

MODELING A REGIME SHIFT IN A KELP FOREST ECOSYSTEM CAUSED BY A LOBSTER RANGE EXPANSION

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ABSTRACT

The South African West Coast rock lobster, *Jasus lalandii* (H. Milne-Edwards, 1837), has expanded its range to the southeast, where its abundance has increased radically. The ecological consequences of this “invasion” are likely to be considerable. We employed a minimally realistic model to simulate the “invasion” and to explore interactions of *J. lalandii* with the sea urchin, *Parechinus angulosus* (Leske, 1778), and the abalone, *Haliotis midae* Linnaeus, 1758, juveniles of which shelter beneath this urchin. Model fits to empirical data were good, although species-interaction terms were difficult to estimate. Base-case trajectories indicated: (1) Lobster biomass peaked at about 1000 t in 1994 and was then reduced by fishing to a stable value approximately 50% lower by 2008. (2) Urchins remained close to carrying capacity in “noninvaded” areas but collapsed to local extinction by 1997 in the invaded area. (3) Abalone declined over 2000–2008 in noninvaded areas because of illegal fishing and collapsed to near zero in the “invaded” area because of illegal fishing combined with increased lobster abundance. Sensitivity analyses favored the hypothesis that the invasion was due to adult immigration rather than larval recruitment. Modeled 50-yr projections indicated that urchins will remain locally extinct in the invaded area, even 50 yrs into the future. The abalone collapse in the invaded area would persist >50 yrs, even if lobsters were absent. We argue that the lobster “invasion” triggered an alternative stable state, making a return to pre-invasion conditions unlikely.

The collapse of many marine ecosystems has been attributed to severe overfishing during the 20th century (Roberts 1995, Turner et al. 1999, Steneck et al. 2004, Frank et al. 2005, Österblom et al. 2007), combined with more recent stressors such as human-caused climate change, water pollution, habitat degradation, and invasive species (Jackson et al. 2001). Although reversibility of collapsed systems is possible, strict management procedures are required, and even then decades may pass before a system shows any sign of recovery (Frank et al. 2011).

The idea of top-down control was first proposed by Hairston et al. (1960) and concerns control of ecosystem structure and functioning by predators, which alter prey abundance and have indirect effects on lower trophic levels that are referred to as “trophic cascades.” The removal or reduction of species at a high trophic level shifts the dominance and impact of consumers to lower trophic levels (Steneck 1998). Through both natural effects (e.g., climate) and those arising from humans (e.g., fishing), trophic cascades can drive regime shifts, changing the ecosystem from one relatively stable state to another (Scheffer et al. 2000, 2001, Daskalov et al. 2007, Österblom et al. 2007, Möllmann et al. 2008). Depending on the likelihood of a shift reversal and the path taken to reverse a shift, these states are referred to as either “alternate stable states” or “phase states” (Lewontin 1969, Holling 1973, Done 1992; see Scheffer et al. 2001, Beisner et al. 2003, Scheffer and Carpenter 2003, for reviews).

Sea urchins are well known in many parts of the world for their grazing abilities (Lawrence 1975, Andrew 1993, Ling and Johnson 2009) and frequently play a major role in controlling kelp communities (Estes and Palmisano 1974, Vadas 1977, Harrold and Reed 1985). They are particularly infamous for their role in transforming kelp forests into “urchin barrens” dominated by encrusting (nongeniculate) corallines. This process has been documented predominantly but not exclusively in the Northern Hemisphere (see e.g., Breen and Mann 1976, Tegner and Dayton 1991, Steneck 1997, Estes et al. 1998, Babcock et al. 1999, Ling and Johnston 2009). In the Southern Hemisphere, several species of urchins feed more on drift algae than on attached plants (Castilla and Moreno 1982, Dayton 1985, Day and Branch 2002b, Vanderklift and Kendrick 2005), so urchin-induced kelp deforestation is not as common there (see review by Steneck et al. 2002).

The intense grazing exerted by sea urchins on kelp communities is often controlled by the top-down effects of predators. These include sea otters (Estes and Palmisano 1974, Watson and Estes 2011), fishes (Shears and Babcock 2002, Steneck et al. 2002, 2004), and both clawed and rock (or spiny) lobsters (see e.g., Cowan 1983, Tegner and Levin 1983, Mayfield and Branch 2000, Shears and Babcock 2002, Ling et al. 2009).

The West Coast rock lobster, *Jasus lalandii* (H. Milne-Edwards, 1837), is a significant predator in South African marine ecosystems and feeds on a wide variety of prey (Pollock 1979, Mayfield et al. 2000a,b, 2001, Van Zyl et al. 2003, Haley et al. 2011), although it is selective and shows a preference for mussels and urchins (Mayfield et al. 2000a,b, 2001, Haley et al. 2011). In the absence of preferred prey, however, these lobsters can maintain their populations by feeding on unorthodox prey such as barnacle recruits and are therefore not necessarily limited by depletion of preferred prey (Barkai and Branch 1988c). Comparisons of adjacent areas in which *J. lalandii* is abundant and rare have revealed radically different communities (Barkai and Branch 1988a, Barkai and McQuaid 1988), and experimental deployment of caged and uncaged settlement plates implicate this lobster as the cause (Barkai and Branch 1988b). As a consequence, any radical change in the abundance of *J. lalandii* can be expected to have substantial effects on benthic invertebrate communities.

A decline in the catches of *J. lalandii* on the west coast of South Africa, partly due to reduced growth rates, occurred from the late 1980s. No satisfactory single explanation has been found for this slow growth, but it is thought to be linked to a combination of reduced primary productivity, scarcity of preferred food, increased frequency of low-oxygen waters, and other environmental anomalies (Pollock and Shannon 1987, Shannon et al. 1992, Pollock et al. 1997, Mayfield et al. 2000b). While *J. lalandii* was decreasing along the west coast, however, a substantial increase in its abundance took place along the southwest coast in an area known as “East of Cape Hangklip” (EOCH; Tarr et al. 1996, Cockcroft et al. 2008). This increase is considered to be due to changes in environmental conditions. Although long-term data for the southwest coast inshore region are insufficient to resolve the question (Cockcroft et al. 2008), cooling of inshore waters has been observed along the south coast (Roy et al. 2007, Rouault et al. 2009). The exact mechanism behind the lobster “invasion” is also unclear but is thought to be either (1) a migration of adult rock lobsters or (2) increased larval settlement in the area.

The increase in rock-lobster abundance EPOCH coincided with a rapid decline in the urchin *Parechinus angulosus* (Leske, 1778) (Tarr et al. 1996) that was almost certainly directly attributable to the increase in lobsters. In addition to the lobster

invasion and subsequent urchin decline, illegal fishing of abalone escalated (Hauck and Sweijd 1999, Hauck 2009). Given the critical relationship between juvenile abalone and urchins (Day and Branch 2000a,b), the decline and then virtual disappearance of urchins, combined with overexploitation of abalone parent stock, has substantially depleted the abalone resource. What was once a lucrative commercial fishery underwent temporary closure, and a rock-lobster fishery has developed in the area EPOCH instead. Despite harvesting, rock-lobster densities remain high, urchins remain absent, and the future for abalone in this region is bleak. A kelp forest system once dominated by herbivores—particularly urchins (*P. angulosus*), abalone (*Haliotis midae* Linnaeus, 1758), and large winkles (*Oxystele* and *Turbo* spp.)—has been transformed into one now dominated by rock lobsters (*J. lalandii*) and foliar algae (Blamey et al. 2010).

Our approach was to develop an ecosystem model to explore regime-shift dynamics in the kelp forest ecosystem EPOCH (Fig. 1). We did so by means of a minimally realistic model (MRM; Punt and Butterworth 1995). Considerably simpler than whole ecosystem models (e.g., ECOPATH with ECOSIM, EwE; Walters et al. 1997), MRMs represent a limited number of species believed to have the most important interactions with the target species; only a small part of the ecosystem is modeled therefore. This simplification reduces the number of interspecific links that must be modeled, particularly eliminating those links that can be construed as weak (Yodzis 1998, Plagányi 2007). We chose this approach for four main reasons: (1) strong links were known to exist among a limited set of species; (2) exploratory work of a similar nature on the ecosystem (Plagányi 2004) provided a platform from which we could build; (3) applying EwE to answer the types of questions we were posing presented difficulties (see Plagányi and Butterworth 2008); and (4) the data necessary for modeling many of the other component species of the ecosystem were lacking.

First, we developed the model to simulate the situation in which lobsters had invaded the area EPOCH and attained high densities. Second, we fitted the model to empirical data to assess how realistic it was. Third, we performed sensitivity analyses to determine how sensitive the estimated parameters were to the adjustment of certain variables. Finally, we used the model to predict the future status of urchin and abalone populations in the absence of lobsters. Specifically we used the model to address the following questions:

1. In the presence of high densities of lobsters, what is the status of the urchin population, and what are the consequences of this status for abalone?
2. Would the “lobster invasion” have differed had it been initiated by larval settlement rather than an influx of adult lobsters?
3. In the absence of rock lobsters, what would be the likely future of abalone and urchin populations east of Cape Hangklip?
4. What biomass would the future rock-lobster population attain under various catch scenarios?
5. Could the ecosystem shift back to its former state?

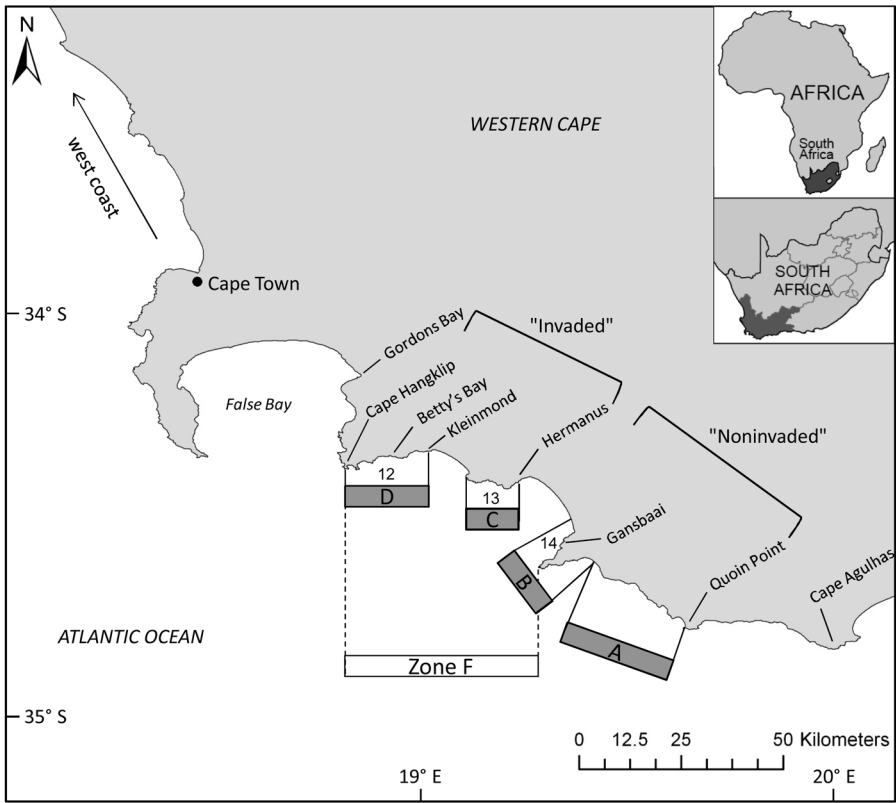


Figure 1. Map of the southwest coast of South Africa showing sites mentioned in the text and the fishing zones east of Cape Hangklip. Zones A–D are the commercial abalone fishing zones, and zone F is the West Coast rock-lobster fishing zone. Zone F is subdivided into three areas: Area 12 Kleinmond, Area 13 Hermanus, and Area 14 Gansbaai. “Invaded” marks the zone into which rock lobsters have recently extended their ranges; “Noninvaded” marks the zone in which they are still so rare as to seem absent.

METHODS

STUDY AREA

The west and southwest coasts of South Africa are divided into commercial fishing zones for both the abalone and rock-lobster fisheries (Fig. 1). East of Cape Hangklip are four abalone fishing zones, A–D (Tarr 2000), which overlap with the one rock-lobster zone, F, itself subdivided into three areas: area 12 Kleinmond, area 13 Hermanus, and area 14 Gansbaai (Cockcroft et al. 2008). On the basis of rock-lobster densities, the area EPOCH was divided into an “invaded” area with high densities and a “noninvaded” area with low densities (Blamey et al. 2010, Blamey and Branch 2012). The invaded area incorporates abalone zones C and D and rock-lobster areas 12 and 13. The noninvaded area includes abalone zones A and B and rock-lobster area 14.

Our model concentrated on the invaded area, specifically abalone zone D, which coincides with rock-lobster area 12. The noninvaded zone B was simultaneously modeled within the same framework, partly for parameter estimation, but for direct comparison of invaded and noninvaded ecosystems. This approach permitted separate estimation of abalone mortality due to (1) the biological effects of lobsters and urchins and (2) fishing (particularly illegal

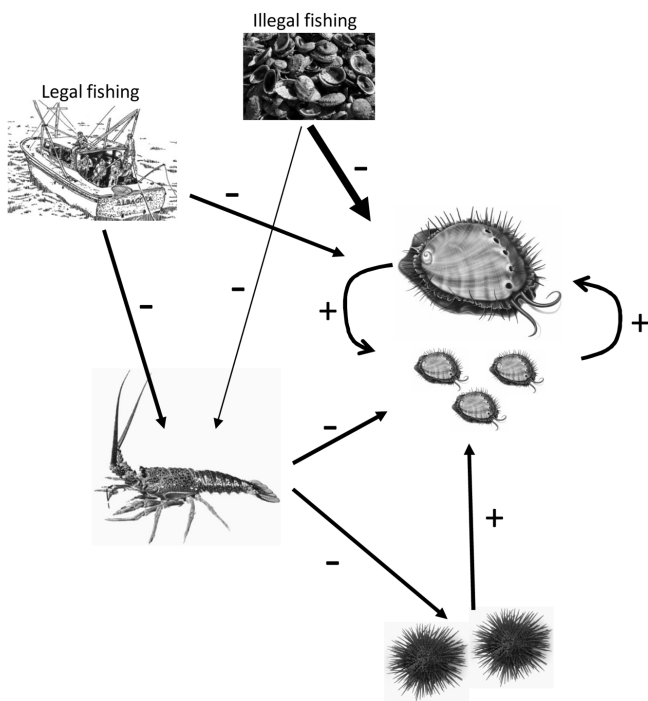


Figure 2. Constituents of the base-case multispecies model, showing positive (+) and negative (–) interactions in the model among rock lobster, abalone, and urchins, as well as the harvesting of rock lobsters and abalone.

fishing), as these mortality sources are confounded if only a single area with both fishing and lobster effects is considered (Plagányi and Butterworth 2010).

CONSTITUENTS OF THE MRM MODEL

We focused on the positive and negative biological interactions among the rock lobster *J. landanii*, the urchin *P. angulosus*, and both juveniles and adults of the abalone *H. midae*, coupled with the effects of both legal and illegal fishing on lobsters and abalone (Fig. 2).

DATA

Rock-Lobster Data.—The model used rock-lobster commercial catch data and recreational and poaching catch estimates. Additional indices of abundance to which the model was fitted included rock-lobster commercial catch per unit effort (CPUE) and fishery-independent monitoring surveys (FIMS) conducted by the South African Department of Agriculture, Forestry and Fisheries.

Commercial catch data for the rock-lobster fishery extend back to the late 19th century (Melville-Smith and van Sittert 2005), but they are almost entirely from the west coast, as the small-scale commercial fishery in the invaded area EPOCH was developed only in the early 2000s (Cockcroft et al. 2008). These new commercial fishing grounds fall under zone F (Fig. 1), and because the fishery is so recent, catch data for this region were available only for the period 2000–2008. No total allowable catch was allocated in 2003, and zero catch was assumed for that year. The minimum size limit for the commercial fishery is 75 mm carapace length (CL), and the fishing season runs from 15 November of model year $y - 1$ until 30 June of model year y .

Estimates of the total recreational catch EPOCH were available for 1992–1995, and for the area between Gordons Bay and Cape Agulhas for 2003–2007. Area 12 was assumed to account

for a representative proportion, namely one quarter of the values for that area (appendix 2 and table A2.03 of Blamey 2010). No recreational catch data are available for the interval between these periods, but because the recreational fishery was operating, the mean catch of the four preceding years (1992–1995) was assumed for the period 1996–2002. Recreational catches are limited to lobsters ≥ 80 mm CL.

Illegal lobster fishing was considered to be negligible before 2000. Thereafter (2000–2008), it was taken to be 10% of the commercial catch for area 12, consistent with the approach used in stock assessment (Johnston and Butterworth 2011).

Rock-lobster data used in model-fitting were from two sources: (1) nonstandardized CPUE data ($\text{kg boat}^{-1} \text{d}^{-1}$), calculated from the commercial catch data from area 12 for the period 2004–2008, and (2) annual FIMS data (number of lobsters hoopnet $^{-1}$) for areas ECH were available for 2002–2005.

Male and female rock-lobster lengths were taken from Johnston and Butterworth (2001) and averaged over the model period 1980–2007; the result was mean lengths at age for both females and males. By means of Heydorn's (1969) length-weight conversion formula, male and female masses at age were calculated. Rock lobsters were treated as one sex in the model, so, on the assumption of a 50:50 sex ratio, a mean length at age and mass at age were used.

Abalone Data.—The abalone component of the model included catch data, catch-at-age information, and indices of abundance. Catch data comprised commercial catch data, recreational catch estimates, and confiscation trends used to estimate illegal catches. Commercial catch data and recreational catch estimates extend back to 1951 (appendix 1 of Plagányi and Butterworth 2010) and poaching confiscation records (from South African law enforcement) back to 1994.

Several indices of abundance were used in the model-fitting process, including standardized commercial CPUE, fishery-independent abalone survey (FIAS) data, and a large amount of catch-at-age data. Standardized commercial CPUE data were available for 1980–2006 and FIAS data for 1995–2007. Finally, the catch-at-age information included data from the commercial, recreational, and illegal (confiscations) fishery sectors and also from fishery-independent and industry surveys, as detailed in Plagányi and Butterworth (2010).

Juvenile Abalone and Urchin Data.—Counts of juvenile abalone and urchin densities at Betty's Bay in zone D, covering 1986–1995, were derived from Tarr et al. (1996). For the model, the average numbers of juvenile abalone and urchins per model year (defined as October of year $y - 1$ to September of year y) were used.

Data for Interactions among Species.—Data used in the multispecies interactions are largely from published work done in the area ECH: see Appendix 1 (Tables A1.1 and A1.2) in online supplementary material.

MODEL DESCRIPTION AND EQUATIONS

Abalone.—The abalone constituent of the multispecies model was based on the single-species integrated statistical model currently used for stock assessment of *H. midae* (Plagányi and Butterworth 2010, Plagányi et al. 2011). It is an age-structured production model with five individual zones modeled simultaneously but split into inshore and offshore components. In brief, the discrete updating equation for the inshore number of abalone of age a at the beginning of model year y ($N_{y,a}^I$) accounts for inshore-offshore movement and natural mortality (the predation mortality component of natural mortality was modeled separately), as well as three sources of mortality (legal fishing, illegal fishing, and predation) that are subtracted as part of a summed catch term (shown here for the inshore sector) $C_{y,a}^I$:

$$N_{y+1,a+1}^I = ((1 - \rho) \cdot N_{y,a}^I e^{-\frac{M_a}{4}} - C_{y,a}^I) e^{-\frac{3M_a}{4}} \quad 5 \leq a \leq 13 \quad (\text{Eq. 1})$$

where ρ is the proportion of inshore animals of age a ($5 \leq a \leq z$) that move offshore at the beginning of model year y , and M_a is the (time-invariant) natural mortality rate for abalone age a .

Abalone natural mortality was assumed to be age dependent according to the formula:

$$M_a = \mu + \frac{\lambda}{a+1} \quad (\text{Eq. 2})$$

where the parameter $\mu = 0.126$ was estimated in the model-fitting process and λ set equal to a constant (0.2). Further details of the model and model equations appear in Plagányi and Butterworth (2010), and modifications to account for interspecies interactions are described below.

For our study, only zone B (which was not invaded by rock lobsters) and zone D (invaded by rock lobsters) were considered, and the focus was on the inshore areas. The abalone model beginning year was 1951 for both zones B and D, but the multispecies effects were only added (to zone D) from 1985, to coincide with the rock-lobster invasion in the early 1990s (Tarr et al. 1996).

Rock Lobster.—The West Coast rock-lobster stock assessment uses a detailed size-structured model (Johnston and Butterworth 2005) to generate an annual recommended total allowable catch (Johnston and Butterworth 2005, Butterworth 2008). A size-structured approach was used, but size data can be converted into age data on the basis of the growth rate of lobsters derived from annual tagging, and a length-at-age matrix calculated (Johnston and Butterworth 2001). We used an age-structured production model to model the rock-lobster component, assuming that the mean length of each age adequately captured the overall dynamics.

The rock lobsters were modeled in quarterly time steps, and the remaining numbers from any given season contributed to the following season. As with the abalone model, the rock-lobster catch was assumed to have been taken as a pulse at midyear (season 2). For the first few years, no catches were made; recreational catches began in the early 1990s, and commercial catches in 2000. Parameters and variables used in the rock-lobster component of the model are given in Appendix 1 (Tables A1.3 and A1.5, respectively) in the online supplementary material.

The rock-lobster deterministic age-structured production model was as follows:

Numbers at age

$$J_{y+1,0} = R_{y+1}^J \quad (\text{Eq. 3})$$

$$J_{y+1,a+1} = J_{y,a}^4 e^{\frac{-M^J}{4}} \quad (\text{Eq. 4})$$

$$J_{y+1,a+1}^2 = (J_{y+1,a+1}^1 - C_{y+1,a}^J) e^{\frac{-M^J}{4}} \quad (\text{Eq. 5})$$

$$J_{y+1,a+1}^3 = J_{y+1,a+1}^2 e^{\frac{-M^J}{4}} \quad (\text{Eq. 6})$$

$$J_{y+1,a+1}^4 = J_{y+1,a+1}^3 e^{\frac{-M^J}{4}} \quad (\text{Eq. 7})$$

where y refers to model year from October of calendar year $y - 1$ to September of year y , a refers to age in years, $J_{y,a} = J_{y,a}^I$ for simplicity of notation, $J_{y,a}^q$ is the number of rock lobsters in age class a during quarter q of year y , M^J is the rock lobster annual natural mortality rate, R_y^J is the number of rock-lobster recruits to age class 0 at the beginning of year y , and $C_{y,a}^J$ is the total catch of rock lobsters from age class a during year y .

Further details on modeling the rock-lobster component (i.e., the relationship between spawning biomass and recruitment, lobster starting age structure, total biomass, total catch, catches at age, and length-weight conversions) are given in Appendix 2 (Equations A1–A19) in the online supplementary material.

Urchins.—

(a) Initial starting population: As with the rock lobsters, the urchin population was introduced into the model in 1985 for zones B and D. The initial starting populations were assumed to be at carrying capacity, which was approximated as the mean maximum urchin density recorded in the region, multiplied by the reef areas of the respective zones:

$$K_u = (U_{pristine} \cdot (Area^z \cdot hfact)) \cdot W_u \quad (\text{Eq. 8})$$

where K_u is the carrying-capacity biomass in metric tons; $U_{pristine}$ is the maximum number of urchins per square meter recorded in Roman's Bay (zone B), a noninvaded site (assumed to be equivalent to the carrying capacity); $Area^z$ is the area covered by kelp forest in zone B and zone D (Tarr 1993); $hfact$ is a habitat multiplication factor adjusting for the way in which bottom topography increases the effective habitat area (see Plagányi 2004); and W_u is the mean weight of an adult urchin in metric tons.

(b) The urchin surplus production model: The urchin populations in the two zones were modeled with a surplus production model:

$$U_{y+1} = U_y + r_u U_y \left(1 - \frac{U_y}{K_u}\right) - C_y^{UJ} \quad (\text{Eq. 9})$$

where U_y is the biomass of urchins in year y , r_u is the urchin intrinsic growth rate parameter, and C_y^{UJ} is the biomass of urchins consumed by rock lobsters in year y .

The zone B population remained at carrying capacity in the absence of rock lobsters, whereas in zone D, urchins were eaten by large rock lobsters. Parameters and variables used in the urchin component of the model appear in Appendix 1 (Tables A1.4 and A1.5, respectively) in the online supplementary material.

Multispecies Interactions.—

(a) Lobster-abalone and lobster-urchin interactions: Rock lobsters must exceed 65 mm CL to be able to consume small abalone (Van Zyl et al. 2003) and >68 mm CL to consume urchins (Mayfield and Branch 2000), corresponding to ages of 11 and 12 yrs, respectively. Predation by rock lobsters was modeled with a Holling type II function, where lobsters ≥ 11 yrs could prey on abalone aged 0 and 1 yrs and lobsters ≥ 12 yrs could consume urchins of all sizes. The lobster's selectivity for abalone younger than 1 yr was set at 50%, as recruits take time to grow sufficiently large to be eaten; for 1 yr olds it was assumed to be 100%. Equations detailing these interactions appear in Appendix 2 (equations A20–A25) in the online supplementary material.

Predation by rock lobsters was assumed to affect the dynamics of urchins and abalone but not vice versa, because (1) urchins and abalone make up a small component of the lobster diet (Pollock 1979, Mayfield et al. 2000a), (2) rock lobsters are significant predators with the ability to alter ecosystem structure (Barkai and Branch 1988a), and (3) although they are selective foragers (Mayfield et al. 2000a,b, 2001, Haley et al. 2011), lobsters readily switch between prey types and can maintain dense populations in the absence of preferred prey (Barkai and Branch 1988c). This view is corroborated by maintenance of high densities of rock lobsters ECH despite decreases in urchin and abalone populations (Mayfield and Branch 2000).

(b) Urchin-abalone relationship: In the region investigated, juvenile abalone (3–35 mm shell length) depend on concealment beneath urchins for survival (Day and Branch 2000b, 2002a). Mayfield and Branch (2000) calculated that urchin densities below 25–30 urchins m^{-2} would

limit survival of juvenile abalone. The urchin-abalone interaction was incorporated into the model in the form of juvenile abalone survival relative to urchin densities, where abalone survival decreased exponentially below a specified urchin-density threshold U_{thresh} (0.3 of the carrying capacity of urchins, equivalent to about 30 urchins m^{-2}). Equations detailing this relationship appear in Appendix 2 (Equations A26–A27) in the online supplementary material.

Likelihood Function.—We fitted the model to all available data to estimate model parameters by minimizing the negative of the log likelihood function for these data. The abalone component included several likelihood contributions from fitting to empirical abundance indices and catch-at-age data (described above and in Plagányi and Butterworth 2010). New contributions to the total likelihood, which became necessary when the model was extended to a multispecies form, included rock-lobster commercial CPUE and FIMS and counts of juvenile abalone and urchins. All equations are given in Appendix 2 (Equations A28–A33) of the online supplementary material and were developed from those in Plagányi and Butterworth (2010).

PARAMETERS

In addition to the 30 pre-existing parameters previously developed for the abalone single-species model (Plagányi and Butterworth 2010), six new parameters were estimated within a maximum likelihood framework and AD Model Builder™ (v 7.1.1, Otter Research, Ltd.), together with associated 90% Hessian-based confidence intervals:

1. B'_{90} : initial total rock lobster biomass in 1985.
2. $\alpha_{Ab,J}$: lobster-abalone interaction parameter 1.
3. $\beta_{Ab,J}$: lobster-abalone interaction parameter 2 (for a Holling type II functional response).
4. $\alpha_{U,J}$: lobster-urchin interaction parameter 1.
5. $\beta_{U,J}$: lobster-urchin interaction parameter 2 (for a Holling type II functional response).
6. K_j^{sp} rock lobster spawning-biomass carrying capacity for zone D.

SENSITIVITY ANALYSES

A wide range of sensitivity tests was conducted (Blamey 2010), but only those that provided insight are reported here:

(1) Abalone natural mortality: our multispecies model was designed to generate an explicit representation of mortality due to interspecific interactions. The different potential sources of mortality were difficult to estimate because natural mortality, legal fishing, illegal fishing, and interspecific effects were confounded. In the sensitivity analyses, the abalone natural mortality parameter (μ), which had been fixed in the base-case model, was estimated instead.

(2) Rock-lobster natural mortality M' was fixed at 0.10 in the base-case model, whereas sensitivity analyses were run with a 50% increase and 50% decrease in M' . In addition, a scenario was run that attempted to estimate M' .

(3) Suggested causes of the rock-lobster invasion (Cockcroft et al. 2008) have yielded two hypotheses: (1) immigration of large lobsters and (2) increased rock-lobster recruitment, eventually leading to the observed increase in abundance. To explore their relative plausibility, we tried three scenarios of rock-lobster starting age structures in the model (Fig. 3). The base-case model used a starting age structure that mimicked a sudden invasion by large lobsters in the early 1990s (Fig. 3), corresponding to adult immigration. Accordingly, at the beginning of the model period, the population was set to constitute uniform proportions of individuals in age groups 0–10, allowing time for individual growth to generate a population that would resemble the arrival of immigrants exceeding the 68-mm CL threshold required to consume urchins.

Two additional scenarios were then used for the sensitivity analyses. The first (model S31) used an age structure that yielded a population by 1990 that would have mimicked the second hypothesis—establishment of the population by larval settlement. For large rock lobsters to have increased in the early 1990s, increased larval settlement would have had to happen in

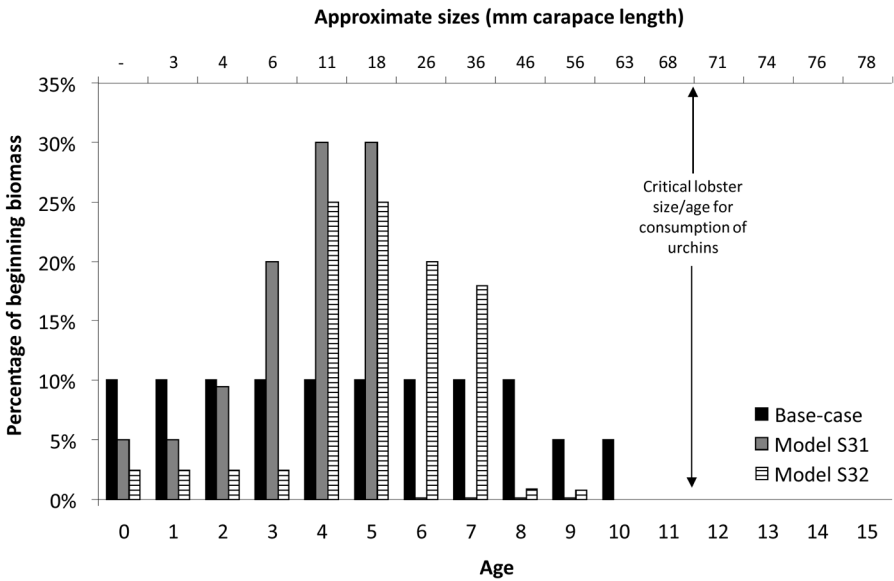


Figure 3. The percentage starting biomass for each rock-lobster age class used in the base-case model starting in 1985 and in two sensitivity analyses, model S31 and model S32. The base-case model used an age structure that, by 1990, would have mimicked an adult rock-lobster immigration into the area east of Cape Hangklip; model S31 used an age structure that would, by 1990, have produced a population that mimicked increased juvenile settlement in the early 1980s, and model S32 used an age structure that was intermediate between the base case and model S31.

the late 1970s/early 1980s. Therefore, when the model period began in 1985, the majority of the starting biomass was set to comprise 3 to 5 yr olds, with few very young rock lobsters and none over 5 yrs old (Fig. 3). The second scenario (model S32) was intermediate between model S31 and the base case, with a starting biomass of mostly 4- to 7-yr-old rock lobsters, plus small proportions of very young lobsters and an even smaller proportion of lobsters large enough to consume urchins (Fig. 3).

FUTURE PROJECTIONS

Future projections were explored for five scenarios: first, for urchin and abalone biomass with (1) or without (2) rock-lobster predation and, second, for rock-lobster biomass, on the assumption of (3) zero legal capture but ongoing illegal capture, (4) capture continuing at 2007 levels, and (5) a 10-fold increase in illegal catches but zero legal take.

RESULTS

PARAMETER ESTIMATION

Six new parameters (B'_{y0} , $\alpha_{Ab,J}$, $\beta_{Ab,J}$, $\alpha_{U,J}$, $\beta_{U,J}$, K^{sp}_J), in addition to those from the single-species abalone model, were estimated together with associated 90% Hessian-based confidence intervals (Table 1). The full set of base-case model-parameter estimates is given in appendix 5 (table A5.01) of Blamey (2010).

The initial rock-lobster beginning biomass, B'_{y0} , of 314 t was not well estimated (90% confidence interval = 0–942 t). The lobster-abalone interaction parameters, $\alpha_{Ab,J}$, $\beta_{Ab,J}$ and the lobster-urchin interaction parameters, $\alpha_{U,J}$, $\beta_{U,J}$ proved the most difficult to estimate (see parameter estimates and 90% confidence intervals in Table 1).

Table 1. Estimated model parameters with Hessian-based 90% confidence intervals.

| Parameter description | Notation | Value | 90% confidence interval |
|--|-----------------|------------|-------------------------|
| Beginning lobster biomass (t) | B_{y0}^l | 314.0000 | 0.0000–942.0000 |
| Lobster-abalone interaction parameter 1 | $\alpha_{Ab,J}$ | 0.0070 | 0.0000–16.1400 |
| Lobster-abalone interaction parameter 2 | $\beta_{Ab,J}$ | 5.7680 | 0.0000–19,679.0000 |
| Lobster-urchin interaction parameter 1 | $\alpha_{U,J}$ | 0.0019 | 0.0000–0.0063 |
| Lobster-urchin interaction parameter 2 | $\beta_{U,J}$ | 0.0002 | 0.0001–0.0004 |
| Lobster spawning biomass carrying capacity (t) | K_j^{sp} | 1,510.6000 | 1,085.7000–1,935.5000 |

Rock-lobster spawning biomass carrying capacity, K_j^{sp} , was estimated to be 1510 t, with narrower 90% confidence interval (Table 1).

POPULATION TRAJECTORIES AND CATCH TRENDS

Abalone.—The model estimates of inshore abalone spawning biomass were 3500 t for zone B and 5500 t for zone D in 1951 (Fig. 4A,B). Subsequently, both zones underwent steep declines in biomass due to high exploitation levels during the 1950s and 1960s. In 1970, fishing regulations were introduced, and as a result the spawning biomass remained relatively stable or rose slightly for the next 25–30 yrs, but by the mid-1990s illegal fishing had begun, initially in zone D and shortly afterward in zone B. The model therefore yielded a rapid decline in the spawning biomass, particularly for zone D, where the invasion by rock lobsters augmented the decline due to overexploitation, culminating in virtual disappearance of abalone by 2007.

Rock Lobster.—We assumed an absence of lobsters from zone B (Fig. 4C). In zone D, the model estimated an initial rock-lobster spawning biomass of approximately 50 t in 1985 (Fig. 4D) and predicted a rapid increase to a maximum of just less than 1000 t in 1994, followed by a decrease until 2001, then relative constancy between 2001 and 2006, and finally a slight drop.

Urchins.—Urchin biomass was modeled for both zones, but rock lobsters would only have had an impact on urchins in zone D. In zone B, the urchin carrying capacity was calculated as approximately 14,600 t, and in the absence of lobsters, it was predicted to remain at that level (Fig. 4E). In zone D, the urchin carrying capacity was calculated to be just under 15,000 t in 1985 (Fig. 4F), with an initial decline in the late 1980s, growing steeper by the early 1990s, and resulting in their complete disappearance from 1997 onward (Fig. 4G).

EVALUATION OF MODEL FITS TO THE DATA

Abalone CPUE and FIAS.—Both zones B and D showed an increase in standardized commercial catch rates between 1980 and the mid- to late 1990s, followed by a decrease over the decade leading up to 2006 (Fig. 5A,C). A general decrease in abalone population density was also evident in the FIAS data over this period (Fig. 5B,D). The model yielded acceptable fits to both indices (Fig. 5A–D; Appendix 1, Table A1.6, in online supplementary material), but during the 1990s the CPUE values were sometimes higher than the predicted model values for zone D for reasons outlined by Plagányi and Butterworth (2010).

Rock Lobster CPUE and FIMS.—Although CPUE data were limited, commercial catch rates for lobsters showed a gradual decline (Fig. 5E), suggesting a decrease

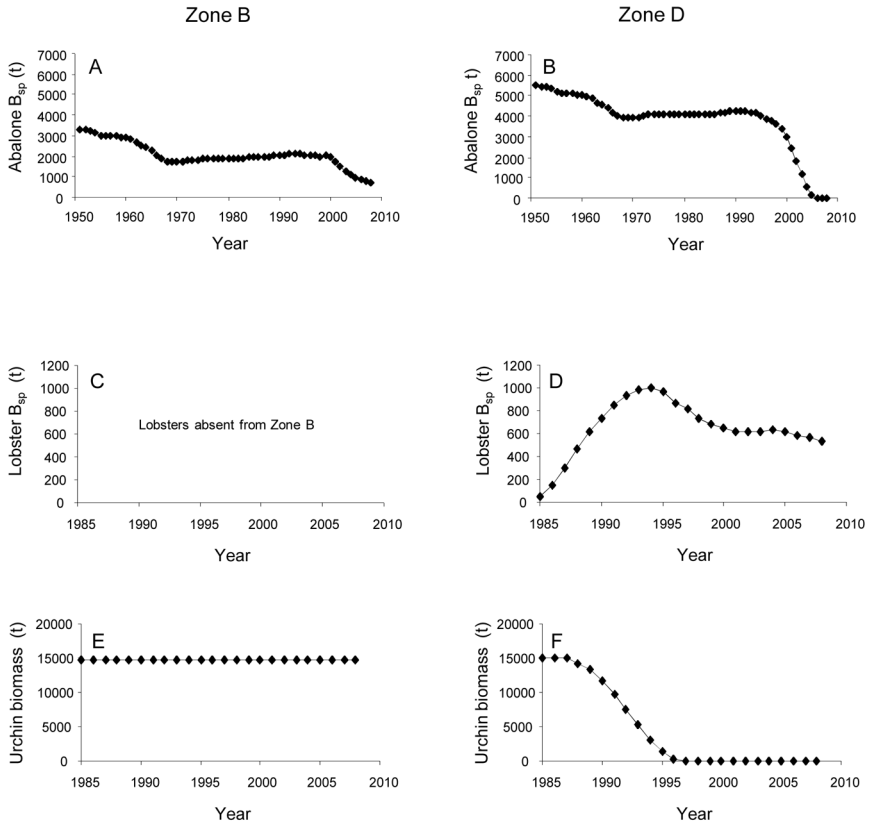


Figure 4. Population trajectories in metric tons (t) for (A,B) abalone inshore spawning biomass, (C,D) rock-lobster spawning biomass, and (E,F) urchin biomass, for zones B (noninvaded) and D (invaded by lobsters).

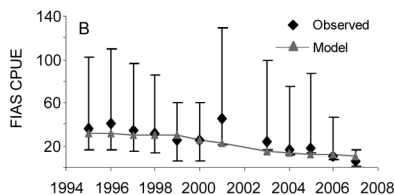
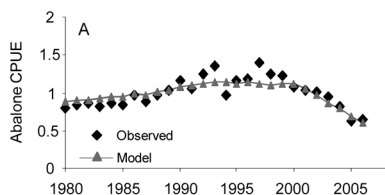
in the biomass in zone D. FIMS data showed no trend, because the surveys EPOCH spanned only 2001–2005. The model showed good fits to both sets of observed CPUE (Fig. 5E,F; Appendix 1, Table A1.6, in online supplementary material). The best fit for FIMS data showed no obvious change in predicted catch rate over the 4 yrs (Fig. 5F).

Urchins and Juvenile Abalone.—Urchin numbers underwent a striking sudden decline in 1994 in zone D and virtually disappeared in 1995 and 1996 (Fig. 5G). Initially numbers of juvenile abalone increased slightly, then fell substantially in 1995–1996, although sampling variability was substantial (Fig. 5H). Model fits were good in both cases (Fig. 5G,H).

SPECIES INTERACTIONS

Despite a decline in urchin biomass, juvenile abalone biomass initially remained relatively constant, declining only when urchins dropped below 4000 t (Fig. 6A). Survival of juvenile abalone (0- to 1-yr olds) was extremely sensitive to urchin biomass (Fig. 6B). Mayfield and Branch (2000) estimated from field observations that, if urchins fall below 25–30 urchins m^{-2} , juvenile abalone survival would be limited. Therefore, in our multispecies model, survival of juvenile abalone was set to decline

Zone B



Zone D

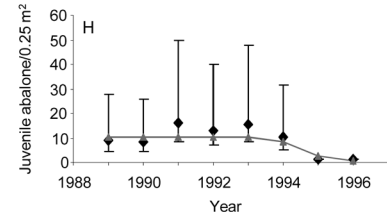
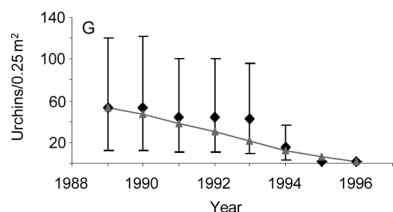
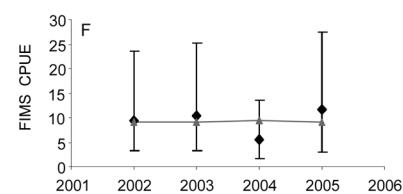
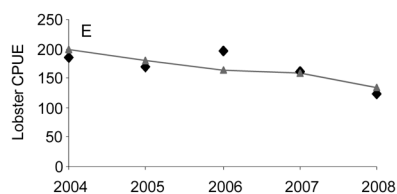
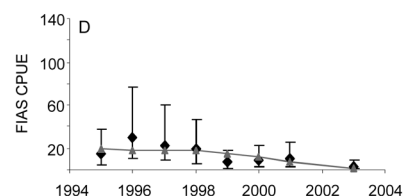
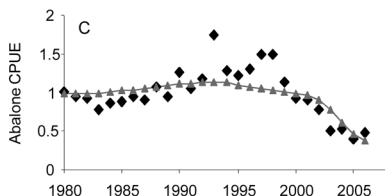


Figure 5. Model fits: observed and predicted catch per unit effort (CPUE) for (A–D) the abalone commercial fishery (standardized to kg min^{-1}) and the Fishery Independent Abalone Survey, FIAS (number of abalone per 60 m^2) in zones B and D; (E) the rock lobster commercial fishery ($\text{kg boat}^{-1} \text{ d}^{-1}$); (F) the rock-lobster Fishery-Independent Monitoring Survey, FIMS (number trap $^{-1}$); (G) urchin survey; and (H) juvenile abalone survey for zone D. Error bars are 90% confidence intervals.

when urchin biomass dropped below a third of the carrying capacity (equivalent to the density calculated by Mayfield and Branch 2000), as seen in Figure 6B. Estimating the parameters describing this urchin-abalone relationship was not possible, given limited data from which to estimate the other interaction parameters simultaneously.

In the trajectory of the relationship between urchins and lobsters (Fig. 6C), urchin biomass decreased as rock-lobster biomass increased and failed to recover, even after declines in rock lobster after about 1995. Abalone biomass (Fig. 6D) remained fairly constant until rock-lobster biomass reached almost 1000 t and thereafter

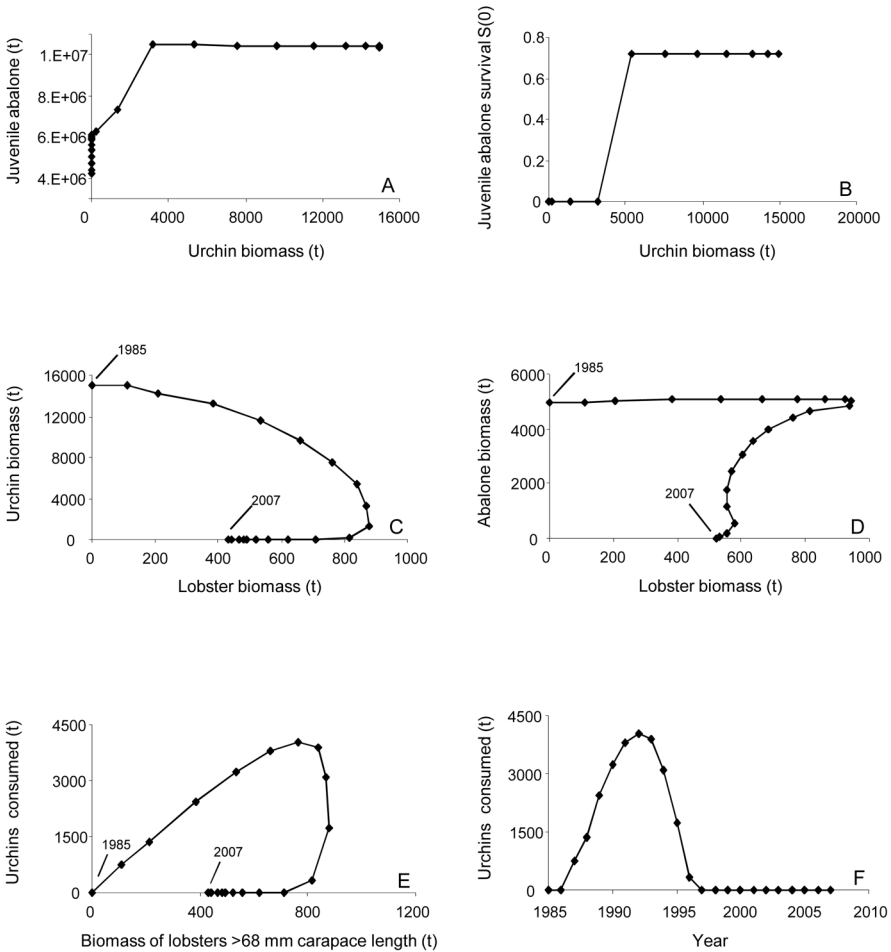


Figure 6. Species interactions in the invaded zone D showing (A) juvenile abalone biomass and (B) juvenile abalone survival relative to urchin biomass, (C) urchin biomass and (D) inshore abalone biomass relative to lobster biomass through model time course (1985–2007), (E) consumption of urchins over time, and (F) urchins consumed over the model time period, relative to biomass of lobsters larger than 68 mm carapace length (the minimum size of lobsters able to eat urchins). t, metric tons.

progressively collapsed. This collapse was due to the combined effects of increased illegal fishing and the rapid decline in urchins and is therefore only indirectly linked to predation by rock lobsters, given the relatively small impact of direct predation on abalone.

The consumption of urchins by rock lobsters initially increased with lobster biomass (Fig. 6E); 4052 t—almost a third of the original biomass—was consumed in 1992 (Fig. 6F). Afterward, urchin consumption declined because of the diminishing urchin population.

SENSITIVITY ANALYSES

Sensitivity analyses revealed that the natural mortality values for both abalone and rock lobsters, which were inputs into the base-case model, were reasonable.

Reestimation of μ for abalone mortality in the multispecies model resulted in a value of 0.128 (very similar to the original single-species estimate of 0.126), with very little effect on any of the other parameters, and the likelihood showed an improvement of only 0.06. This result indicated that the single-species estimation of the relative contributions to total mortality from “natural” and interspecific-interactions-related causes were unlikely to have been in error because of the inclusion of the indirect effects of the lobster invasion, validating the use of the simplified single-species representation in stock assessments and its incorporation into our multispecies model.

The model was sensitive to changes in rock-lobster natural mortality M' ; rock-lobster biomass, B'_{y0} , increased by approximately 50% when M' was increased from 0.105 to 0.150. An increase in natural mortality resulted in increased rock-lobster productivity, which could explain this increase in lobster biomass. The opposite took place when M' was halved; biomass decreased by about 50%. Estimating M' resulted in a value of 0.087, equivalent to a natural survivorship of 0.92. This is not an unrealistic estimate of M' given that rock lobsters are long lived and that in some cases *J. lalandii* natural survivorship has been estimated to be as high as 0.95 (Johnston and Bergh 1993), but the likelihood did not improve when this parameter was estimated, and the associated Akaike information criterion value was less than that of the base-case model. The fixed M' value of 0.105 used in the base-case model was therefore considered the most appropriate choice.

The age-structure used in model S31 (simulating arrival of lobsters by larval settlement, see Fig. 3) produced a significantly worse likelihood (−135.9) than did the base-case model version, in which lobsters arrive by immigration of adults (−156.7). An increase in both the beginning biomass and in the spawner carrying capacity was observed, as well as large changes in the interaction parameters as the model tried to fit the data. Although the overall abalone likelihood for zone D improved, the likelihoods for urchin and juvenile abalone surveys were significantly worsened.

The calculated fishing-mortality (F) proportions were used as an additional check of the validity of model estimates because high values (combined with reasonably reliable catch information) suggest biomass is underestimated and low values that it is overestimated. Fishing-induced mortality for the recreational sector ($F^{L,rec}$) hit the upper bound of 0.95 in 1995, suggesting almost complete removal of the rock-lobster biomass available to recreational fishers in that year. This scenario is unrealistic, suggesting underestimation of the number of large lobsters by model S31. In addition, when model S31 was employed, the urchin population crashed only in 1999, again indicating that this model would not have yielded a realistic sufficiency of “large” rock lobsters during the early 1990s.

Model S32, which represented an intermediate age structure, showed an improvement in the likelihood (−154.5) and Akaike information criterion (−296.9) over that with Model S31, but was still significantly worse than the base-case model. Once again, the overall abalone fit improved, but the urchin and juvenile-abalone surveys showed worse fits to the data. $F^{L,rec}$ values were less than those in model S31 but hit 0.7 yr^{-1} (70% removal of large lobsters) in 1993, again suggesting the biomass of large lobsters was underestimated. Commercial fishing-induced mortality ($F^{L,comm}$) values were above 0.3 yr^{-1} for the period 2002–2007. The base model thus remains the preferred one and, by inference, favors the hypothesis of adult immigration into the area ECH.

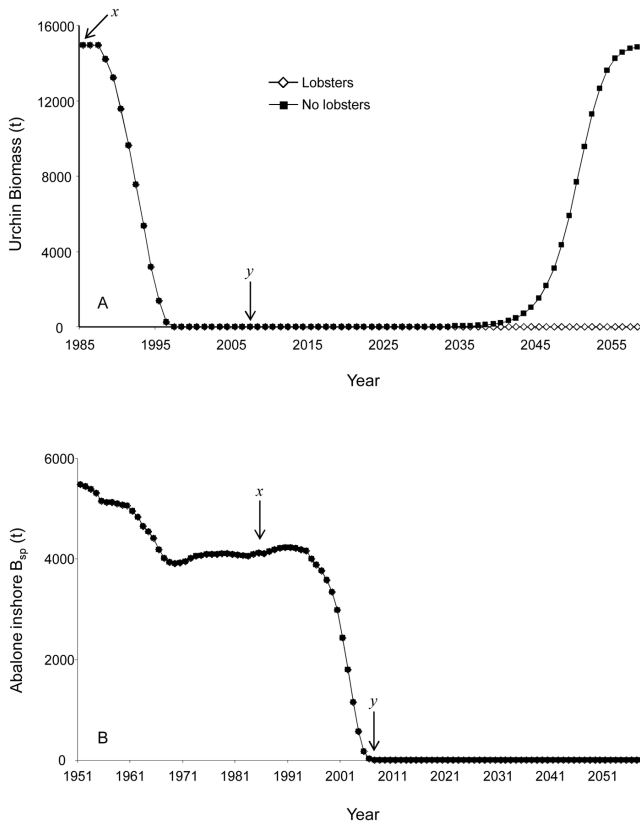


Figure 7. Future projections for (A) urchin biomass for the period 1985–2058 and (B) the abalone inshore spawning biomass for the period 1951–2058. “Lobsters” indicates the base-case model continued for 50 yrs into the future with no changes to the model, i.e., with ongoing lobster predation. “No lobsters” indicates the removal of rock lobsters from 2008–2058, i.e., an absence of lobster predation. For the period up to 2033 in (A) and for the entire duration in (B), the data for “lobsters” and “no lobsters” track identical paths; *x* denotes the year in which lobsters were introduced into the model (1985), and *y* denotes the base-case model end year (2008), after which future projections were run for 50 yrs.

FUTURE PROJECTIONS

In the base-case model for zone D, the urchin population crashed in 1996–1997 and remained severely depleted until the end of the period modeled, in 2007 (Fig. 4F). Future projections were run for 50 yrs after the end of the base-case model. Under scenario 1 (Table 2), in which lobsters were present and lobster catches remained at the 2007 level, future projections predicted that the urchin population would not recover (Fig. 7A). Less anticipated was that, even under scenario 2 (Table 2), which excluded lobsters, the urchin showed signs of recovery only by the mid-2030s, and only by 2058 did it reach carrying capacity (Fig. 7A).

The inshore abalone population crashed in 2006–2007. Future projections were similarly modeled for 50 yrs after the end of the period modeled, under scenarios 1 and 2 (i.e., in the presence and absence of lobster predation). Although legal abalone catches were halted by 2008 and future legal catches set at zero, illegal catches

Table 2. Five scenarios under which future biomass projections were made. Rock lobster catches are in metric tons per annum.

| Scenario | Urchin and abalone biomass | | Rock lobster biomass | | |
|----------------------------|--|---|-------------------------|------------------------------|-------------------------------------|
| | Scenario 1: rock lobster predation | Scenario 2: no rock lobster predation | Scenario 3: no catch | Scenario 4: current catch | Scenario 5: 10× illegal catch |
| Rock lobsters | Present | Absent | Present | Present | Present |
| Commercial lobster catch | 91.0 | 0 | 0 | 91.0 | 0 |
| Recreational lobster catch | 20.5 | 0 | 0 | 20.5 | 0 |
| Illegal lobster catch | 9.0 | 0 | 9 | 9.0 | 90 |

continued and were (probably conservatively) set as the mean take of the last two model years (2006 and 2007). In the presence of rock-lobster predation, the abalone population showed no recovery (Fig. 7B). Even in the absence of lobsters, the abalone population failed to recover within the 50-yr period of the projection (Fig. 7B).

Scenarios 3–6 differed in future projections for rock-lobster spawning biomass for the period 2008–2028 (Fig. 8; Table 2). Closure of both the commercial and recreational rock-lobster fisheries, but continued illegal catches (scenario 3), resulted in a projected increase in rock-lobster spawning biomass, which later leveled off. Continuation of the 2007 levels (scenario 4) would lead to an initial decrease in spawning biomass, leveling off after 2014. A 10-fold increase in the illegal catch (scenario 5) would have the strongest influence, resulting in the most rapid and most substantial decline in spawning biomass, even in the absence of commercial and recreational fishing. This result arises because the illegal sector does not respect size limits, removing lobsters below the size at which they reach sexual maturity. The legal size limits are set above this size, allowing opportunity for lobsters to reproduce before capture.

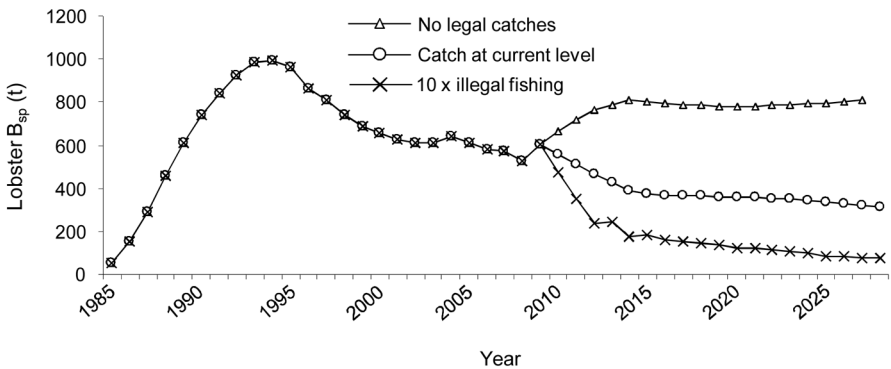


Figure 8. Future projections for rock-lobster spawning biomass in zone D under different rock-lobster catch scenarios employed for the period 2008–2028. t, metric tons.

DISCUSSION

BASE-CASE MODEL

Parameter Estimation.—In the initialization of the model, the starting age structure was kept below the lobster age/size necessary to consume urchins and juvenile abalone, allowing the lobsters time to grow to the size at which they could prey on urchins at a date that coincided with the observed urchin decline. Surveys conducted in zone D before 1990 recorded no rock lobsters (Field et al. 1980, Blamey et al. 2010), lobsters were almost certainly not completely absent. Rather their numbers were probably too low for detection in transects, or they were located mainly offshore in waters deeper than those surveyed. Despite poor estimation of the rock-lobster beginning biomass, the estimated value did appear realistic, given that a lower value would result in an insufficient biomass to sustain known recreational harvest rates, and a higher value would have caused premature urchin depletion.

Although many ecosystem models have now been constructed worldwide, exceedingly few (e.g., Kinzey and Punt 2009) have attempted estimation of interspecific interaction parameters by fitting models to data. Estimation of the lobster-urchin interaction parameters was made possible because the urchin data reflected a sudden decline that could be directly attributable to lobsters in the model. Similarly, data on the decline in the numbers of juvenile abalone assisted in estimation of lobster-abalone interaction parameters, but these parameters were extremely difficult to estimate, and confidence intervals were especially wide for the abalone-lobster parameters. Additional contrasting data reflecting the reverse process, wherein lobsters declined and urchins recovered, would improve estimation of the interaction parameters, but these data do not exist. Field experiments employing lobster-exclusion cages could assist with parameterization. One of the problems is the paucity of data on lobster numbers in the region ECH over the critical 1990s period, and this lack cannot be rectified. Moreover, the lobster catch information contains little contrast. Given the paucity of data, estimation of the urchin-lobster interaction parameters was more successful than expected (Table 1). Comparisons between model outputs for zone B (noninvaded) and zone D (invaded) yielded outcomes that corresponded strongly with empirical data (Tarr et al. 1996, Mayfield and Branch 2000, Blamey et al. 2010), boosting confidence in the model.

Rock-lobster spawning-biomass carrying capacity, K^s , was relatively well estimated. The planar area of Zone D is 4,474,754 m², and if suitable habitat is assumed to be 1.5 times this value (accounting for bottom topography; see Plagányi 2004) and the mean weight of a mature lobster to be 270 g, a rock-lobster biomass of 1500 t corresponds to approximately 0.83 rock lobsters m⁻² (see Appendix 1, Table A1.5, in online supplementary material for details). The greatest mean rock-lobster density recorded in zone D was 0.94 m⁻² (K Reaugh-Flower, University of Cape Town, unpubl data), but most of the mean densities recorded during the mid- to late 1990s ranged between 0.2 and 0.5 m⁻² (Mayfield and Branch 2000, Blamey 2010, Blamey et al. 2010), so the model estimate is not unrealistic.

Evaluation of Model Fits to the Data.—On the whole, the model yielded a good fit to all indices except for the relatively high abalone CPUE values in the 1990s (Figs. 5A,C), which were the result of area changes made to zone D that altered access and

resulted in unusually high CPUE values for 1993 and the next few years. These data should be omitted from future analyses.

Systematic annual survey data do not exist for lobster abundances over the 1990s to reveal whether spawning biomass did rise to a peak in 1994 and then decline, as the model trajectories suggest, but early surveys by Field et al. (1980) do confirm that lobsters were virtually absent in 1978, and the highest recorded densities in zone D were during the mid-1990s (Mayfield and Branch 2000), coincident with peak values in the trajectory of the model.

Both urchin and abalone populations declined substantially in the mid-1990s, leading to population crashes to low levels that have persisted to date. Given the dependency of juvenile abalone on urchins in this region, the observed crash in juvenile abalone is not surprising, as no urchins were found in 1995 and 1996, coincident with the disappearance of juvenile abalone. Previous experimental removal of urchins led to a collapse of the juvenile abalone population (Day and Branch 2002a). Several lines of empirical data therefore support the trends forecast by the model.

ADULT MIGRATION OR LARVAL SETTLEMENT?

The two mechanisms most likely to explain the increase in rock-lobster abundance are: (1) immigration of adult lobsters or (2) increased larval settlement. Sensitivity analyses revealed that an increase in larval settlement could not explain the observed increased abundance and size structure of adult rock lobsters during the early 1990s. It is more likely that the increased abundance was due to an abrupt arrival of large rock lobsters—i.e., immigration of adults. Lobster migrations have been observed for a number of species (see, e.g., Annala and Bycroft 1993, Pezzack and Duggan 1986), some of which can travel hundreds of kilometers (Moore and McFarlane 1984, Groeneveld and Branch 2002). Most *Jasus* species undergo some form of inshore–offshore migration associated with molting or reproduction (see review by Booth 1997); significant alongshore migrations are not common (Kelly 2001, Atkinson and Branch 2003, Barrett et al. 2009), but in New Zealand, small proportions of populations of *Jasus edwardsii* (Hutton, 1875) do undergo large-scale migrations in response to changing environmental conditions (McKoy 1983, Annala and Bycroft 1993), and mass alongshore migrations of *Jasus verreauxi* (H. Milne-Edwards, 1851) also take place (Booth 1997).

Whether the increase in *J. lalandii* EPOCH was caused by an inshore migration or a southeast alongshore migration remains unknown, but the latter seems unlikely, given the evidence of Atkinson and Branch (2003) that long-shore movement of at least adult males is limited. The inshore-migration hypothesis is supported by similarities in size composition and sex ratios between offshore and inshore lobster stocks (Cockcroft et al. 2008).

A number of other species have also shifted eastward (Fairweather et al. 2006, Coetzee et al. 2008, Bolton et al. 2012; A Mead, University of Cape Town, unpubl data). The reasons for these shifts remain unknown, and although they may be linked to changes in environmental conditions (see Roy et al. 2007, Rouault et al. 2009), long-term data for the inshore region EPOCH are inadequate for assessment of this possibility (Cockcroft et al. 2008). The increase in lobster abundance could also be linked to a scarcity of predators. Large predatory fish that would normally prey on lobsters are overexploited and scarce along the southwest coast (Griffiths 2000), but most species were depleted before the 1980s (Griffiths 2000). Although their scarcity

may therefore not explain the abrupt arrival of lobsters, the “invasion” could probably not have taken place in the presence of pristine populations of predators (Blamey 2010). After the arrival of lobsters, juveniles (<65 mm CL) were frequently recorded on FIMS and other independent surveys conducted in the 2000s (Haley et al. 2011), suggesting that the lobsters are now recruiting into the system sufficiently to maintain their high densities.

ROLE OF URCHINS

In the region where we worked, the behavior of urchins is strikingly different from that in other parts of the world. *Parechinus angulosus* fulfills a facilitative rather than destructive role. Because of turbulent sea conditions and its relatively small size, *P. angulosus* cannot feed on live kelp fronds or ascend the plants to graze (Fricke 1979, Anderson et al. 1997), and it does not significantly reduce standing crop of macroalgae, as has been demonstrated by field experiments involving its removal (Day and Branch 2002a). Instead, *P. angulosus* feeds by trapping drift algae and, in doing so, allows juvenile abalone (3–35 mm shell length) to shelter under its spines, where they gain both protection from predators and nourishment from pieces of drift algae trapped by the urchins (Day and Branch 2002b). Even *Strongylocentrotus franciscanus* (A. Agassiz, 1863), known for its destructive grazing (Harrold and Reed 1985), shelters conspecific juveniles (Tegner and Dayton 1977).

URCHIN AND ABALONE PROJECTIONS

In our model, the urchin population crashed in 1997, and approximately 50 yrs would be needed for the urchin population to recover fully; and even then recovery would take place only in the absence of lobsters. Although useful as a first estimate of recovery time, this result is highly uncertain and subject to the following caveats: (1) The prediction is based on an intrinsic population growth rate for urchins of 0.5 (Appendix 1, Table A1.4, in online supplementary material) that takes into account the likely longevity of urchins, but this input is uncertain, particularly as no information is available about the potential population growth rate of *P. angulosus* during recovery, only a record of how quickly its population declined. (2) The model prediction for recovery assumed a complete absence of rock-lobster predation on urchins, but some future predation is more probable. (3) Additional factors influencing urchin population growth, such as disease, other predators, recruitment, and larval dispersal from adjacent areas were not considered. Other urchin species are known for their sporadic and sometimes pulsed recruitment events (Ebert 1968, Dayton 1975), and survival of the recruits has been linked to the presence or absence of macroalgal cover, predators, and adult urchins (Tegner and Dayton 1977, 1981). Very little is known about *P. angulosus* recruitment, but an exceptionally heavy, pulsed recruitment event could conceivably bring larvae into the region. Foliar algae and silt dominate the substratum (Blamey et al. 2010, Blamey and Branch 2012, LKB pers obs), however, because herbivores have been depleted by lobster predation, and we would expect such conditions to influence larval settlement.

Not only does the model predict a long time course for any urchin recovery, it also forecasts even greater delays for abalone recovery, which was not even initiated in the 50-yr modeled time scale. Given the critical relationship between urchins and abalone, the regional recovery of abalone populations, and consequently restoration of the “original” EOC ecosystem, seems unlikely for several reasons. (1) The lobster-urchin-abalone effect is most obvious in the shallows (0–5 m), where any

reduction in lobsters by commercial rock-lobster fishing will be low because fishing operates in waters deeper than 5 m. (2) If rock lobsters remain at a density above 0.25 m^{-2} (Mayfield and Branch 2000), urchins on which juvenile abalone depend (Tarr et al. 1996, Day and Branch 2000a,b, 2002a) will be unable to achieve sufficient density to support juvenile abalone (Mayfield and Branch 2000). (3) Since the substantial depletion of herbivores by lobsters EPOCH, macroalgae have increased, and siltation rates have risen (Mayfield and Branch 2000, Blamey et al. 2010, LKB pers obs). (4) Increased siltation and macroalgal growth are likely to smother and outcompete encrusting corallines, upon which abalone recruitment depends (Day and Branch 2000a). (5) Intense illegal fishing of abalone combined with the invasion of lobsters has depleted the abalone stock to levels at which recruitment failure is likely. (6) Model simulations predict that, should rock lobsters decline, even under a best-case recovery scenario (i.e., immediate complete elimination of lobsters, zero future catches of abalone, and no impediments such as adverse changes to the substratum), urchin recovery could take up to 50 yrs and abalone recovery even longer (Fig. 6). Recovery of both urchins and abalone would be even slower than predicted by the model if these species were subject to an Allee effect, whereby fertilization collapses below a threshold adult density (Allee et al. 1949, Stephens et al. 1999). Our model results estimate near-zero remaining densities of abalone in the zone D inshore region, highlighting that the stock there may already be below the threshold for an Allee effect. As abalone recruitment is very localized (Prince 2005, Miller et al. 2009, Saunders et al. 2009), Allee effect is not an unreasonable assumption, but even if neighboring abalone populations (which have also declined because of overfishing) were to supply recruits to the invaded zone D, the proliferation of macroalgae and shortage of suitable substratum there would probably inhibit settlement.

LOBSTER PROJECTIONS UNDER DIFFERENT CATCH SCENARIOS

The complete removal of lobsters is highly unlikely, and even under increased fishing effort, model simulations predict that lobster biomass will remain at around 400 t unless smaller individuals are included, as they are in the illegal catch. Even under such conditions, urchin and abalone recovery would be slow or improbable, particularly given the additional complications mentioned above.

ALTERNATE STATES

Two theories have developed to explain how communities shift from one alternate stable state to another (Fig. 9). The first assumes a constant environment in which a large perturbation causes state variables (e.g., population density) to shift. The second suggests that the underlying parameters (i.e., landscape or environment) shift, influencing the state variables and thereby resulting in an alternate state (Lewontin 1969, Sutherland 1974, Scheffer et al. 2001, see review by Beisner et al. 2003). Although both lead to new states, in the first case, no intrinsic reason prevents restoration of the original state by means of a reversal of the processes that led to its alteration, whereas in the second, the underlying parameters would have to be transformed to allow restoration of the original state. In most cases, a lag is involved in the reversal process, known as hysteresis, and the route taken to shift from one state to the other differs from the route required to reverse the shift (Beisner et al. 2003). Considerable debate has surrounded the question of what constitutes an alternate stable state, and at least three criteria must be fulfilled. First, the change must occur within the same physical habitat; second, it must result from a pulse perturbation; and third, the

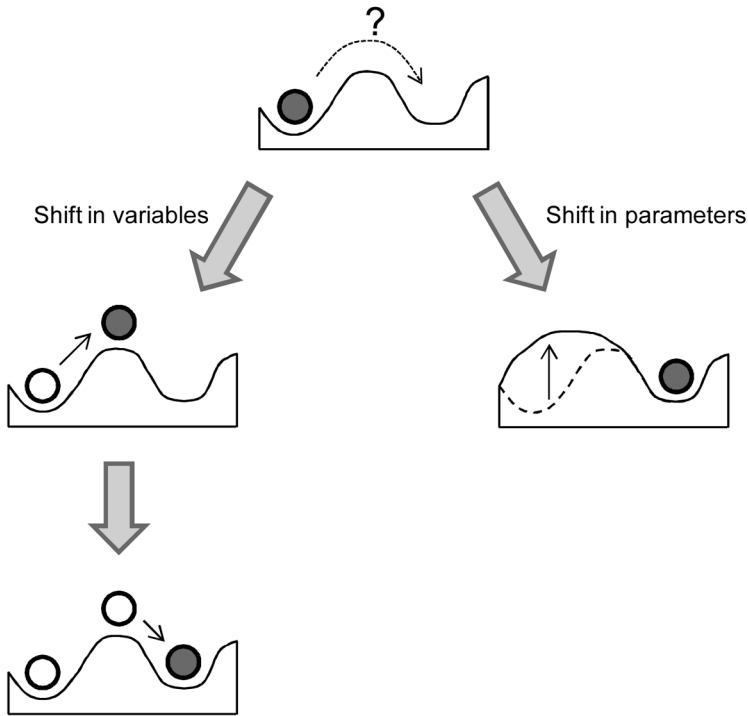


Figure 9. Ball-in-cup diagrams showing the two ways in which an ecosystem (the ball) can shift from one state to another: either a shift in the state variables (left) causes the ball to move or a shift in parameters (right) changes the landscape and ultimately causes the ball to move (redrawn from Beisner et al. 2003).

change must be long enough to be self-sustaining (Connell and Sousa 1983, deYoung et al. 2004, Petraitis and Dudgeon 2004).

On the basis of these criteria and arguments given in a parallel paper (Blamey and Branch 2012), we would argue that the ecosystem EPOCH can be considered a case of alternate stable states, but the mechanism causing the shift from one ecosystem state to another remains unclear. Increased rock-lobster densities would suggest that this state variable has changed, but reasons for the increase remain uncertain, although they are probably the result of changes in environmental conditions (Cockcroft et al. 2008). What is apparent is that the environment or landscape has changed since the shift from one state to another; herbivores have been depleted, macroalgal abundance has increased, siltation of reefs has increased, and encrusting corallines have declined. For reasons outlined above, reversibility to the former ecosystem state seems unlikely, as in the similar situation observed on coral reefs in the Caribbean (Hughes 1994). Beisner et al. (2003) maintain that most ecosystem “landscapes” are asymmetrical and that alternate stable states often show hysteresis. In our model simulations, we found this to be the case. Even after modeled removal of all lobsters from zone D, urchins took at least 50 yrs to recover, and abalone showed no signs of recovery.

The invasion by rock lobsters EPOCH, combined with the illegal harvesting of abalone, has had substantial impacts on both the ecosystem and fisheries. The once

highly lucrative abalone fishery has been replaced by a small-scale commercial rock-lobster fishery, despite which lobster densities have remained high. Herbivores have virtually disappeared, and abalone recruitment failure has probably occurred. Just east of the invaded area, rock lobsters are either rare or absent. Urchins and other herbivores are abundant, but the abalone population has been substantially depleted by illegal fishing. Nevertheless, the abalone there probably constitute the most important adult stocks that could supply recruitment to the invaded area. Even then, recovery of abalone there would require suitable habitat, the presence of sufficient urchins, and a greatly reduced rock-lobster biomass. Our model therefore supports the hypothesis that the lobster range-expansion caused a regional regime shift in the kelp forest ecosystem and predicts that this shift will not be reversible within 50 yrs.

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