



## Summary of East-of-Hangklip lobster-abalone-urchin models and abalone projections

Éva E Plagányi

MARAM (Marine Resource Assessment and Management Group)  
 Department of Mathematics and Applied Mathematics  
 University of Cape Town, Rondebosch 7701, South Africa

November 2005

### SUMMARY

A complicated ecosystem interaction is impacting South African abalone *Haliotis midae* and rock lobsters *Jasus lalandii* along the East of Hangklip (EoH) coastline. The lobsters have dramatically reduced sea urchin *Parechinus angulosus* populations, thereby indirectly negatively impacting juvenile abalone, which rely on the urchins for shelter. This ecosystem change effect is incorporated in the spatial and age-structured assessment model for abalone, with model projections predicting steep declines in abalone spawning biomass in the lobster-infected areas. In practice, multi-species considerations have been incorporated in an *ad hoc* manner only in the assessment, because of the difficulties both in the conceptualisation and parameterisation of a more complicated multi-species model capable of explicitly representing the various interactions. However, a preliminary abalone-urchin-lobster multi-species model has been developed as a first step to explore the problem, to investigate the data needs and to test the potential sensitivity of model results to the choice of parameter values. Indications from preliminary investigations were that the predicted recovery of the abalone resource may be slower than that predicted by a model that does not explicitly take the various interactions into account.

### INTRODUCTION

This document is drawn from Plagányi (2004) and summarises multi-species aspects pertaining to the South African abalone *Haliotis midae* fishery. Core problems facing the South African abalone *Haliotis midae* include illegal fishing and recent ecosystem change in the form of a movement of rock lobsters *Jasus lalandii* into a major part of the range of the abalone. It seems that the lobsters have dramatically reduced sea urchin *Parechinus angulosus* populations, thereby indirectly negatively impacting juvenile abalone, which rely on the urchins for shelter (Mayfield and Branch 2000, Day and Branch 2002). A spatial and age-structured production model (ASPM) (Plagányi 2005, Plagányi and Butterworth in prep) has provided the basis for management advice for the abalone resource over recent years by projecting abundance trends under alternative future catch levels. As evident from spawning biomass projections in the lobster-invaded Zones C and D, the resource is predicted to decline even in the absence of fishing because of the “recruitment failure effect” (Fig. 1).

Some preliminary analyses were done in 2002 in response to proposals regarding a possible experimental take of rock lobsters from East of Hangklip (EoH) to advantage abalone. Johnston (2002) projected the EoH rock lobster population forward under three future constant catch scenarios. Her analysis suggested, for example, that a future annual commercial catch of 500 MT (i.e. total removals of 900 MT) would have the effect of reducing the biomass of lobsters above 75 mm down to 18% of the

2002 estimate by 2008. The extent to which this level of removal of lobsters would advantage the abalone resource is not known and is difficult to predict.

***Multi-species model: abalone, urchins and lobsters***

A preliminary abalone-urchin-lobster multi-species model (see Appendix 1) was constructed in 2002 as a tool to explore proposed multi-species management scenarios in the East of Hangklip (EoH) region (Plagányi 2004). As a first look at the potential recovery of abalone in response to fairly large reductions in rock lobster biomass having been effected by 2008, a linear increase from 2002 to 2008 in juvenile abalone survival rate in Zone C is assumed to occur from the current estimated value of 2.1% up to 50% of the pre-1990 survival rate of 71.3%. From 2008 onwards, the juvenile survival rate remains constant at 35.6% per annum.

The model extends on the base-case abalone age- and spatial-structured population model as follows:

- i) A discrete logistic equation is added to model the dynamics of urchins, under the assumption that the biomass of urchins consumed by rock lobsters can be described using a Holling type II interaction term;
- ii) Two discrete logistic equations with added inshore/offshore and longshore migration terms are used to model the inshore and offshore components of the EoH rock lobster resource;
- iii) Below a threshold urchin density, the mortality rate of 0-yr old juvenile abalone is assumed to increase exponentially with decreasing urchin biomass; and
- iv) The consumption of abalone by lobsters is accounted for by including rock lobsters as an additional “fishing fleet” in the abalone population model.

The model highlighted the difficulties in parameterising even a simple multi-species model. A preliminary sensitivity analysis for abalone spawning biomass indicated that model predictions are particularly sensitive to a) the urchin growth rate parameter, b) the urchin-lobster interaction parameter, c) the long-shore lobster migration rate and d) the initial (1990) lobster biomass level assumed. An illustrative application of the model suggested that the predicted recovery of the abalone resource may be slower than that predicted using a single species modelling approach only.

Much more work is necessary before this model might be considered useful in a management context. However, there is some utility in experimenting with the model in the interim, and hence a single example of a model run is presented here (Figs 2-3). The parameter settings used in this initial run are given in Plagányi (2004). The base-case demonstration model run predicted that in ten years’ time the abalone resource would be at 31% of the current level whereas in 30 years’ time it would be at 36% of the current estimated level.

The basic aim of the demonstration simulation was to roughly capture the observed changes in EoH lobster and urchin biomass, so as to see what the effects on the projected abalone biomass might be. Note that the rock lobster predation effect on abalone may be included in the model to a greater or lesser degree following further investigations. Little time has been spent at this stage in trying to fine tune parameters, but nonetheless preliminary investigations were useful in highlighting the following.

- To simulate the crash in the Zone C urchin population as having occurred over a relatively short timespan, it was necessary to use a relatively large urchin-lobster interaction term. The result of this was that urchin populations are extremely slow to recover (and hence there was no obvious immediate benefit to abalone of removing lobsters) unless a high urchin growth rate was assumed. Once a more accurate estimate of urchin growth rate is input to the model, the model will potentially be very useful in predicting the timescale of a recovery of the abalone resource (assuming this is possible!). The sensitivity of model results to the urchin growth rate is positive in the sense that this is likely one of the easier parameters to measure

in the field or laboratory and that (raw) data are potentially available to quantify this parameter.

- The sensitivity of model results to the lobster migration rates highlight the importance of trying to quantify these parameters.
- Although no great reliability should be accorded to the parameter values chosen for this illustrative application of the model, there were nonetheless indications from preliminary investigations that the predicted recovery of the abalone resource may be slower than that predicted by a model that does not explicitly take the various interactions into account.

The 2002 BENEFIT Stock Assessment Workshop (BENEFIT 2002) agreed that the modelling exercise as presented here was useful as a first step to explore and bound the problem (in the sense of an upper limit in particular), to investigate the data needs and to test the potential sensitivity of model results to the choice of parameter values. Specific recommendations for improving the model included:

- Taking account of the strong size effect in interactions between lobsters and urchins;
- Giving due consideration to explicitly incorporating the important role of associated changes in the substrate and more specifically in the availability of coralline algae; and
- Re-examining and refining the interaction terms, in particular to test sensitivity to having used the strongest possible interaction terms and to consider reflecting the role of the habitat in mediating the urchin – abalone interaction.

The Workshop agreed that no biological reasons were presented that justified closing the EoH area to lobster fishing. Moreover, there was general consensus that lobsters do appear to impact abalone but that there is considerable uncertainty as to whether the current situation is potentially reversible. Part of this uncertainty resides in the possibility that the observed changes are due in part to an environmental or regime shift. The Workshop supported the use of both short-term experimental and modelling studies to assist in elucidating the nature and extent of the underlying causal mechanisms. There is already a considerable amount of data available to assist in parameterising the model (G.M. Branch, UCT, pers. comm) and experimental demonstrations (using caging) have already successfully been applied to confirm that both sediment composition and urchin populations can show some recovery when protected from predation effects (G.M. Branch, UCT, pers. comm). These issues are being addressed to some extent by a MSc project currently underway. Nonetheless, the possibility should not be excluded that ecosystem change may occur in a manner contrary to expectations, as occurred at Malgas and Marcus Islands off the west coast of South Africa, where rock lobster removals resulted in an explosion in the abundance of a number of benthic species but not abalone (Barkai and Branch 1998).

### ***Multi-species modelling recommendations pertaining to South African abalone and lobsters***

#### ***1. Modelling the relative economic gains and losses from the abalone and rock lobster resources in the East of Hangklip (EoH) area***

Detailed modelling of the abalone – rock lobster – urchin multi-species interactions is complex and not immediately feasible. However, given pressures to increase rock lobster quotas in the EoH region, an immediate priority relates to gaining an improved understanding of the trade-offs involved in harvesting rock lobster heavily in this region with the aim (in theory at least) of allowing some recovery of the abalone resource. The long time-scale (approx. 10-20 years) required for any appreciable recovery of the abalone resource in the “lobster-invaded” areas is demonstrated in Fig. 3. A practical starting point to address this issue would involve a relatively simple extension of the approach described in Appendix 1, which builds on the current abalone and rock lobster stock assessment models.

## 2. Modelling the abalone – rock lobster – urchin multi-species interactions

Given the paucity of available data and lack of full ecosystem understanding, it is debatable whether a detailed ecosystem approach to this problem will yield practically meaningful conclusions. The complexity of these interactions is also not easily accommodated within the relatively rigid structure of preset models such as Ecopath with Ecosim (Walters *et al.* 1997). A more pragmatic approach would be to extend the current abalone stock assessment model to include interactions with rock lobsters, urchins and possibly the substrate. This approach would be extremely flexible in permitting experimentation with a range of different interaction representations and scenarios. It has the added advantage that the consequences for management are immediately obvious within this framework, as results would be output in the same form as for current abalone assessments.

The approach described here is similar to that of Livingston and Methot (2000) and Hollowed *et al.* (2000b) who explicitly modelled predation mortality in a catch-at-age stock assessment model applied to the Gulf of Alaska walleye pollock. They modelled the effect of three predators: arrowtooth flounder (*Atheresthes stomias*), Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumetopias jubatus*) by defining predation mortality as a type of fishery. Two important features of this approach were the use of a flexible functional response form capable of simulating varying levels of predator satiation, and the use of statistical methods to fit the model to the data. Tjelmeland and Lindstrøm (in press) provide a further example of the incorporation of predators into standard fish stock assessment models. They incorporated predation by northeast Atlantic minke whales in the SeaStar herring stock assessment model and estimated the parameters of the consumption formula by directly including the consumption term in the total log-likelihood function.

## 3. Development of an OMP for abalone that takes account of multi-species interactions

Ideally, an OMP needs to be developed for the abalone resource in the main fishery Zones A-D. As a first step, the current population model could be used as the operating model for the underlying dynamics. Decision models would then need to be developed to take account of three critical factors:

- a) the recent trend in poaching in each secondary zone (or TURF);
- b) the recent trend in CPUE and survey indices in each secondary zone, as determined from finer spatial scale data than that input to the operating model; and
- c) an assessment of the impact of multi-species interactions.

The last of these could be based on any or several of the following:

- i) Data on abalone recruitment success from a dedicated recruitment survey or from a full population survey with coverage in at least one lobster-invaded and one “lobster-free” zone (as was the case for the 2002 MCM/Industry survey).
- ii) Information on the EoH proportion of the rock lobster TAC, in the event that it can be demonstrated that sufficient numbers of rock lobsters have been harvested to allow some recovery of the abalone resource. This relates to item 1. above – note also that this would become relevant only in a few years time given the time-scale needed for a noticeable recovery. Unfortunately it appears that the current EoH rock lobster allocations have *not* been constrained (for social reasons) to be taken from a sufficiently small area to be able to assist in starting to shed further light as to both the likelihood and extent of a possible reversal of the “rock lobster effect”.
- iii) Information from models of abalone - rock lobster – urchin interactions. These could either be relatively simple models or more complicated whole ecosystem models. Indications from these models of a short-term enhancement or reduction of the “rock lobster” effect could be fed into a decision model, provided such multi-species / ecosystem models are carefully parameterised and have demonstrated sufficient robustness of their conclusions to uncertainty in the data as well as to a range of plausible alternative hypotheses. In the case of abalone, the development of a tactical ecosystem model as the basis for computing harvest limits within an OMP itself would seem to be a very long way off.

Arguably the most important issue relates to the need for an overall strategic goal by the resource managers regarding the abalone and rock lobster resources in the East of Hangklip region (e.g. should effort be concentrated on removing rock lobsters from the EoH region – or even just from east of Danger Point – or should an optimal mix [if possible] of the two resources be attempted?).

Although the discussion above focuses on a modelling perspective, the best approach to this problem would likely depend on experimental studies and an adaptive management approach (e.g. Walters 1986, Hilborn and Walters 1992, Sainsbury *et al.* 2000). For example, an actively adaptive management strategy applied to the Australian multi-species fishery was successful in resolving key uncertainties about resource dynamics and sustainable resource use (Sainsbury *et al.* 1997). The approach involved identifying four different plausible hypotheses and adopting an experimental process involving the sequential closure of areas to trawl fishing. After a period of a few years, the experiment was successful in discriminating among the competing hypotheses (Sainsbury *et al.* 1997, 2000).

### LITERATURE CITED

- Day, E. and G.M. Branch 2002. Effects of sea urchins (*Parechinus angulosus*) on recruits and juveniles of abalone (*Haliotis midae*). *Ecol. Monogr.* 72: 133-149.
- Hilborn, R. and C.J. Walters 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman & Hall, New York.
- Hollowed, A.B., Ianelli, J.N. and P.A. Livingston. 2000b. Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock. *ICES J. Mar. Sci.* 57: 279-293.
- Johnston, S.J. 2002. A first look at East of Hangklip (EoH) west coast rock lobster biomass estimates and projections. Marine & Coastal Management, South Africa, Internal Rock Lobster Working Group Report, WG/08/02/WCL27.
- Livingston, P.A. and R.D. Methot. 2000. Incorporation of predation into a population assessment model of eastern Bering Sea walleye pollock. In *Fishery Stock Assessment Models*, Alaska Sea Grant College Program, AK-SG-98-01.
- Mayfield, S. and G.M. Branch 2000. Interrelations among rock lobsters, sea urchins, and juvenile abalone: implications for community management. *Can. J. Fish. Aquat. Sci.* 57: 2175-2185
- Mayfield, S., Branch, G.M. and A.C. Cockcroft 2000. Relationships among diet, growth rate, and food availability for the South African rock lobster (*Jasus lalandii*) (Decapoda, Palinuridea) *Crustaceana* 73: 815-834.
- Plagányi, E.E. 2004. Walking the bridge from single- to multi-species approaches in southern African fisheries management. PhD thesis, University of Cape Town, Rondebosch, South Africa.
- Plagányi, É.E. 2005. A summary of the assessment and management approach applied to South African abalone in Zones A-D. Marine and Coastal Management document WG/AB/05/06/03: 20 pp
- Plagányi, É.E. & D.S. Butterworth. In prep. A spatial and age-structured assessment model to estimate poaching and ecosystem change impacting the management of South African abalone *Haliotis midae*.
- Sainsbury, K.J. 1991. Application of an experimental management approach to management of a tropical multispecies fishery with highly uncertain dynamics. *ICES Mar. Sci. Symp.* 193: 301-320.
- Sainsbury, K.J., Campbell, R.A., Lindholm, R. and Whitelaw, W. 1997. Experimental management of an Australian multispecies fishery: examining the possibility of trawl-induced habitat modification. In: *Global Trends: Fisheries Management*. Pikitch, E.L., Huppert, D.D. and M.P. Sissenwine (Eds). *American Fisheries Society Symposium* 20: 107-112. Bethesda, Maryland, USA
- Sainsbury, K.J., Punt, A.E. and A.D.M. Smith 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J. Mar. Sci.* 57: 731-741.
- Tjelmeland, S. and U. Lindstrøm. (In press). An ecosystem element added to the assessment of Norwegian spring spawning herring: implementing predation by minke whales. *ICES J. Mar. Sci.*
- Walters, C.J. 1986. *Adaptive management of renewable resources*. Macmillan, New York.
- Walters, C.J., Christensen, V. and D. Pauly 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish. Biol. Fish.* 7: 139-172

## APPENDIX 1 – SUMMARY OF MODEL

The model is applied in the first instance to Zone C (including both subareas CNP and CP) and is basically an extension of the abalone assessment model (with specifications as given in Plaganyi 2005, Plaganyi and Butterworth in prep).

### 1.1 Modelling urchin dynamics

A discrete logistic equation is applied to model the dynamics of the sea urchin *Parechinus angulosus* as follows:

$$u_{y+1} = u_y + r_u u_y \left( 1 - \frac{u_y}{K_u} \right) - \frac{\alpha_{u_l} u_y J_y^I}{1 + \beta_{u_l} u_y} \quad (1)$$

where  $u_y$  is the biomass of urchins at the start of Model year  $y$ ;  
 $r_u$  is the intrinsic growth rate of urchins;  
 $K_u$  is the urchin carrying capacity in Zone C;  
 $\alpha_{u_l}$  is an urchin-lobster interaction parameter;  
 $\beta_{u_l}$  is a second urchin-lobster interaction parameter; and  
 $J_y^I$  is the total inshore biomass of rock lobsters in Zone C in Model year  $y$ .

A logistic growth term was considered most appropriate given that the urchin population needs to be modelled as declining from a relatively high level relative to pristine down to a very low level followed by a possible recovery in biomass in response to lobster removals.

The sea urchin *P. angulosus* is an important component of the diet of both juvenile and adult west coast rock lobsters (Mayfield *et al.* 2000). However, Mayfield *et al.* (2000) found that despite very large differences in prey availability at different sites on the West Coast of South Africa, rock lobsters consume similar prey species in roughly equal proportions and amounts. Based on this, the biomass of urchins removed by rock lobsters is modelled using a simplified form of a Holling type II functional response. This formulation was chosen because it approximates a scenario in which the *per capita* consumption of urchins by rock lobsters remains approximately constant at high urchin densities, but declines with decreasing urchin density. Sensitivity to alternative interaction formulations can easily be considered.

### 1.2 Modelling rock lobster dynamics

The current *Jasus lalandii* stock assessment model (Johnston 2002) is rather complex and not suitable for inclusion in the model proposed here. Instead, the following equations are used to respectively model the inshore and offshore Zone C rock lobster populations:

$$\begin{aligned} J_{y+1}^I &= J_y^I + r_J (J_y^I + J_y^O) \left( 1 - \frac{(J_y^I + J_y^O)}{K_J} \right) - C_y^{J^I} + m_J^I + \rho_J J_i^O - \rho_J^* J_i^I \\ J_{y+1}^O &= J_y^O + r_J (J_y^I + J_y^O) \left( 1 - \frac{(J_y^I + J_y^O)}{K_J} \right) - C_y^{J^O} + m_J^O - \rho_J J_i^O + \rho_J^* J_i^I \end{aligned} \quad (2)$$

where  $J_y^O$  is the total offshore biomass of lobsters in Zone C in Model year  $y$ ;  
 $r_J$  is the intrinsic growth rate ( $\text{yr}^{-1}$ ) of EoH lobsters;  
 $K_J$  is the lobster carrying capacity in the Zone C region;  
 $C_y^{J^I}$  and  $C_y^{J^O}$  are respectively the total inshore and offshore annual catches of rock lobsters in Model year  $y$ ;  
 $m_J^I$  and  $m_J^O$  are constants depicting the annual net longshore immigration of lobsters (biomass per year) into the inshore and offshore areas of Zone C respectively;  
 $\rho_J$  is a constant representing the annual proportion of lobsters in the offshore region that migrate inshore; and  
 $\rho_J^*$  is a constant representing the annual proportion of lobsters in the inshore region that migrate offshore.

A logistic rather than simpler exponential growth term is used in this instance because the EoH lobster population is currently considered to be close to carrying capacity (S. Brouwer, Marine & Coastal Management, pers. commn.)

Note that whilst the lobsters are modelled as impacting both the urchin and abalone (see below) populations negatively, the lobster dynamics are modelled as independent of these two populations. The justifications for choosing a one-way interaction representation are first because it is likely that the feedback loops are relatively small, and secondly to avoid getting into much more complicated details. For example, if the contribution of abalone and urchins to the diet of lobsters is to be explicitly considered, it has to be done in the context of the availabilities of the full spectrum of other prey items selected by lobsters.

Rock lobsters can occur in deeper water than abalone, and it is particularly important to note that they will have the largest effect on abalone populations in the shallow inshore waters where the majority of abalone recruits and juveniles are to be found. It was therefore considered necessary to model the inshore and offshore proportions of the resource separately. This was also considered useful to be able to investigate the effects of removing lobsters differentially from the inshore and offshore regions.

Migration/immigration parameters are difficult to estimate but are considered critical in this context where it is necessary to quantify the biomass of lobsters that overlaps directly with the primary distribution of juvenile abalone. This preliminary model assumes that the longshore migration rate is constant, but this could be modified, given sufficient evidence, to include a time trend in this migration rate. Given that the inshore region may be a preferred habitat for lobsters, it is important to consider the possible “reseedling” of the inshore region with lobsters from the offshore region under a scenario where lobsters are preferentially removed from the inshore region. Further thought is required as regards the validity of assuming a constant offshore to inshore migration rate compared, for example, to assuming that this rate is a function of inshore (and perhaps offshore) lobster biomass. Tagging studies currently underway (S. Brouwer, Marine & Coastal Management, pers. commn) may assist in quantifying some of these parameters.

### 1.3 Modelling abalone dynamics

#### *a) Explicitly including the negative effect of decreasing urchin biomass on the juvenile abalone survival rate*

Increases in 0-yr old survival rate are explicitly linked to urchin biomass using the relations:

$$\begin{aligned} M_0(y) &= M_{\max} e^{-\nu u_i} && \text{for } u_i < K_u / \eta_u \\ M_0(y) &= M_0^{\text{base}} && \text{for } u_i \geq K_u / \eta_u \end{aligned} \quad (3)$$

where  $M_0(y)$  is the (time-variant post 1989) natural mortality rate in Model year  $y$  on abalone of age  $a < 1$ ;

$M_0^{\text{base}}$  is the (time-invariant) natural mortality rate on abalone of age  $a < 1$ , as estimated to apply over the pre-1990 period (it is also the minimum 0-yr old natural mortality rate);

$M_{\max}$  is the maximum 0-yr old natural mortality rate (given very low urchin biomass);

$\nu$  is a constant controlling the rate at which  $M_0$  increases in response to decreasing urchin biomass; and

$\eta_u$  is a constant determining the threshold urchin biomass (relative to pristine  $K_u$ ), below which the survival rate of juvenile abalone is negatively impacted.

Mayfield and Branch (2000) indicated that there is a threshold urchin density below which the survival of juvenile abalone is affected.

#### *b) Explicitly accounting for the predation mortality on abalone due to rock lobsters*

The following is based on the assumption that rock lobsters predate on young abalone as proposed by some. The natural mortality parameter  $M$  used in single-species models implicitly takes into account the predation effects of a suite of “background” predator species and should be a reasonable approximation in all but situations where there is a dramatic sustained increase or decrease in the biomass of and associated predation mortality caused by one of the predators. Given the large recent increases in the EoH rock lobster population, it is thus desirable to explicitly include the associated increase in abalone mortality rates due to predation by lobsters in the model. The simplest method to introduce a biological interaction into a model appears to be to include the predator as a fishing fleet. The EoH inshore rock lobster population has therefore been included in the model as an “additional fishing fleet” operating since 1990, with the proportion of the abalone resource consumed by lobsters each year ( $F_y^J$ ) given by:

$$F_y^J = C_y^J / B_y^{prey} \quad (4)$$

where the biomass of abalone prey available for consumption by rock lobsters is computed as:

$$B_y^{prey} = \sum_{a=0}^{z-1} S_a^J w_{a+\frac{1}{4}} (N_{y,a}^I + N_{y,a}^O) e^{-M_a/4} \quad (5)$$

where  $S_a^J$ , the fishing selectivity-at-age for the lobster “fishing fleet”, can be interpreted as the predator feeding preferences for abalone of age  $a$  (assumed not to change over time). The summation is shown over ages 0 to  $z-1$ , where  $z$  is the plus group age, as it is unlikely that plus group animals are preyed upon by lobsters.

The consumption of abalone by lobsters is given by a simple Lotka-Volterra interaction term:

$$C_y^J = \alpha_{a-l} J_y^I B_y^{prey} \quad (6)$$

where  $\alpha_{a-l}$  is an abalone-lobster interaction parameter that in essence captures the “availability” of prey to the predator. However, this is a particularly strong interaction form and some experimentation was conducted with alternative forms such as:

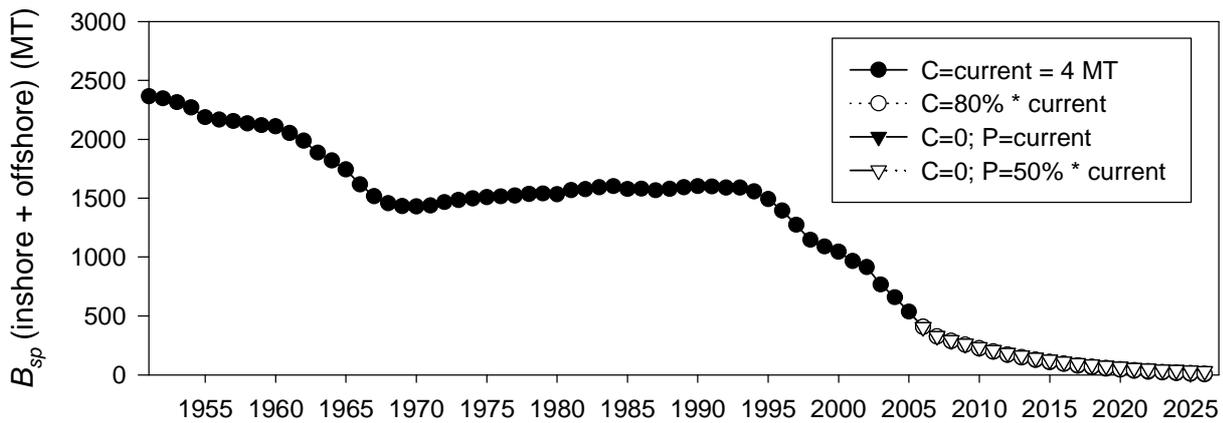
$$C_y^{pred} = a^{pred} B_y^{pred} B_y^{prey} / (1 + b^{pred} B_y^{prey}) \quad (7)$$

which allow for predator satiation. More complicated functional response formulations (such as the various Holling functional response formulations or ECOSIM’s foraging arena formulation) can readily be incorporated in a simple model of this form.

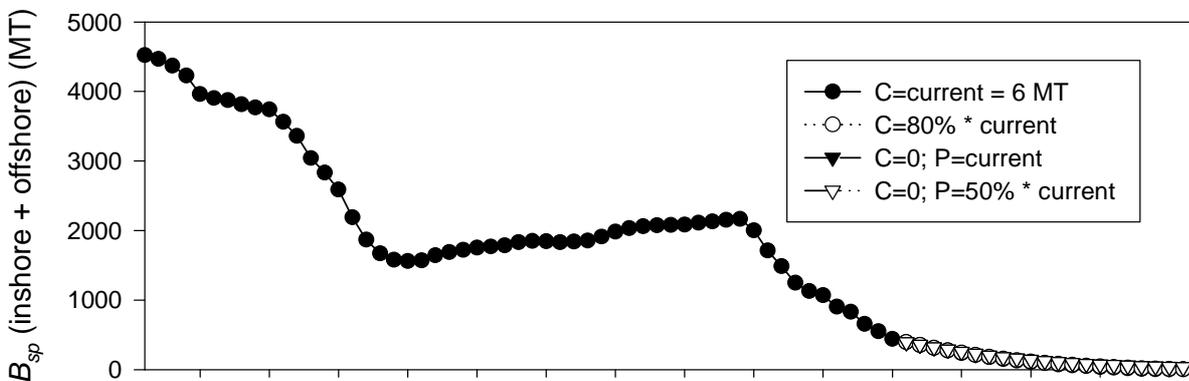
It follows that the abalone numbers-at-age consumed by lobsters each year is given by:

$$C_{y,a}^J = S_a^J F_y^J (N_{y,a}^I + N_{y,a}^O) e^{-M_a/4} \quad (8)$$

a) Zone CNP Spawning biomass projections  
 FUTURE POACHING CONTINUES AT CURRENT LEVEL



b) Zone CP Spawning biomass projections  
 FUTURE POACHING CONTINUES AT CURRENT LEVEL



c) Zone D Spawning biomass projections  
 FUTURE POACHING CONTINUES AT CURRENT LEVEL

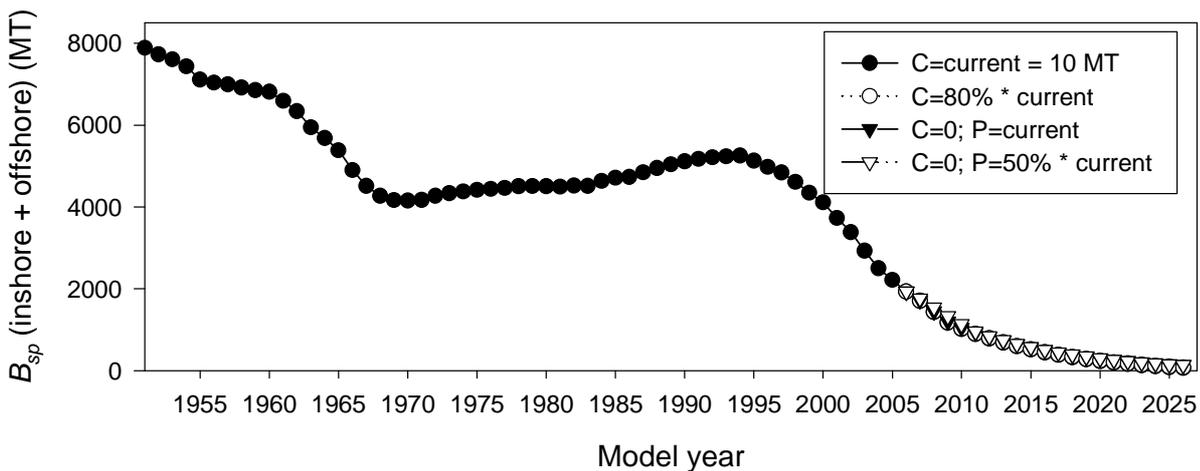


Fig. 1. Spawning biomass trajectories and 20-yr projections for Zone C subareas a) CNP and b) CP as well as for c) Zone D obtained using a Spatial- and Age-Structured Production Model (Plaganyi 2005, Plaganyi and Butterworth in prep). The projected commercial (C) and poaching (P) catches are in tonnes. Future catch scenarios shown include future commercial catches constant at the current level, reduced by 20%, or set to zero, as well as one illustrative scenario with future poaching assumed reduced by 50%. Results were near identical under each of the future scenarios investigated because the declines in these zones is dominated by the recruitment failure effect.

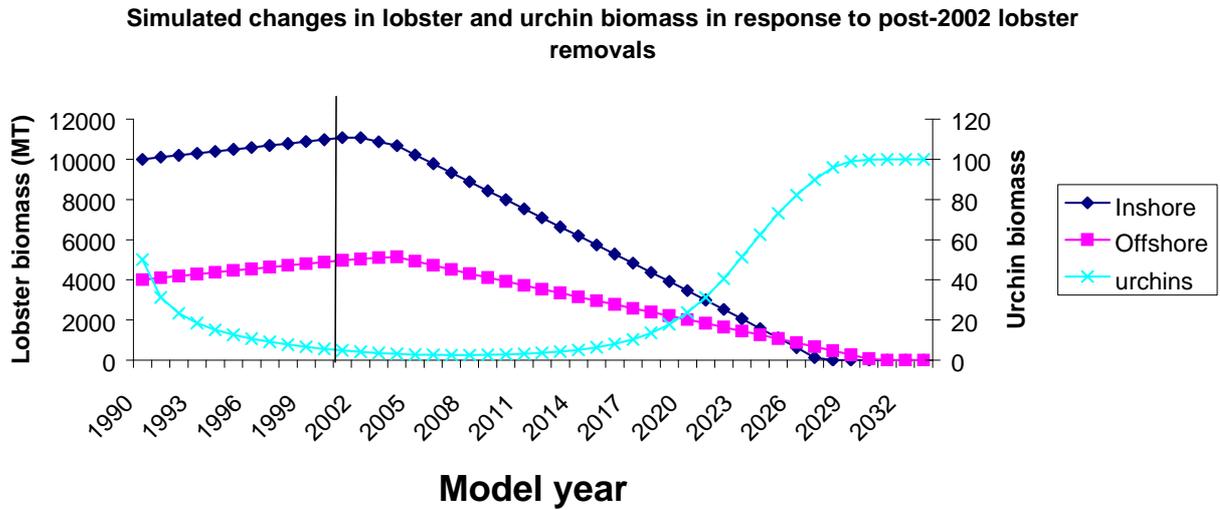


Fig. 2 Example inshore and offshore lobster and urchin biomass trajectories obtained using input parameters as detailed in Plagányi (2004) and under a scenario in which lobster catches are increased substantially post-2002.

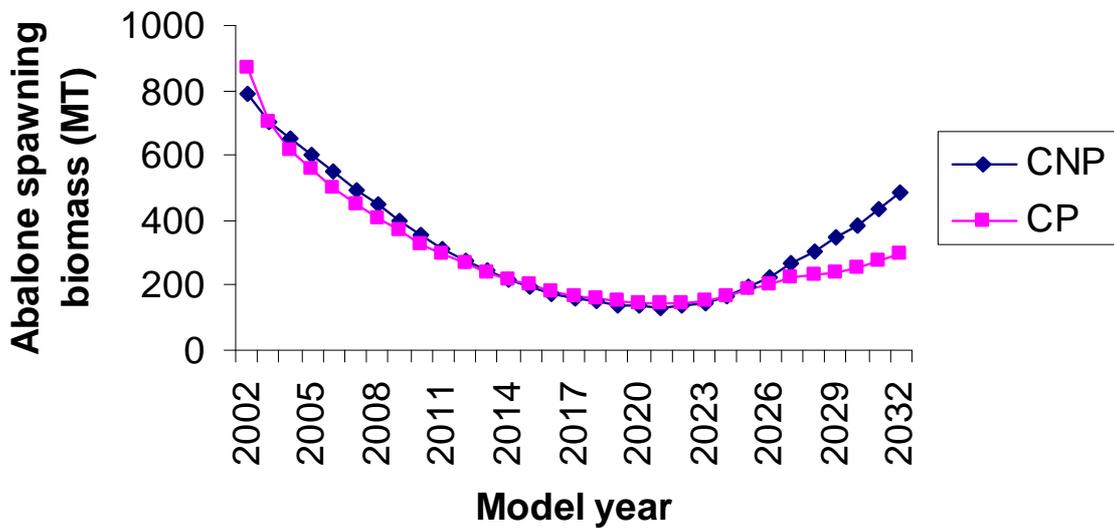


Fig. 3. Abalone spawning biomass (inshore + offshore combined) projections in subareas CNP and CP of Zone C given associated lobster and urchin biomass trajectories as shown in Fig. 1.

