

Figure 7. *Scenario 3, continued.*

No fishing, 5% larval connectivity, no reserve. Larval connectivity allowed both populations to persist at a greater range of SST. Mean total population size was largest at the same temperatures for the case with no larval connectivity (fig. 7a–c). The proportion of local recruitment was highest at the extreme SST values (while extant) because no larvae were produced by the other population (extinct), and lowest when one population was at unfavorable SST (fig. 7f). At temperatures lower than 11.5°C, approximately half of the populations went extinct (fig. 7g) after 90 years (fig. 7h). At SST at and above 16°C all the population runs ended in extinction, with the time to extinction decreasing with increasing SST. The populations all persisted between these SST values. For temperatures at which the population persisted, 90% of females had eggs fertilized (fig. 7i) in all years (fig. 7j). The number of years of recruitment was highest at the same SST for highest recruitment (fig. 7k). The number of years of recruitment was reduced in the middle of the SST range due to the increase in population size, which reduced density-dependent settlement. The final total, adult, and legal population sizes were largest at 14.5°C, 15°C, and 12.5°C respectively (fig. 7l–n).

30% fishing level, 5% larval connectivity, no reserve. With 30% of the surviving legal-sized abalone removed every year, and with larval connectivity between the populations, there was little difference in mean total population size compared with the previous two cases (fig. 7a). Mean adult and legal population sizes were largest at the same temperatures as before; however, the values were lower (fig. 7b,c). Total catch was greatest at 12.5°C for the cold and 13°C for the warm population (fig. 7d). Recruitment patterns were similar to the previous cases (fig. 7f). At temperatures lower than 11.5°C, both populations went extinct (fig. 7g) after about 50–60 years (fig. 7h). As before, at SST above 16°C all the population runs ended in extinction, with the time to extinction decreasing with increasing SST. The populations all persisted when the SST was between these values. Fertilization and recruitment patterns were similar to the previous cases (fig. 7i–k). The final total, adult, and legal population sizes were largest at 14°C, 13.5°C, and 13°C, respectively, and were reduced at all SSTs compared with the previous cases (fig. 7l–n).

30% fishing level, 5% larval connectivity, 25% reserve area. The final future SST scenario included 25% of the model area reserved from fishing, in addition to 30% of the legal-sized abalone removed every year and 5% connectivity between the population. This reserve portion somewhat compensated for the fishing, with mean total and adult population sizes the same as the first two cases, across the SST range (fig. 7a,b). The mean legal population size was now halfway between the fishing and no-fishing versions across the SST range (fig. 7c). Total catch was only slightly reduced compared to the previous version and was greatest at 13°C for both populations (fig. 7d). Recruitment patterns were similar to the previous cases (fig. 7f). At temperatures lower than 11.5°C, both populations went extinct (fig. 7g) but persisted longer than without a reserve, about 80 years (fig. 7h). As before, at or above 16°C all the model runs ended in population extinction, with the time to extinction decreasing with increasing SST and little difference in extinction time compared with the previous cases. Fertilization and recruitment patterns were again similar to the previous cases (fig. 7i–k). The final total, adult, and legal population sizes were greatest at 13.5°C, 13.5°C, and 13°C, respectively, and were either the same or higher than the nonfishing experiments across the SST range (fig. 7l–n).

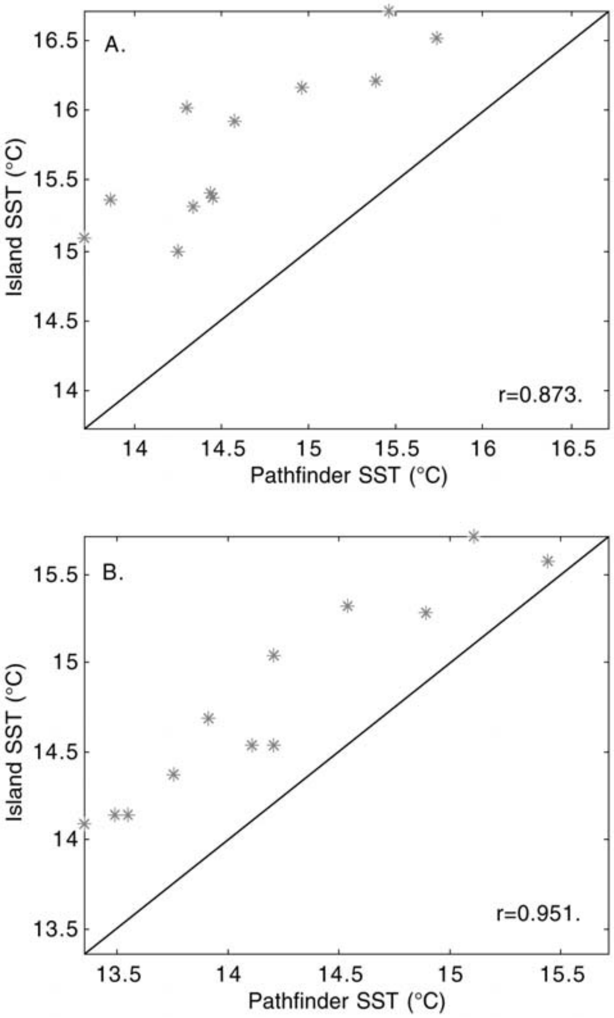

Figure 8. Correlation between the island SST and the Pathfinder SST extracted for the box closest to the island location (1987–98). *A*, Santa Cruz Island. *B*, San Miguel Island.

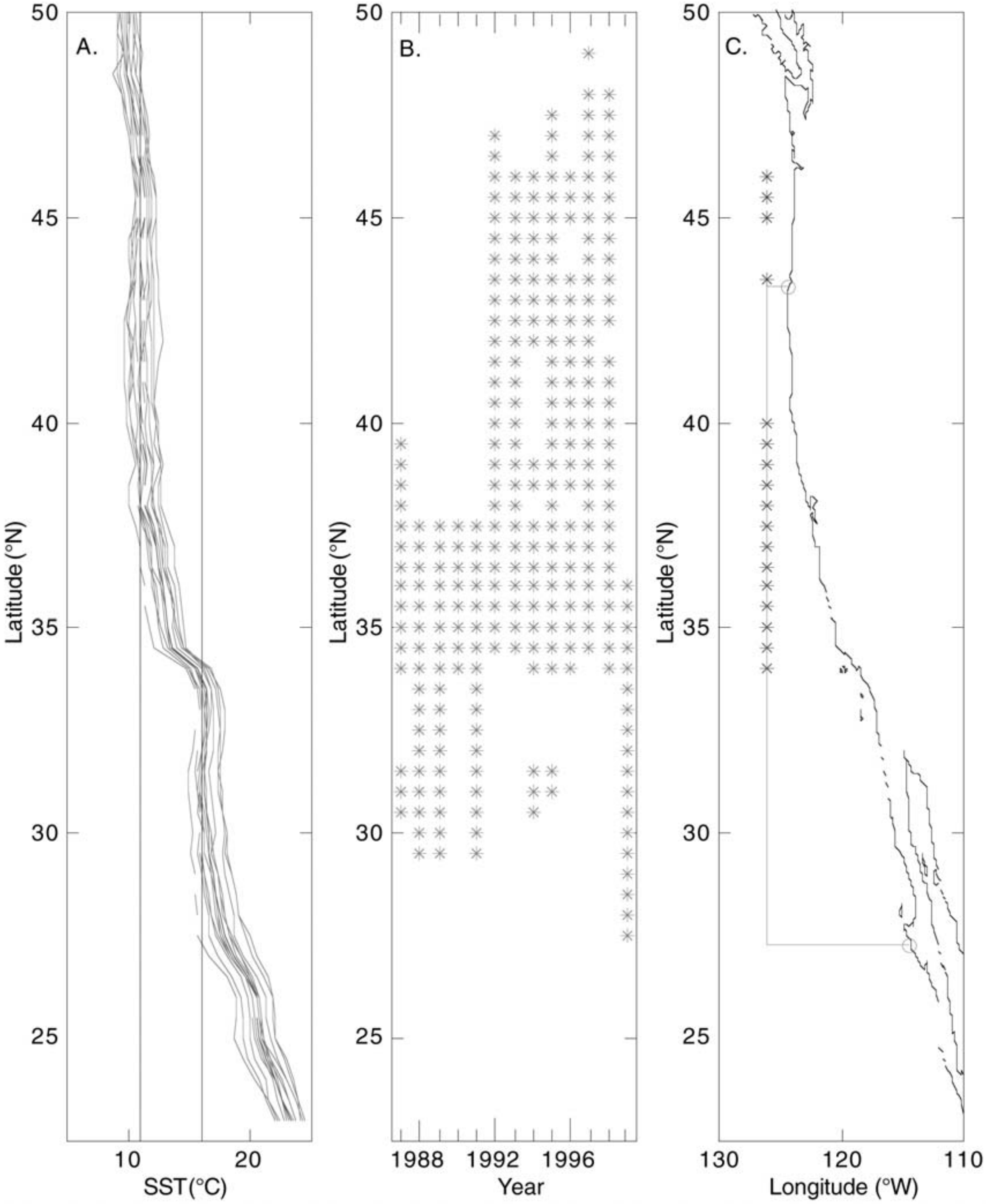

Figure 9. Corrected Pathfinder data extracted for 0.5° latitude bins along the west coast of North America (1987–99). *A*, SST by latitude for each year of data. The vertical lines indicate the suitable abalone SST range (11–16°C) estimated from Scenario 3 models. *B*, Latitudinal ranges for model red abalone within the suitable SST range. *C*, Suitable overall mean SST along the coast for model abalone (*stars*), together with the historical latitudinal range for red abalone (*H. rufescens*) (*line*).

Future SST and Range Changes

The correlation between the overlapping 12 years of island SST and Pathfinder SST for a similar latitude was high ($r = 0.873$ at Santa Cruz Island, $r = 0.951$ for San Miguel Island) (fig. 8). The Pathfinder data showed slightly cooler temperatures than the in situ data at these two locations (1.14°C and 0.57°C, respectively), perhaps because the Pathfinder data was averaged over a larger area and thus included regions where upwelling occurs. With a slight correction of the average difference over the latitudinal range considered (+ 1°C), the (corrected) Pathfinder SST data was suitable for extrapolating the abalone model findings based on the island data to the whole coast.

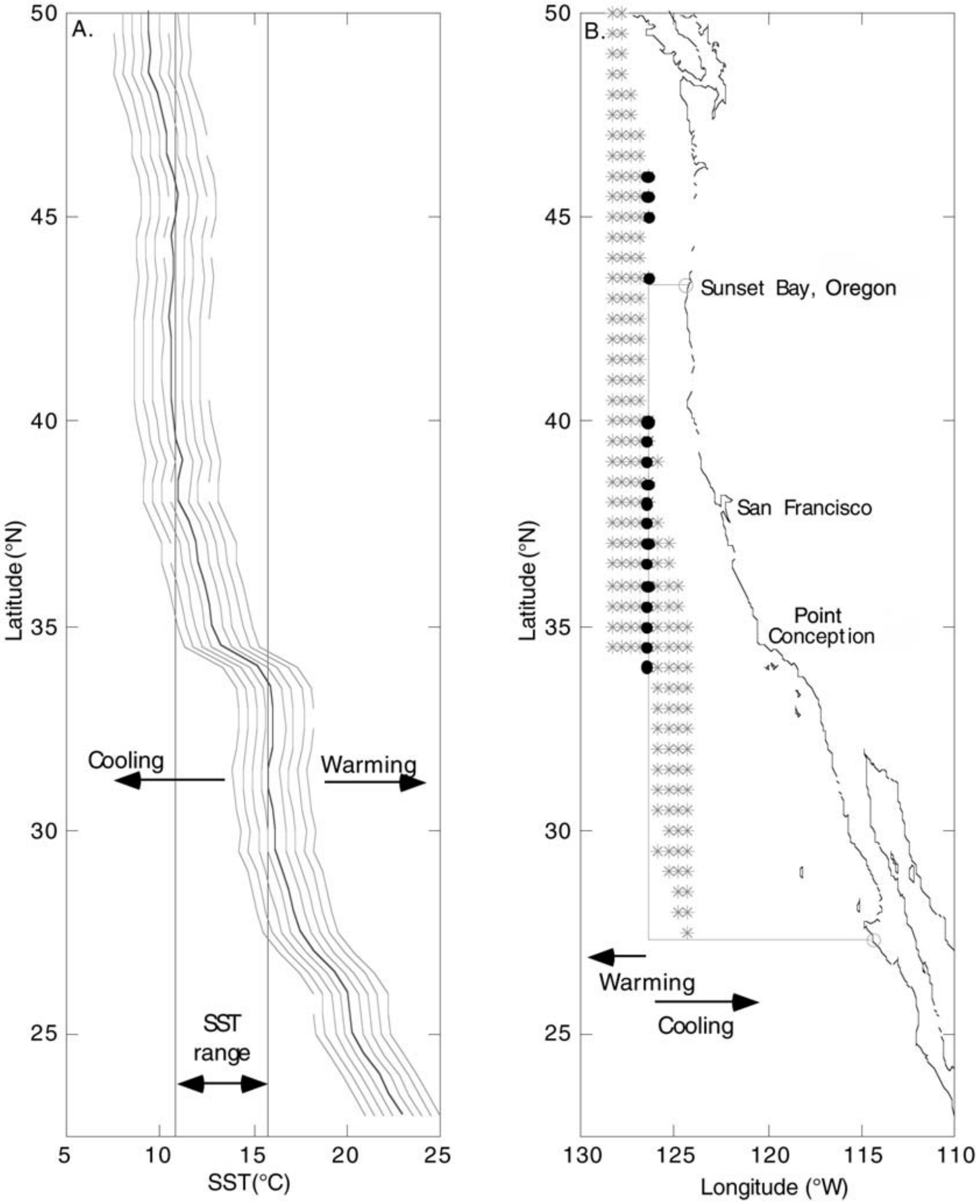

Figure 10. Potential future red abalone (*H. rufescens*) latitudinal ranges. *A*, Expected changes in SST with latitude for 0.5°C changes above and below current mean SST from corrected Pathfinder data (1987–99). Vertical lines indicate the suitable model abalone SST range (11–16°C). *B*, Expected changes in the latitudinal range of suitable red abalone habitat. The two open circles at the coast indicate the historical range, and filled circles indicate the current range of suitable SST; vertical columns of asterisks (*) to the left and right of the filled circles indicate the expected latitudinal range for increasing or decreasing SST respectively (± 2°C incremented by 0.5°C).

Analysis of mean annual SST by latitude (fig. 9a) showed that if red abalone populations can persist at temperatures between 11°C and 16°C (as indicated by the results of scenario 3), the suitable range along the U.S. west coast would be from 27.5°N to 49°N (fig. 9b), which is similar to the historical range. If the median of the annual range limits based on these temperature limits is used to define a latitudinal range for the model populations, then under current mean SST conditions the suitable range has moved north compared with the historical red abalone range (fig. 9c).

If climate change causes a general increase in SST, it will likely increase SST at each latitude. Increases in SST of 0.5°C and the subsequent northward migration of the southern limit of the range of red abalone indicate that southern portions of its range will soon be unsuitable (fig. 10a,b).

DISCUSSION

These model scenarios indicate patterns that might occur in real red abalone populations under similar circumstances. Although red abalones do not generally live at the surface, and so SST may not be a direct measure of this species' environment, they do live at depths where temperatures are similar to those observed at the surface. At worst these SST values are a correlated proxy for the actual conditions.

The results reported here were for a model area of 1 ha, which allowed experiments to be completed in a timely fashion (6 hours per experiment). The results were very similar to those obtained when the model was run for smaller areas, with the exception that extinction occurred slightly more frequently in smaller domains. Real populations of abalone exist at these smaller scales, as well as at larger ones. Model results for simulations with areas up to 10 ha were identical; however, the assumption of random settlement over these larger areas may not be valid and would need to be modified. Density dependence in settlement was required to constrain the model, and similar results were obtained when higher densities were allowed.

Summary, Scenario 1

All model runs based on the SST signal over the past 100 years showed a decline in population size with increasing fishing pressure, although the inclusion of a 25% reserve area reduced this decline. In both populations this reserve proportion led to a 15–20% decline in total catch across a range of fishing levels. The models with a reserve also showed an increase in the proportion of females with eggs fertilized as a result of higher densities within the reserve area. The inclusion of larval connectivity between the two populations did not markedly change the outcomes, suggesting that under this SST environment both populations are self-supporting. The final adult population size in the absence of fishing was close to the maximum allowed adult density for the cold San Miguel population, and about half the maximum allowed for the warm Santa Cruz population. In the absence of fishing, both populations persisted under this SST scenario. With the addition of fishing, the cold adult population was reduced to about half the maximum density, and the warm population was reduced to about 20% of maximum density.

Summary, Scenario 2

The model simulations based on the current island SST conditions showed large impacts on the warm population representing Santa Cruz Island. Without larval connectivity this population went extinct in all cases, and the process was accelerated if fishing was permitted. Allowing some larval connectivity increased the size of the warm population but did little for the cold population, which served only as a larval source for the warm population (hence a sink). Under these SST conditions, inclusion of a 25% reserve area also did little to increase the size of the warm population and changed little in the cold population.

In general, the size of the cold population was reduced to levels found for the warm population in the previous 100 years (scenario 1), and the size of the warm population was reduced to very low levels if there was any fishing exploitation. These results are similar to the real situation observed at these two islands (Karpov et al. 2000).

Summary, Scenario 3

The range of model versions using SST environments different from those currently found at the islands assume there is no evolution or adaptation to the changing conditions. If adaptation occurs, the results will be conservative. In general, all the models showed that the population at the cold location persisted, whereas at the warmer location an increase of only 1°C dramatically reduced the population. Larval connectivity slightly increased the range of temperatures at which the population could persist. At SST values higher than 16°C and lower than 11°C the populations did not persist. Fishing reduced the population sizes and decreased the time to extinction where it occurred. Adding a reserve component somewhat compensated for the effect of fishing, and only slightly reduced the total catch, by about 10–15% for a 25% reduction in fishing area. This indicates that within the range of suitable SST, a reserve would be an effective tool but outside that range it was obviously of no consequence.

Summary, All Scenarios

All scenarios showed that model populations of red abalone are sensitive to changes in SST. Declines of real exploited abalone stocks have also been linked to changes in SST (Shepherd et al. 1998; Tegner et al. 1989). Larval connectivity and fishing influenced the model outcomes, buffering or increasing the sensitivity of the populations to changes in the environment to varying degrees. The historical level of fishing is unknown in these real populations, so we used a range of possible values in this study. At even moderate fishing levels, however, the most dramatic changes had already occurred, suggesting the results are robust to uncertainty about the real level of fishing, which was certainly high (Karpov et al. 2001).

Although fertilization of eggs occurred often in the model runs, the frequency of recruitment was lower than fertilization. This was due to density-dependent settlement and environmental conditions unsuitable for larval survival. These two factors often compound to make stock-recruitment relationships of little value in real abalone population management (e.g., Shepherd 1990; but see Shepherd and Partington 1995). In real populations, irregular recruitment has been observed (Tegner et al. 1989; McShane 1992; Shepherd and Daume 1996) and is indicated by size-frequency distributions that are strongly skewed with an accumulation of old individuals; both were features of model runs in this study.

The proportion of recruitment that is local is an indicator of source/sink population status. Scenarios based on SST from the last 100 years and from the current period show that the warm population received more of its recruits from the cold population and can be considered a sink population. Protecting a sink population, perhaps through a marine reserve, at the expense of a source population is undesirable (Jennings 2001).

This abalone model incorporated local fertilization, and higher fertilization occurred when local adult density was high. Fishing reduces the density of adult abalone, and it has been suggested that fishers who target abalone aggregations can decrease reproductive success (Prince et al. 1987; Sluczanowski 1984; Shepherd 1986). Reserves are the best solution for the maintenance of natural aggregations for species like abalone where the ability to aggregate after settlement is low (e.g., Jennings 2001). This model could be further refined to explore the outcome under various reserve proportions.

The effects of abalone facilitators, competitors, and predators were ignored in this simulation study; however, the abundance of sea otters and urchins, for example, has fluctuated in the last century (e.g., Tegner and Dayton 2000) and this may also influence the population dynamics of red abalone (Rogers-Bennett and Pearse 2001). Alternative hypotheses for the decline of red abalone populations, such as that it is due to the fishing-related reduction in red urchins (*Strongylocentrotus franciscanus*) that provide spine canopy protection to juvenile abalone (Tegner and Dayton 1977, 2000; Rogers-Bennett and Pearse 2001) remain unexplored. More complex ecosystem models may provide insight on the effects of other species on abalone population dynamics.

Trigger Points for Management

These model simulations demonstrate the sensitivity of red abalone populations to the SST environment. When the environment is poor, extra pressure through fishing exploitation increased the magnitude of model abalone population declines. A management option might be to close an area to fishing when environmental conditions deteriorate (e.g., Shepherd et al. 1998). This would then protect the remaining animals at a time when recruitment, growth, and survival are in jeopardy. Management would need to be regional; since temperature varies regionally only some portions of the range would need to be closed to fishing at any one time.

With the future SST scenarios, trigger points for closure can be identified, such as temperatures at which the population would not persist if the conditions persisted. Under such criteria, trigger points for temporary fishery closure for these model populations would be 11°C > SST > 16°C. Alternative trigger criteria might include SST values that would lead to a 50% decline in population size at a certain fishing level or when recruitment fell to 50% of the maximum.

If a trigger point for closure for the year was 16°C, then based on the time series for the past 100 years (scenario 1) the cold population at San Miguel Island would have been closed to harvesting once and the warm Santa Cruz Island closed on ten occasions. Closures would have occurred in the El Niño years of 1958, 1983, and 1993, when observations indicated abalone growth and reproduction was reduced (Cox 1962; Haaker et al. 1998). There would have been no closures based on the lower trigger point of 11°C. Considering just the 18 years of in situ SST data at the islands, there would have been seven closures at Santa Cruz Island and one closure at San Miguel Island. Extrapolating to the 100-year periods used in scenario 2, closures would have occurred for 39% and 6% of years, respectively, at the warm and cold populations. As SST increases, so does the number of years of closure in the southern portion of the range. Model simulations could incorporate such management strategies to evaluate their effectiveness, comparing them to simulations with the same number of randomly selected closure years.[3] In an operational sense, a potential problem is that in situ SST data is only available after the fact; however, SST forecasts are now available and could be incorporated into management decision frameworks.[4]

Future SST and Range Changes

Increases in SST and the likely northward migration of the southern range limit for red abalone indicate that some portions of the historic range will soon be unsuitable, as they are for other marine species along the California coast (e.g., Barry et al. 1995; Veit et al. 1996; Oedekoven et al. 2001). The current mean SST for Santa Cruz Island (15.8°C) suggests that this abalone population is at the limit of suitable SST, with the caveat that real populations in California will be influenced by adap-

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[3] A. Hobday, unpubl. data.

[4] See, for example, Scripps Institution of Oceanography's Joint Environmental Data Analysis Center, <www.acw.ucsd.edu>.

tation as well as protected in refuges created as a result of submergence (moving to deeper, cooler waters) and localized upwelling.

Red abalone is only one of several species of abalone currently at risk in California. Commercial fishing is prohibited for all species, but if the environment is also contributing to population declines for the other species, then different management action must be taken. It is assumed, based on past observations (Roemmich and McGowan 1995; Levitus et al. 2000), that climate change will increase surface water temperatures more than temperatures at depth. Thus, the shallow-living abalone species, black (*H. cracherodii*) and green (*H. fulgens*), are more likely to be affected by temperature changes than those living deeper, pink (*H. corrugata*) and white (*H. sorenseni*) abalone. In fact, increased water temperature has already been shown to increase the susceptibility of green[5] and black abalone to disease (Alstatt et al. 1996; Friedman et al. 1997).

Management strategies that rely on restricting fishing or creating marine reserves may be unsuccessful in conserving abalone stocks if potential changes in the environment (such as SST) are not considered. Efforts to restore depleted red and other abalone populations should focus on locations where the environment is likely to be suitable over the long term. In the case of red abalone such locations are likely to be north of Point Conception (34.5°N) if SST increases by more than 1°C from current levels. An additional conservation problem for red abalone is that in several locations north of Point Conception, predation by sea otters is a significant additional source of abalone mortality (e.g., Wendell 1994).

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APPENDIX 1

Population dynamics model for red abalone. Example output from one model run of scenario 2 (100 years of current SST), where fishing level was 30% and larval connectivity was 5%. Panels on the right show the cold population, those on the left the warm population. The top two panels show the final distribution of abalone in each model area, the middle two the size distribution at the end of the run, and the bottom two the population trajectories. In the bottom panels, the upper line is the size of the total population, the middle the adult population, and the lower the legal population; the vertical line at year 50 indicates the start of fishing.