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Modelling the impact of poaching on metapopulation viability for data-limited species

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Abstract

We developed a spatially-explicit simulation model of poaching behaviour to quantify the relative influence of the intensity, frequency, and spatial distribution of poaching on metapopulation viability. We integrated our model of poaching with a stochastic, habitat-based, spatially-explicit population model, applied it to examine the impact of poaching on northern abalone metapopulation dynamics in Barkley Sound, British Columbia, Canada, and quantified model sensitivity to input parameters. While demographic parameters remained important in predicting extinction probabilities for northern abalone, our simulations indicate that the odds of extinction are twice as high when populations are subjected to poaching. Viability was influenced by poaching variables that affect the total number of individuals removed. Of these, poaching mortality was the most influential in predicting metapopulation viability, with each 0.1 increase in mortality rate resulting in 22.6% increase in the odds of extinction. By contrast, the location and spatial correlation of events were less important predictors of viability. When data are limited, simulation models of poaching combined with sensitivity analyses can be useful in informing management strategies and future research directions.

Keywords

Illegal harvest, population dynamics, sensitivity analysis, endangered species, conservation

18 **Introduction**

19 Considered to be one of the primary threats to biodiversity, overexploitation has led to the
20 decline and disappearance of many species worldwide (Wilcove et al. 1998; Venter et al. 2006),
21 with significant consequences for the structure and functioning of ecosystems (Pauly et al. 1998;
22 Jackson 2001). In particular, the illegal harvest (i.e., poaching) of wild resources is unregulated
23 and operates as an open access system (Berkes et al. 1989), which can contribute to the
24 overexploitation of target species (Berck 1979; Bulte et al. 1995). Poaching of rare and
25 threatened species can also drastically exacerbate extinction risks when rarity leads to higher
26 economic values that offset the increasing costs and risks of poaching (Courchamp et al. 2006;
27 Hall et al. 2008). Managing species threatened by poaching requires not only an understanding of
28 the non-compliant behaviours (Arias 2015), but also of their consequences on the species'
29 dynamics (Fa and Brown 2009). Here, we focus on understanding the relative impact of
30 poaching, as compared to the impact of other spatial and demographic factors, on the extinction
31 risk of the target species.

32 Understanding the consequences of poaching on species population viability requires sufficient
33 knowledge of the amounts and patterns of exploitation (Fa and Brown 2009). However,
34 obtaining accurate information about poaching behaviours is often difficult due to the covert
35 nature of the activity. While information on poaching activity may be obtained through various
36 means, for instance, directly through self-reporting, or indirectly through law-enforcement
37 records and signs of illegal activity, these methods are subject to inherent biases. In particular,
38 poachers may be reluctant to divulge information regarding their activities, which can have
39 implications for the reliability of the data (Gavin et al. 2010; St. John et al. 2010; Bergseth et al.
40 2015).

Modelling approaches can be useful in predicting the effects of different aspects of poaching behaviour and management actions when data are limited. For instance, previous studies have used regression models to identify factors that may be useful in predicting poaching levels (e.g., Gavin et al. 2010). Information on poaching can be incorporated into population models to assess its impact on population viability (e.g., Tian et al. 2011) or evaluate the potential effects of management and enforcement strategies on poaching levels (Milner-Gulland and Leader-Williams 1992). The spatial distribution of poaching effort can also be incorporated into statistical models to identify locations where monitoring and enforcement actions should be allocated (e.g., Kritzer 2004; Haines et al. 2012), or into spatially-explicit simulation models to examine the effects of spatial preferences in harvest effort on the target population (Bedford et al. 2013).

Models of the impact of poaching are subject to varying degrees of parameter uncertainty due to the difficulties in obtaining accurate information about poaching behaviour. Sensitivity analyses can be performed to examine the extent to which uncertainties in input parameters influence the model outputs – that is, the sensitivity of model outputs to changes in input values (Cariboni et al. 2007). Sensitivity analyses are often conducted by varying model parameters one at a time by a small amount around an estimated value, and measuring the resulting change in model predictions (McCarthy et al. 1995; Naujokaitis-Lewis et al. 2009). By contrast, a global sensitivity analysis involves varying all parameters simultaneously, thereby allowing an assessment of parameter influence averaged over the entire range of variation of other input parameters (Saltelli et al. 1999; Naujokaitis-Lewis et al. 2009). Parameters wherein changes in values result in large changes in model output are considered to be highly influential, and can then be targeted for future research efforts to reduce uncertainty in parameter estimates. Within a

management context, sensitivity analyses can also be used to identify variables to target for management (Naujokaitis-Lewis and Curtis 2016).

Here, we developed a model of poaching to simulate the intensity, timing, and spatial distribution of poaching events. We then incorporated the poaching model into a spatially-explicit population model to examine the effect of poaching on metapopulation viability. In the absence of detailed information about poaching, we used Monte Carlo simulation combined with a global sensitivity analysis to evaluate the influence of poaching relative to the effects of other spatial and demographic parameters. We applied this approach to evaluate the influence of a range of poaching behaviours on the persistence and recovery potential of northern abalone (*Haliotis kamtschatkana*) in British Columbia, Canada, and identify influential parameters that should be the focus of management and future research efforts.

Materials and Methods

Poaching simulation model

We simulated a poaching event as a sequence of poaching activity occurring on a number of populations during a single, uninterrupted session. In this model, the occurrence and impact of poaching events are determined by four key parameters: 1) the intensity of poaching, simulated as the mortality rate from poaching, 2) the extent of poaching, which determines the number of populations affected by a given poaching event, 3) the frequency of poaching, which determines the timing of occurrence of poaching events, and 4) the spatial pattern or distribution of poaching, which identifies the subset of populations that will be affected by a given poaching event.

When a poaching event occurs, its effect is simulated in a population model as an additional source of mortality for the selected populations, with the magnitude of impact determined by the intensity and extent of poaching. Estimates of poaching frequencies are used to develop a schedule of poaching events for the time horizon of interest: the time steps in which poaching events occur are determined by sampling from a binomial distribution, such that for each time step, the probability of a poaching event occurring is equal to the estimated poaching frequency. To determine which populations will be affected by a given poaching event, each population is assigned a probability of being poached based on its proximity to preferred locations or distance from sites that are typically avoided. In the absence of any location preferences, populations are assigned equal probabilities of being poached. These probabilities are used to identify the subset of populations affected by poaching, with those having the highest probabilities selected first. However, if poaching is spatially correlated, only the first population to be poached is identified based on location preferences; subsequent populations poached are instead selected based on their proximity to the first population. Additional details on the poaching simulation algorithm is provided in Appendix A.

Northern abalone case study

Poaching is a major threat to the long-term persistence of the northern abalone (*Haliotis kamtschatkana*), a broadcast spawning marine mollusc found along the west coast of North America from Alaska to Baja California (Campbell 2000). As with congeneric species, the northern abalone spawns in aggregations (Breen and Adkins 1980) and likely subject to Allee effects, given that sufficient adult densities are required for successful fertilization (Babcock and Keesing 1999; Zhang 2008). These characteristics, combined with a short planktonic larval phase (Sloan and Breen 1988), low fishing costs, and high market value (Campbell 2000), make

abalone species vulnerable to overexploitation (Rothaus et al. 2008). Traditionally harvested by First Nations, increased market demand and technological advances led to the development and peak of a commercial fishery in the 1970s (Sloan and Breen 1988), followed by a significant population decline that prompted fishery closures in the 1990s in the United States and Canada (McDougall et al. 2006). Harvest continues to be an important threat to northern abalone through poaching, with instantaneous fishing mortality (F) estimates of 0.06-0.26 in Canada despite fishery closures (Lessard et al. 2007). The ongoing decline in population abundance combined with low recruitment (Fisheries and Oceans Canada 2007; COSEWIC 2009) poses a significant threat to the viability of northern abalone populations and has resulted in its designation as Endangered in Canada (*Species at Risk Act* S.C. 2002, Schedule 1) and globally (McDougall et al. 2006). Achieving short-term recovery targets for northern abalone may require a reduction in abalone poaching removals to half the current levels (Chadès et al. 2012). To do so cost-effectively, however, requires an understanding of how different poaching behaviours influence population dynamics.

Spatially-explicit population and poaching models

We simulated northern abalone population dynamics and poaching behaviours over time and space within Barkley Sound, British Columbia (BC), Canada (Fig. 1), one of four areas in BC deemed to encompass critical habitat for this species (Fisheries and Oceans Canada 2012). The habitat-based, spatially-explicit population dynamics model used in the simulations integrated a habitat suitability (HS) index with a stage-structured population model and a model of dispersal using RAMAS GIS 5.0 (Akçakaya and Root 2005), a widely used population viability analysis (PVA) software (Naujokaitis-Lewis et al. 2009). Input parameter values, ranges and sources for our habitat-based population dynamics model are detailed in Table 1 and Chadès et al. (2012).

A habitat suitability index was developed for northern abalone in Barkley Sound by Jamieson et al. (2004) based on the presence of suitable depth, substrate characteristics, kelp distribution, tidal currents and wave exposure. Maps of habitat depth, substrate characteristics, kelp distribution, tidal currents, and wave exposure were combined to create a map of habitat suitability for northern abalone, wherein each map cell is assigned a habitat suitability index value ranging from 0 - 4. The HS map was used as the basis for defining the location of 92 discrete patches of suitable abalone habitat with RAMAS GIS (Akçakaya and Root 2005), assuming a threshold HS index value of 3 for suitable habitat (Joanne Lessard, pers. comm.), and a maximum neighbourhood distance of 230m between map cells that belong to the same habitat patch (Table 1). The HS map was linked to the population model described below through two functions that related population-specific carrying capacity and initial abundances to total habitat suitability within each patch (Table 1).

The stage-structured population model was based on field survey data and stock-recruitment analyses (Zhang et al. 2007) of abalone in British Columbia and is described in Chadès et al. (2012). The model included 10 stages subject to a logistic or Ricker type density dependence, which affected all stage-specific survival and fecundity rates at each time step. When population density falls below a specified Allee threshold, RAMAS GIS applies an Allee effect by reducing fecundities by half (Akçakaya and Root 2005). Populations were also linked through larval dispersal, which was simulated with a dispersal distance function that uses the distance between a population pair to determine the rate of dispersal from one population to the other (Jamieson et al. 2004) (Table 1). In this baseline scenario, 91.7% of population pairs were connected through dispersal, and the median annual dispersal rate between populations was 0.032 (range = 0-0.039).

The impact of poaching was introduced into the abalone population model as a source of mortality for affected populations. Due to the limited availability of information on northern abalone poaching, we simulated a range of poaching behaviour scenarios using parameter values derived from data on poaching convictions, published literature on harvest patterns for other abalone species (Sloan and Breen 1988; McShane and Smith 1989; Hobday et al. 2001; Tailby and Gant 2002; Dowling et al. 2004a; b; Raemaekers and Britz 2009), and expert knowledge on the extent, frequency, and impact of abalone poaching (Table 2). The range of parameter values used to characterize poaching behaviours in our scenarios are described in detail in Appendix A.

Sensitivity analysis

We carried out a global sensitivity analysis to account for uncertainties surrounding parameters used in the population dynamics and poaching models. To achieve this in a computationally-efficient manner, we used GRIP 2.0, a script written and executed in R (R Core Team 2013) for global sensitivity analysis of models constructed with RAMAS GIS (Curtis and Naujokaitis-Lewis 2008a; b; Naujokaitis-Lewis and Curtis 2016).

GRIP 2.0 varies habitat-related and demographic parameters in the baseline model by creating replicate simulations, each with a unique set of input parameter values. For continuous variables, values were drawn randomly from specified probability distributions that reflect the best available information for northern abalone and its habitat – that is, the current best estimate of parameter values (our baseline values) were used to determine the mean and, where possible, the standard deviation of the probability distribution (Table 1). Where no prior information is available to provide a baseline estimate for a given parameter, such as dispersal survival, we sampled values from a uniform distribution (Marino et al. 2008), so that all values within the

range had an equal probability of being selected (Table 1). For the type of density dependence, which is a categorical variable, one function was randomly selected from a set of three possibilities: a logistic or Ricker function (the baseline value), which models scramble competition, a Beverton-Holt function, which models contest competition, and a ceiling model, which allows for exponential population growth until the population reaches the ceiling value (e.g., carrying capacity), after which the population is maintained at that level until a decline reduces the population to below the ceiling (Akçakaya and Root 2005).

To assess model sensitivity to uncertainty in poaching parameters, we varied the parameter values in the poaching model, such that for each replicate simulation, a unique poaching mortality rate, extent, and frequency were drawn randomly from the range of baseline poaching model parameters (Table 2 and Appendix A). We also accounted for uncertainty in the spatial distribution of poaching by varying the poaching location preference and the occurrence of spatial correlation (Table 2) for each replicate simulation, thus resulting in changes to the poaching probabilities and therefore the selected subset of populations affected by poaching.

We ran a total of 9000 replicate simulations in our sensitivity analysis, half of which incorporated poaching. For each replicate simulation, the probability of metapopulation extinction over 100 years was calculated and converted into a binary measure of metapopulation viability. Metapopulations with extinction probabilities greater than or equal to 0.1 were considered to be at risk of extinction, while those with probabilities less than 0.1 were classified as viable. This 0.1 threshold corresponds to criteria for listing species as Vulnerable globally (IUCN 2012) or as Threatened in Canada (COSEWIC 2010). Our binary response variable was used in subsequent analyses to determine the sensitivity of extinction probability to the spatial, demographic, and poaching parameters used in the PVA model.

198 Due to high correlations among spatial parameters (Table S1⁴), we used a principal components
199 analysis (PCA) to select a smaller subset of uncorrelated parameters for analysis. The PCA
200 identified four principal components with eigenvalues greater than one, which explained a total
201 of 83.1% of the total variance across all axes. Based on the strength and pattern of correlation of
202 spatial parameters with the principal components (Table S1⁴), we retained one parameter each
203 from the first four principal components that had the strongest correlation with the principal
204 component: total area of all habitat patches, mean edge length of each patch, mean habitat
205 suitability per patch, and the proportion of population pairs that are connected by dispersal.

206 Model sensitivity to input parameters was assessed using logistic regression, with our binary
207 measure of metapopulation viability as the response variable (Cross and Beissinger 2001; Curtis
208 and Naujokaitis-Lewis 2008a). The relative influence of model parameters on metapopulation
209 viability was evaluated by comparing their standardized logistic regression coefficients (SLRC)
210 (Menard 2004), which were obtained by performing the logistic regression on predictors
211 standardized to a mean of 0 and a standard deviation of 1 (Agresti 2007).

212 To determine how various spatial and demographic parameters influence metapopulation
213 viability, model-averaged coefficient estimates for each parameter were estimated using an
214 information-theoretic (I-T) approach to model selection (Burnham and Anderson 2002; Johnson
215 and Omland 2004). Coefficient estimates were obtained using a genetic algorithm in the glmulti
216 package in R (Calcagno and de Mazancourt 2010), which was run 4 times to generate 4 sets of
217 100 candidate models each. Once duplicate models were removed, the remaining models were
218 used to generate model-averaged coefficient estimates.

⁴ Supplementary data

To assess the importance of poaching activity relative to other spatial and demographic parameters, we combined the data from simulations with a poaching effect and those without by using a dummy variable to code for the presence or absence of poaching in the simulation. The relative importance of poaching parameters, specifically frequency, extent, mortality rate, location, and spatial correlation, on metapopulation viability were assessed in a separate standardized logistic regression analysis that included these poaching parameters, along with important spatial and demographic parameters, as predictor variables.

Results

Our baseline scenario of northern abalone metapopulation dynamics in the absence of poaching led to an expected equilibrium density of 2.57 adults per m² across all 92 populations in Barkley Sound, and within the range of historical abundances (Sloan and Breen 1988). This is higher than the density predicted by Chadès et al. (2012), who also simulated the effects of sea otter depredation, but is consistent with an estimated unfished density of ~2.5 adults per m² and within the range of historical abundances observed during fishery-independent surveys (Sloan and Breen 1988). In our baseline scenario (Table 1), which excluded poaching, extinction probability was nil over a 100 year time horizon.

Relative importance of spatial and demographic parameters

Based on the outcomes of the global sensitivity analysis, the most influential parameters on viability included density dependence parameters, including the Allee threshold density, the model of density dependence, and the maximum population growth rate (Fig. 2 a). The degree of connectivity among populations (measured as the proportion of population pairs connected by dispersal) and the survival rate of dispersers had larger magnitude of effects, based on the

standardized logistic regression coefficients (SLRC), on metapopulation viability than poaching. Spatial parameters that describe the mean habitat suitability of each patch and the total habitat area had less influence on metapopulation viability than the occurrence of poaching (Fig. 2 a). In general, the probability of metapopulation extinction increased as the Allee threshold, the strength of density dependence, connectivity, and dispersal survival increased, and as maximum population growth rate, mean habitat suitability, and total habitat area decreased (Fig. 3). Replicate simulations that assumed a ceiling model of density dependence were pessimistic, and all but one resulted in extinction, while extinction occurred in 77% of simulations using a Beverton-Holt model and in only 41% of simulations with a logistic or Ricker model. Because almost all simulations with the ceiling model of density dependence resulted in extinction, we excluded all replicate simulations using this model from the analysis to prevent complete separation in the logistic model.

Effect of poaching on metapopulation viability

While uncertain parameters that govern density dependent population growth were most influential in our model, poaching had a large impact on northern abalone viability. In a comparison of scenarios with and without poaching, poaching activity increased the odds of being at risk of extinction (that is, having an extinction probability greater than 0.1) by 2.22 times ($B=0.798$, $se=0.090$, $z=8.910$, $p<0.001$), based on the logistic regression coefficients. This corresponds to an increase in the probability of being at risk of extinction from around 0.73 in the absence of poaching to 0.86 when poaching occurs. More specifically, the probability of metapopulation extinction increased with the frequency of poaching events, the number of populations poached per event, and the poaching mortality (Fig. 4). Of the poaching parameters

investigated, poaching mortality was the most influential in predicting metapopulation viability (Fig. 2 b), with each 0.1 increase in poaching mortality rate resulting in 22.6% increase in the odds of being at risk of extinction ($B=2.038$, $se=0.266$, $z=7.668$, $p<0.001$). The number of local abalone populations poached during each poaching event and the frequency of poaching events also influenced viability, while the spatial distribution of poaching did not (Fig. 2 b).

Discussion

In Canada, the primary threat to endangered northern abalone populations is poaching (COSEWIC 2009). Given this species' aggregative behaviour (Breen and Adkins 1980), high market value (Campbell 2000), and limited mobility, poaching can lead to serial depletions (Hobday et al. 2001). A non-spatially-structured simulation-optimization model indicated that populations are likely to continue to decline in abundance unless poaching is significantly curtailed (Chadès et al. 2012). Modelling the effects of a range of poaching behaviours on the metapopulation viability of northern abalone, as done here, can help identify the poaching parameters that had the most influence on extinction risks, and that should therefore be managed or reduced to prevent further population declines and promote recovery.

Demographic processes ultimately determine population growth, abundance, and distribution, and therefore remain important in predicting population viability for endangered species.

However, the occurrence of poaching also appears to have influenced the relative importance of these demographic factors in our study (Fig. 2). For instance, as sedentary broadcast spawners, abalone become increasingly susceptible to reduced fertilization rates when poaching reduces populations to densities below a particular threshold, which can range from 0.15 to 0.33 individuals $\cdot m^{-2}$ for various abalone species (Jamieson 1993; Babcock and Keesing 1999; Zhang

2008). Such an Allee effect can result in recruitment failure (Rothaus et al. 2008; Bouma et al. 2012), thus decreasing the likelihood of population recovery and hindering successful recolonization of locally-extirpated habitat patches.

Allee effects may partly explain the positive relationships between extinction risk and connectivity and between extinction risk and dispersal survival that were observed in our study (Fig. 3). For spatially-structured populations, greater connectivity and dispersal are typically expected to reduce metapopulation extinction risks by facilitating the recolonization of extinct or disturbed habitat patches (Higgins 2009; Altermatt et al. 2011). However, sufficiently low recolonization success due to Allee effects likely weakens or negates the effect of connectivity and dispersal on extinction risk. As dispersing individuals are also removed from the source population, thus reducing the population density at the source (Morel-Journel et al. 2015), greater connectivity and dispersal combined with low recolonization success may instead result in higher extinction risks.

Low recolonization success due to Allee effects may also partly explain the relatively low influence of spatial correlation in poaching on metapopulation viability. Previous simulation studies have shown that spatially correlated disturbances lead to higher population extinction risks and shorter mean times to extinction compared to randomly distributed disturbances (Johst and Drechsler 2003; Vuilleumier et al. 2007) by preventing the recolonization of disturbed patches by individuals from adjacent patches that may also have been affected by the same disturbance (Johst and Drechsler 2003; Kallimanis et al. 2005; Vuilleumier et al. 2007). In our simulations, however, Allee effects may have prevented the successful recolonization of exploited patches in both randomly distributed and spatially correlated poaching scenarios. The resulting impact on metapopulation viability may therefore have been of similar magnitude

regardless of the presence or absence of spatial correlation in poaching, thus reducing the relative effect of spatial correlation in poaching on metapopulation viability.

Our poaching simulations suggest that northern abalone metapopulation viability is primarily sensitive to poaching mortality. The number of populations affected during each poaching event and the frequency of such events also influenced viability, although to a lesser degree. These influences can be explained in terms of their effects on population demography: all else being equal, increases in any one of these variables leads to increases in the number of abalone removed per unit of time, and therefore, to a reduction in average population density.

While the poaching estimates used in our simulations are reasonable given the paucity of data, high demand and values placed on increasingly rare species can offset the rising cost and associated risks of detection, thus allowing poachers to continue to profit while driving species to extinction (Courchamp et al. 2006; Hall et al. 2008). In addition, inadequate enforcement of regulations can result in a de facto open access system (Berkes et al. 1989), which promotes overexploitation and higher extinction risks for those species with a low cost of harvest relative to revenues (Gordon 1954; Schaefer 1957; Berck 1979). Although we explore a range of poaching scenarios based on the best available information, it is possible that poaching for northern abalone occurs at greater intensities, frequencies, and extents than considered in our sensitivity analyses, likely resulting in even greater impacts on metapopulation viability. This may be the case when, for example, poachers do not have perfect information on which populations have been recently poached by others, thus harvesting from the same site. Harvesting from a particular site too frequently, without allowing for a sufficient recovery period in between harvest, could lead to further depletion of previously poached populations (Bedford et

al. 2013) and possibly local extinction, thus resulting in increased extinction risk for the entire metapopulation.

Various studies have used information obtained from harvest models to assess the sustainability of harvest and determine optimal locations or populations, rates, and individuals to harvest (Bousquet et al. 2001; Saether et al. 2001; Taylor et al. 2006), the impact of different hunting methods and gear types (Damania et al. 2005; Levi et al. 2009), and the effectiveness of various enforcement and/or mitigation efforts (Clayton et al. 1997; Damania et al. 2005; Levi et al. 2009). However, while poaching of northern abalone is a key threat to recovery of this species (Gardner et al. 2000; Jubinville 2000), the covert nature of northern abalone poaching in British Columbia makes it difficult to obtain accurate estimates of poaching rates and patterns, and to identify effective monitoring and enforcement strategies. The lengthy coastline of British Columbia, which exceeds 25,000 km (Sebert and Munro 1972), also makes it difficult to enforce a province-wide fishery closure.

Information on the relative influence of various poaching behaviours could help inform the design of effective management strategies to achieve a reduction in exploitation rate. For instance, our simulation results suggest that strategies aimed at preventing population densities from declining below the suggested Allee threshold densities of $0.15 - 0.33 \text{ individuals} \cdot \text{m}^{-2}$, as estimated for various abalone species (Shepherd and Brown 1993; Shepherd and Partington 1995; Button 2008), will be critical to preventing further population declines and promoting recovery. Modelling the effect of poaching in a spatially-explicit manner also allowed us to determine that costly but spatially limited surveillance and enforcement of fishery closures may be less effective at promoting species recovery than strategies that lead to overall reductions in exploitation rates. In this way, modelling different spatial patterns, rates, and impacts of a given

threat, such as poaching, in a sensitivity analysis can be a useful approach for identifying variables with a high influence on metapopulation viability, and for which greater effort must be spent on research and management.

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588

589 **Table 1** List of input parameters used in a baseline spatially-explicit, habitat-based
590 metapopulation model of northern abalone in Barkley Sound

Submodel	Parameter	Description	Baseline values used for initializing simulations	References/ sources	Range of values used for sensitivity analysis
Habitat suitability model	Habitat	where HS = 0,	0 - 4	Jamieson	sampled from
	suitability	denotes poor		et al. 2004	normal distribution, with
	(HS)	suitability of habitat attributes ^a ; where HS = 4, denotes high suitability of habitat attributes			mean = mean(HS) sd = sd(HS) min = HS threshold
	Habitat suitability threshold	minimum HS value where habitat is highly suitable in 3 of 4 attributes	3	J. Lessard, pers. comm.	sampled from normal distribution, with mean = HS threshold CV ^b = 10%
	Neighbourhood distance, NghbdDistance	based on movement patterns of tagged abalone	230 m	J. Lessard, pers. comm.	sampled from normal distribution, with mean = NghbdDistance, CV = 10%
Population model	Maximum growth rate, R _{max}	based on max. recruitment in highly suitable habitats	1.6	Zhang et al. 2007; Chadès et al. 2012	sampled from normal distribution, with mean = mean(R _{max}) sd = sd(R _{max}) or CV = 10%

Carrying capacity, k	applies to all stages, where ths = total patch habitat suitability	$k = 6500 \cdot ths$	Chadès et al. 2012	sampled from normal distribution, with mean = k , CV = 10%
Density dependence function	Ricker function ^c , based on abundance of all stages	$R(t) = R_{max} \cdot e^{\frac{-\ln(R_{max}) \cdot N(t)}{K}}$	Zhang et al. 2007	Ricker Beverton-Holt: $R(t) = \frac{R_{max} \cdot K}{R_{max} \cdot N(t) - N(t) + K}$ Ceiling
Survival rate	based on survey estimates of age-specific densities	0.818 for all stages	Chadès et al. 2012	sampled from lognormal distribution, with mean = Survival rate, CV = 10%
Fecundities	based on estimates of age-specific densities and weights from survey data	Age 4 = 0.074 Age 5 = 0.1409 Age 6 = 0.2057 Age 7 = 0.2655 Age 8 = 0.3207 Age 9 = 0.3695 Age 10 = 0.4031 Age 11 = 0.4299 Age 12 = 0.4519 Age 13+ = 0.6306	Chadès et al. 2012	sampled from lognormal distribution, mean = mean(Fecundities) CV = 10%

Initial abundances, N_0	abalone abundance in patch i at time 0; assuming population abundance is at 15% of historical abundance (just above % declines since 1978)	$N_0 = 975 \cdot ths$	Lessard et al. 2007	sampled from normal distribution, with mean = N_0 , CV = 10%
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Dispersal model	Dispersal distance function, m_{ij}	proportion of individuals dispersing from patch i to patch j , located x units apart	for $x \leq 23.8$ km, $m_{ij} = 0.1258e^{-0.2148x}$ for $x > 23.8$ km, $m_{ij} = 0$	Jamieson et al. 2004 ^d	not varied
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Dispersal survival	proportion of dispersers that survive movement from patch i to patch j	1	No data available	sampled from uniform distribution between 0 and 1
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Correlation	correlation in	0	No data	based on transformation
distance	survival and		available	coefficient sampled from a
function	fecundity			normal distribution with
	among			mean = 0, sd = 0.1
	populations			

^aHabitat attributes include depth, currents, kelp abundance, physical structure. ^bCoefficient of variation. ^cZhang et al. (2007) reported similar statistical support for Ricker and Beverton-Holt models. ^dFunction fit to simulated data generated by the oceanographic circulation model.

Draft

591 **Table 2** List of input parameters used to model poaching of northern abalone in Barkley Sound

Parameter	Description	Estimated value/units	Range of values used for sensitivity analysis	References/sources
Poaching extent	total number of populations poached for each event	No data available	1 - 10	NA
Poaching location	preferred poaching locations relative to access points	No data available	Random = no preference Far = remote locations preferred Near = accessible locations preferred	Raemaekers and Britz 2009; Tailby and Gant 2002
Spatial correlation	presence of spatial correlation in poaching	No data available	Random = each population poached independently Correlated = nearby populations are poached first	NA
Poaching frequency	frequency of poaching events	0.24 - 0.48 per year	0.24 - 0.48	COSEWIC 2009
Poaching intensity	mortality rate of abalone from each poaching event	0.7 - 0.9	0.05 - 0.95	J. Lessard, pers. comm.

592

Figure Captions

Fig. 1 Habitat suitability map for northern abalone in Barkley Sound (based on Jamieson et al. 2004). High habitat suitability values (HSI) indicate habitat areas with greater suitability. Approximate locations of coastal communities were obtained from the British Columbia Ministry of Energy and Mines (Province of British Columbia 2010)

Fig. 2 Relative importance of parameters using data from a) simulations with and without a poaching effect, and b) simulations with poaching effect only and including parameters that describe the occurrence of poaching (poaching mortality, number of populations poached, poaching frequency, and poaching spatial correlation). Units of the horizontal axis are the absolute values of the standardized logistic regression coefficients; higher values indicate greater parameter importance

Fig. 3 The effect of the seven most important spatial and demographic parameters on the probability of metapopulation extinction. Dashed lines indicate the effect when poaching is present, while solid lines indicate effects in the absence of poaching. Horizontal dotted lines indicate the location of the threshold probability of extinction of 0.1, used to classify simulations as being viable or at risk of extinction. Grey shaded areas indicate 95% confidence intervals for the relationship between the probability of extinction and each predictor variable (logistic regression coefficients)

Fig. 4 Effect of poaching mortality rate, the number of populations poached per poaching event, and the frequency of poaching events on the probability of metapopulation extinction, based on simulations that include a poaching effect. Horizontal dotted lines indicate the location of the threshold probability of extinction of 0.1, used to classify simulations as being viable or at risk of

615 extinction. Grey shaded areas indicate 95% confidence intervals for the relationship between the
616 probability of extinction and each predictor variable (logistic regression coefficients)

Draft

Fig. 1 Habitat suitability map for northern abalone in Barkley Sound (based on Jamieson et al. 2004). High habitat suitability values (HSI) indicate habitat areas with greater suitability. Approximate locations of coastal communities were obtained from the British Columbia Ministry of Energy and Mines (Province of British Columbia 2010)

Fig. 1
215x166mm (300 x 300 DPI)

(a) All simulation results

(b) Poaching simulation results only

Legend

— NoPoach

- - - Poach

Probability of extinction

0.75

0.50

0.25

0.25 0.50 0.75

Poaching mortality

(proportion of abalone/event)

Probability of extinction

0.75

0.50

0.25

2.5 5.0 7.5 10.0

Number of populations poached

(average number/event)

Probability of extinction

0.75

0.50

0.25

20 30 40 50 60

Poaching frequency

(number of events/100 yrs)

<https://mc.manuscriptcentral.com/cjfas-pubs>

Appendix A

Poaching algorithm in GRIP 2.0

Prior to initializing the simulations, we created a map of distances from preferred or avoided locations by calculating the distance of each cell of the habitat suitability map from these locations. This new distance map is read and imported in the user-specified section of GRIP 2.0. We also included lines of code in this section of GRIP to specify a range of values from which to sample the poaching survival rate, the number of populations poached during each poaching event, and the frequency of poaching events, as well as the minimum stage class at which individuals become vulnerable to poaching.

GRIP performs the sensitivity analysis by first creating replicate simulations with varying spatial and demographic parameters. For each replicate simulation, we determined the distance of each population from the preferred or avoided locations using the distance map and the x,y coordinates of the center of each habitat patch identified by RAMAS Spatial. The distance of each population from the preferred or avoided location was transformed into relative weights and used to determine the probability of a population being selected for illegal harvest. For avoidance of particular locations, distance weights were created by dividing the distance value of each patch by the maximum distance value, so that patches located at greater distances from avoided locations have distance weights approaching 1, while those that are closer have values closer to 0. If the location is preferred, distance weights were obtained by subtracting the previous value from 1, so that patches closer to preferred sites have higher values than those further away.

Distance weights were used to select populations to be poached for each time step of the simulation. To do this, we first selected one of the poaching scenarios created that incorporate

both the location preference and spatial correlation of poaching. We also determined the number of populations to be poached for each poaching event by sampling from the range of user-specified values and assuming a random uniform distribution. An initial population was first selected based on poaching location preference: randomly, or using the distance weights as sampling probabilities. Subsequent populations were then selected based on spatial correlation of poaching, which was incorporated using pairwise distances between populations. For scenarios where poaching was spatially correlated, subsequent populations were selected based on their distance from the initial population selected, such that populations at smaller distances from the initial population were poached first. In scenarios where poaching was not spatially correlated, each subsequent population was selected independently using the same sampling probabilities used to select the first population – that is, either randomly, or based on the distance weights. Note that for the northern abalone case study, populations were only selected if they were not poached during the previous three time steps – previously poached populations were either removed from the list of available populations prior to sampling, or, if the total number of populations in the replicate simulation was insufficient, were removed from the list of poached populations after sampling, but prior to running the simulations (Fig. A1). Once selected, populations that were selected for poaching for the current time step were assigned a poaching probability value of 1 while all others are assigned a value of 0. The process was repeated for the remaining time steps, and the probability values stored in a poaching table with the number of rows corresponding to the number of time steps in the simulation, and the number of columns corresponding to the number of abalone populations in the current replicate simulation.

To determine the time steps in which poaching events occur, we sampled the poaching frequency from the range of user-specified values using a random uniform distribution. A schedule of

poaching events is generated by sampling from a binomial distribution, such that for each time step in the simulation, the probability of success – the occurrence of a poaching event – is equal to the sampled poaching frequency value. Time steps wherein a poaching event occurs were assigned a poaching probability value of 1, while those where poaching does not occur were assigned a value of 0. This vector of the probability of poaching events for each time step was used to modify the poaching table, so that in times when poaching does not occur, the poaching probability for all populations during that time step was set to 0.

Prior to running the simulations, we sampled a poaching mortality rate from the range of user-specified values, assuming a random uniform distribution. We also divided each replicate simulation into multiple intervals of varying lengths based on the occurrence of poaching events, such that each interval begins with either the start of the simulations (for the first interval) or with the occurrence of a poaching event, and ends with the time step just before the occurrence of the next poaching event. The interval lengths were used to determine the duration each simulation is allowed to run before a poaching effect is applied.

Once initialized, simulations were run until a poaching event occurs, as determined by the poach schedule and interval lengths. Poaching is applied to the selected populations by multiplying the poaching mortality rate with the age-specific abundances of vulnerable age classes. If poaching occurs on the first time step of the simulation, the poaching effect is first applied to the selected populations, and the resulting population abundances were used to initialize the simulation. If, on the other hand, poaching does not occur on the first time step, then the initial abundances generated by GRIP were used in the simulations. The model simulations were then allowed to continue until the next poaching event occurs, and the process is repeated until the end of the 100 year simulation (Fig. A2).

69 *Northern abalone poaching parameters*

70 To simulate poaching for northern abalone, we derived a range of parameter values for the
71 poaching model using data on poaching convictions, published literature on harvest patterns for
72 other abalone species (Dowling et al. 2004a, b; Hobday et al. 2001; McShane and Smith 1989;
73 Raemaekers and Britz 2009; Sloan and Breen 1988; Tailby and Gant 2002), and expert
74 knowledge on the intensity, extent, frequency, and spatial distribution of abalone poaching.

75 *Intensity*

76 Field observations suggest that up to 70-90% of mature individuals may be harvested from each
77 population during a single poaching event (J. Lessard, 2010, pers. comm.), which corresponds to
78 an estimated poaching mortality rate of 0.7-0.9. However, due to uncertainty in poaching rates,
79 and to quantify model sensitivity, we allowed poaching mortality rate to vary from 0.05 to 0.95
80 in our sensitivity analysis, described below (Table 2). We also assumed that only older, larger
81 individuals are harvested. Juvenile abalone (<70 mm shell length), are more cryptic in their
82 behaviour than larger sized adults and therefore less susceptible to illegal harvest (Zhang et al.
83 2007). Poaching records also revealed that the mean size of poached abalone is estimated to be
84 about 115 mm shell length (SL), with a range of 70-154 mm (COSEWIC (Committee on the
85 Status of Endangered Wildlife in Canada) 2009). To account for size-related variation in
86 poaching, we restricted poaching to individuals age six years (mean size = 85.8 mm SL, Zhang et
87 al. 2007; Chadès et al. 2012) and older.

88 *Extent*

The extent of a single poaching event is not well documented, nor is the distribution of poaching activity relative to the distribution of abalone in our study area. To evaluate model sensitivity to uncertainty in poaching extent, we varied the number of populations harvested for each poaching event by drawing a random number from 1 to 10, assuming a minimum of 0.5 hours to poach from a population and a maximum SCUBA diving bottom time of 5 hours per day.

Frequency

The frequency of poaching events was estimated using data on the number of abalone poaching convictions in British Columbia between 1996-2006 (COSEWIC (Committee on the Status of Endangered Wildlife in Canada) 2009). Over this time period, thirty abalone poaching convictions occurred in BC (COSEWIC (Committee on the Status of Endangered Wildlife in Canada) 2009). Given that only 10-20% of poaching activities are prosecuted (COSEWIC (Committee on the Status of Endangered Wildlife in Canada) 2009), we estimated that approximately 150 to 300 separate poaching events occurred during the same ten year period, for a yearly estimated poaching frequency of 15-30 for the entire BC coast, which is comparable to the numbers of reported poaching events in 2004 (14 events) and 2005 (23 events) (COSEWIC (Committee on the Status of Endangered Wildlife in Canada) 2009). We transformed this value to the appropriate spatial scale using the ratio of the entire coastline length of BC to the coastline length within the study area, both measured at the same map scale, to obtain a range of poaching event frequencies of 0.24 to 0.48 per year, or approximately once every 2-4 years, for Barkley Sound (Table 2).

Spatial distribution

110 We modelled the spatial distribution of poaching events by considering three potential
111 preferences for poaching locations in the model: (1) remote sites (Far), (2) accessible sites
112 (Near), or (3) no location preference (Random) (Table 2). Although limited quantitative
113 information was available from our study region, these characterizations were informed by
114 patterns of abalone poaching in Australia and Africa, where exploitation typically occurs along
115 an axis of accessibility. This means poaching may occur as highly organized boat-based
116 operations that exploit remote locations with higher yields or with lower risks of detection by
117 authorities, or as opportunistic activities by shore-based divers and their families concentrated
118 around access points near population centres (Raemaekers and Britz 2009; Tailby and Gant
119 2002). We used the locations of coastal communities around Barkley Sound outlined by census
120 data (Province of British Columbia 2010) as approximate locations of access points (Fig. 1), and
121 used the distance of each abalone population from the nearest community to determine the
122 probability of each population being selected for poaching during each poaching event. For the
123 Far scenarios, abalone populations at greater distances from the nearest community were
124 assigned higher probabilities of being poached, while the reverse was applied for Near scenarios.
125 In Random scenarios, all populations had equal probabilities of being poached.

126 We also modelled spatial correlation by allowing for either (a) independent selection of each
127 abalone population for poaching (Random) or (b) spatially correlated poaching events
128 (Correlated), where the probability of being poached was higher for populations located near the
129 first population poached (Table 1). When combined with the preference for different locations,
130 this results in six different scenarios of spatial distribution of poaching activity.

131 We assumed that poachers have perfect information about the status of abalone patches, and that
132 they behave optimally to maximize profits (Gordon 1954; Salas and Gaertner 2004; Sanchirico

and Wilen 1999; Schaefer 1957) and are not likely to poach recently exploited populations given the likelihood of diminished economic returns from depleted populations. We therefore assumed that poachers were not likely to return to a recently fished location given the high cost of travel and risk of detection relative to the low benefit of a diminished harvest. To achieve this, we simulated a brief period of population recovery of two years following a poaching event and constrained the frequency of poaching in any one population to a maximum of once every three years. This recovery period approximately corresponds to the amount of time it likely takes for juvenile abalone in a harvested patch to be recruited into the adult population and become vulnerable to poaching; for northern abalone, this typically occurs between age 3 and 4 (Chadès et al. 2012).

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184 **Appendix Figure Captions**

185 **Fig. A1** Summary of algorithm used to select local abalone populations for poaching for each
186 time step of a replicate simulation

187 **Fig. A2** Summary of algorithm used to apply a poaching effect to selected local populations of
188 northern abalone during each poaching event of a replicate simulation

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Supplementary Material

Principal components analysis results

Table S1 PCA loadings of spatial parameters on the first four principal components. All suitable habitat patches are considered to be occupied by abalone populations. Mean values are calculated among populations or pairs of populations within the study area

Spatial Parameters	PC1	PC2	PC3	PC4
Number of habitat patches or populations	0.1449	0.3794	-0.0069	0.0115
Mean distance between pairs of populations	0.2543	-0.0427	-0.0249	0.0147
Number of population pairs connected by dispersal ^a	-0.0384	-0.0172	0.0292	-0.7189
Minimum convex polygon area occupied by populations	0.2460	0.1341	-0.0094	0.0039
Mean dispersal rate among population pairs	-0.0726	-0.1367	0.0222	-0.6590
Mean distance between population pairs connected by dispersal	0.2073	-0.0821	-0.0255	0.0215
Metapopulation carrying capacity	0.2817	0.0845	0.0265	-0.0308
Initial abundance of metapopulation	0.2817	0.0845	0.0263	-0.0315
Habitat suitability threshold	0.0042	-0.0001	0.7042	0.0340
Neighbourhood distance	0.0388	-0.3585	-0.0125	0.0674
Total habitat suitability of all habitat patches	0.2819	0.0847	0.0265	-0.0313
Mean total habitat suitability	0.2345	-0.2590	0.0381	-0.0321
Mean patch habitat suitability ^a	0.0019	-0.0091	0.7049	0.0253
Mean patch area	0.2348	-0.2592	-0.0087	-0.0340
Total area of all habitat patches ^a	0.2821	0.0848	-0.0087	-0.0324
Mean patch core area	0.2671	-0.1001	-0.0084	-0.0606
Mean patch edge:area	-0.2532	0.1350	0.0068	0.0317
Total edge length of all habitat patches	0.2545	0.1023	-0.0142	0.0213
Mean patch edge length ^a	0.1024	-0.4495	-0.0070	0.0291
Total core area of all habitat patches	0.2766	0.0771	-0.0062	-0.0547
Mean shape index	-0.0561	-0.4347	-0.0056	0.1092
Mean fractal dimension	0.0700	-0.2760	-0.0116	0.1163
Total suitable habitat area as a percent of the study area	0.2820	0.0848	-0.0087	-0.0325

^a Spatial parameters selected for further analysis