AN ADAPTIVE, ROTATIONAL HARVEST STRATEGY FOR DATA-POOR FISHERIES ON SEDENTARY SPECIES:
Application to the giant red sea cucumber (*Parastichopus californicus*) fishery in British Columbia

by

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ABSTRACT

This research explores an adaptive rotational harvest strategy using animal size and population density as indicators for allowing harvest. Using sea cucumbers as a case study, I evaluate the relative yield and conservation performance of adaptive rotation and annual harvest strategies under a range of scenarios characterising uncertainty in population dynamics and localised harvest rates. In each scenario, the adaptive strategy achieves the rotation period that maximises long-term yield subject to conservation constraints. Under most scenarios and stochastic variability, adaptive rotation resulted in relatively higher spawning biomass and yield than annual harvest, which performed well only under assumptions of high productivity or low harvest rate. The adaptive strategy is robust to uncertainty in harvest rate and population dynamics, adjusting harvest frequency to meet recovery targets. I modelled the use of "insurance areas", or harvest reserves, to guard against there being no harvestable (recovered) areas under a system of adaptive rotation.

DEDICATION

To my mother, whose contribution to inflammatory breast cancer research and whose strength and determination will inspire me always

ACKNOWLEDGEMENTS

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1 INTRODUCTION

1.1   The problem with conventional fisheries management

In many situations, conventional fisheries management methods estimate target harvest rates based on theoretical estimates of maximum sustainable yield, which often depend on very uncertain parameter estimates, and usually entail assumptions of location-independent and density-independent growth and mortality, with recruitment being the most important density dependent variable. Due to the irreducible uncertainty inherent in these methods, managers often arbitrarily reduce harvest-rate goals to guard against overfishing.

However, it is uncertain whether one can prevent stock decline by reducing harvest-rate goals over some large area, due to environmental variability and high localised harvest rates. Growth and mortality rates, as well as recruitment dynamics, can vary spatially (McCall, 1991), and can change over time due to unpredictable environmental changes, leading to possible overfishing with the potential of stock depletion. In dive fisheries (where animals are harvested subtidally by SCUBA diving), the likelihood of overfishing is compounded because fishing effort is spatially concentrated by economic necessity. In addition, the species targeted by dive fisheries, such as giant red sea cucumbers (*Parastichopus californicus*, hereafter referred to as the sea cucumber), sea urchins, and geoducks have little or no mobility, so immigration into harvested areas is limited. Consequently, aggregations of commercially attractive densities of these animals are particularly susceptible to intensive harvest. Thus, harvest rates at particular locations are likely to be much higher than a biologically conservative harvest rate used to set quotas over some large area.

In addition to intensive harvest and lack of mobility, broadcast spawning invertebrates may be more vulnerable to recruitment overfishing than finfish populations due to possible Allee effects in which recruitment is disproportionately reduced at low population densities (Botsford et al. 1993). For red sea urchins, a minimum density of adults is required for successful fertilization of gametes released into the water column (Levitan et al. 1992). The dependence of fertilization success on adult density in many

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species (Levitan and Sewell, 1998) suggests a generality of this mechanism among harvested broadcast spawning invertebrates. Scientists and harvesters are concerned about potentially severe depletion in fished populations of sedentary invertebrate populations, although hard evidence of this trend is lacking. Washington State and British Columbia have had anecdotal reports of widespread reduction of stocks since the fishery for sea cucumber began (Phillips and Boutillier, 1998). Several management areas have been closed to harvesting of red sea urchins, based on harvesters' request, to allow local populations to recover (Campbell et al. 2001).

Repeated annual harvest of the same areas increases the chance of decline in stock abundance; evidence for this effect is seen in many fisheries. For example, logbook data collected from the sea cucumber fishery between 1985 and 1996 show a 6% to 69% decline in CPUE in beds that were fished annually (Phillips and Boutillier, 1998). Sea cucumber harvesters have also seen a decline in animal size in areas that have been fished annually (K. Ridgway, PSCHA, 5296 Lost Lake Road, Nanaimo, B.C. V9T 5E5, pers. comm., 2004).

1.2   Rotational harvest as an alternative to annual harvest

Rotational or pulse fishing has been suggested as an appropriate harvest strategy for fisheries that occur on sessile and sedentary species, primarily because it allows higher spawning stock abundance than does an annual harvest strategy. A rotational harvest involves opening an area to harvest, and then closing it for a certain period to allow recovery before re-opening. Different areas can be managed in this way, so that some areas are available to harvest in any given year. Simulation modelling studies have found that, compared to annual harvest, rotational harvest resulted in higher egg production and population abundance for red sea urchins (Botsford et al. 1993; Pfister and Bradbury, 1996) and abalone (Sluczanowski, 1984), as well as higher spawning biomass per recruit for horse clams (Zhang and Campbell, 2002), and American sea scallops (Myers et al. 2000). Similarly, Breen (1992) predicted that, at proportional harvest rates above 2%, mean biomass of geoduck clams would increase with the rotation period (number of years between successive harvest events).

Rotational harvest may also provide greater yields than annual harvest. Walters and Bandy (1972) predicted that periodic harvest would increase big-game yields, and that the best interval between harvests depended on the harvest rate and population

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productivity. However, fishery simulation studies show divergent results on this subject. Studies that assumed relatively low proportional harvest rates predicted higher yields for annual harvest than rotational harvest strategies (Zhang and Campbell, 2002; Pfister and Bradbury, 1996; Botsford et al. 1993; Breen, 1992). In contrast, studies that explored a range of harvest rates found that longer periods of rotation resulted in a higher mean annual yield, particularly at higher harvest rates (Lai and Bradbury, 1998; Myers et al. 2000). Because spatial concentration of fishing effort is inevitable in dive fisheries, it is more likely that localised harvest rates are high. Thus, a precautionary approach to management would suggest the assessment of alternative harvest strategies in light of possibly high harvest rates.

While increasing the duration of the period between harvesting events (i.e., rotation period, or cycle length) results in higher spawning biomass, harvesting too infrequently will lead to unnecessary reduction in yield. The "optimal" cycle length will depend on local characteristics of population productivity, which vary over space and time. Zhang and Campbell (2002) showed that the magnitude of depletion of spawning stock biomass resulting from different rotation periods is extremely sensitive to the assumed mortality rate; growth and recruitment rates will also affect these results. Even if one could perfectly estimate these parameters and the rotation period that would prevent depletion of spawning biomass below some acceptable level, severe depletion could still occur due to environmental variability. For instance, in one study for the red sea urchin (Morgan et al. 2000), estimates of rates of growth and natural mortality from data on growth increment and size distributions differed substantially among sites. Urchin reproduction also varies over space (Botsford et al. 1993). In addition, environmental influences on larval survival and transport vary both temporally and spatially (Fogarty et al. 1991). This variation contributes to the irregular, episodic nature of recruitment in many broadcast spawning invertebrates (Winga et al. 2003) as well as unpredictable location-specific differences in recruitment.

Because of this variability in productivity, the period required for populations in harvested areas to recover differs among locations and over years. Rogers-Bennett et al. (1998) found that recovery of isolated urchin beds after intense harvest was highly variable spatially, and depended on bed depth and harvesters' size-selectivity. Sea cucumber harvesters have found that the rate of recovery in numbers after harvest varies between areas (K. Ridgway, pers. comm.). The unpredictable nature of recovery

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time suggests that a fixed rotation cycle (where the frequency of harvest is held constant, for example, at once every 3 years) could result in undesirable stock depletion if the cycle is too short, or unnecessary sacrifice in yield if the cycle is too long.

Botsford et al. (1993) noted the possibility of using different rotation periods for different areas to take advantage of spatial variability in productivity. Perhaps more important than maximizing yield, this approach could maintain spawning biomass where productivity is low. However, temporal as well as spatial variation in productivity suggests that an improved management approach could be based on state-dependent indicators to change the rotation cycle length over time, as well as by location. No studies to date have explored such an adaptive approach to setting the frequency of rotational harvests.

1.3 An alternative to fixed rotation: Adaptive rotational harvest

Given the lack of complete understanding as well as spatial and temporal variability in population dynamics and harvest rates for sea cucumbers, an appropriate management task is to find a harvest strategy that is robust to both high localised harvest rates and the effects of uncertainty in growth, mortality, and recruitment. Toward this end, I extend past studies of rotational harvest by applying the concepts of feedback management.

Walters (1986) advocated experimenting with management actions in order to learn more about the ability of populations to sustain harvest. One approach discussed by Walters was the use of feedback policies. In his description, initial policy actions are calculated based on a model of stock response to harvest, and decision rules (for future actions) are prescribed based on system-state variables, or attributes, such as estimated stock abundance. Because policy actions are varied only in response to changes in estimates of parameters used to assess population state, or of parameters for the model of stock response to harvest, Walters categorised feedback policies as "passive adaptive". In contrast, "active adaptive" policies entail deliberately probing management actions in order to gather data to reduce the uncertainty in parameter estimates and thus learn about the system's response to harvest. Feedback policies that specify what actions are required in response to particular observed attribute values are consistent with the FAO (1995) guidelines on the precautionary approach to fisheries.

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However, using estimates of stock abundance or parameters of a theoretical stock-response relationship (such as rates of fishing mortality, growth, and reproductive rate) to determine harvest policies may not avoid undesirable levels of stock depletion because of uncertainty in these estimates-- particularly for data-poor fisheries. According to Nicol and de la Mare (1993), successful feedback management requires the use of attributes that can be measured robustly. For example, population density and statistics of size distributions are attributes that can be measured with adequate accuracy and precision, despite uncertainties in population abundance and in population response to both harvest and unpredictable environmental changes. In addition, these attributes more directly indicate the state of the population than do rates of fishing mortality, growth or reproduction. In the technique of feedback management described by Nicol and de la Mare, managers decide on specific quantitative targets for attributes of the system that can be measured as indicators of the effects from harvest. A catch limit is put in place that is designed to meet the targets. Later, the effect of harvest is estimated by measuring the attributes; if the targets have not been met, the fishing level is adjusted. By using feedback from the biotic system, this technique helps identify the right targets and fishing levels over time. Management of the fishery proceeds much like an autopilot on a boat constantly adjusts the rudder to reach the destination. I combine this concept of feedback management with that of rotational harvest in a new strategy that allows the frequency of harvest to be adjusted based on feedback from the fished system.

In this study, I develop two variations of an adaptive rotational harvest strategy, using animal size and population density as biotic feedback indicators for determining when to harvest next. The cycle length (i.e., rotation period) would not be fixed; local areas would be harvested at a frequency determined by local recovery rates, which may differ by location and over time. For example, in an unproductive area, an adaptive rotational harvest strategy might lead to a cycle of fishing every five or six years, whereas more productive areas might be harvested every two or three years. If productivity levels change, the cycle length will also change. In the first adaptive rotational harvest strategy that I consider, harvested areas are closed to further harvest until a designated degree of recovery has been assessed, using annual monitoring of the indicators. In the second strategy, areas are re-opened to harvest after a predetermined number of years, at which time feedback indicators are measured; the cycle length is then adjusted if measurements either exceed or fall short of recovery targets. These two variations represent management options with different costs and

benefits. This strategy can be considered an "active adaptive" feedback policy if the recovery targets are changed over time, however I consider only fixed targets here.

The adaptive rotational strategy that I explore here determines empirically the appropriate rotation cycle length without the need to estimate population parameters such as rates of natural mortality and growth in body size. These parameters are difficult to estimate in sea cucumbers because age cannot be determined (see Section 1.5). Simply by monitoring animal sizes and local population density, the adaptive strategy adjusts the frequency of harvesting in each area so that harvested populations recover to set targets for animal size and population density. In addition, temporary reserves for spawning stock are created because harvested areas are closed for several years, during which time the density of adults should increase. This strategy should prevent serial stock depletion, and possibly allow an increased yield from the fishery.

If an adaptive rotational harvest strategy appears theoretically attractive, in the real world we will have to deal with the practical problem of potentially unstable catches over time. Within a system of several areas being harvested using an adaptive rotation, the rotation cycle length is very likely to vary between areas, because of spatial heterogeneity in productivity of the habitat. Consequently, the number of areas open to harvest will likely change from year to year. This property will lead to variation in the annual yield, and the possibility that in some years, none of the harvest areas will be ready for harvest. From the standpoint of the fishing industry, this situation is obviously undesirable.

To mitigate this potential problem, I suggest that several insurance, or spare, areas can be set aside and opened for harvest when needed. For example, if four primary areas are harvested on an adaptive rotation, the management objective might be to have at least one area open to harvest each year. The practical question is: how many insurance areas must be set aside to ensure that this objective is met? As an adaptive rotational harvest system is implemented in the field, we can learn through experience what cycle lengths can be expected and the number of insurance areas needed. Insurance areas that are never or rarely harvested would act as a network of spawning reserves, building on the precautionary nature of this harvest strategy.

We used the fishery for the giant red sea cucumber in British Columbia as a case study to evaluate the potential performance of an adaptive rotational harvest strategy relative to the current practice of harvesting based on annual catch limits.

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1.4 Research Objectives

Given uncertainty and spatial variability in stock dynamics, the objective of this study is to evaluate annual and adaptive rotational harvest strategies under a range of plausible scenarios of population dynamics. This general research objective can be broken down into three specific objectives:

1. **Deterministic comparison of harvest strategies.** Under deterministic conditions,

   a) calculate the "optimal" rotation cycle (that which maximises long term yield) for different scenarios of productivity and recruitment-compensation (recruitment per unit spawning stock biomass at negligible stock size), given a high (50%) localised harvest rate.

   b) determine whether the two adaptive rotational harvest strategies correctly identify this cycle length under each scenario; and

   c) compare the performance of annual, fixed rotational, and adaptive rotational harvest strategies in terms of long-term yield and spawning biomass.

2. **Stochastic comparison of harvest strategies.** Under more realistic conditions of time-varying recruitment and observation error, compare the expected performance of the annual harvest strategy versus the adaptive rotational harvest strategies under different scenarios of productivity, recruitment-compensation and inter-annual variability in recruitment. Performance criteria are:

   a) long-term average annual yield (biomass harvested);

   b) inter-annual variability in yield;

   c) depletion from an unfished state of:

      1) average body mass per sea cucumber (in terms of split weight);

      2) proportion of sea cucumbers over 300 g ("large sea cucumbers") in the population;

      3) population density;

      4) spawning biomass.

3. **Insurance Areas.** Under different scenarios of productivity, recruitment-compensation, and variability in recruitment, determine how many insurance areas are required for each of the two adaptive rotational harvest systems to

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ensure that at least one area will be open to harvest each year, given four primary harvest areas.

1.5 Biology of the Sea Cucumber

The giant red sea cucumber is a holothuroid echinoderm distributed from California to Alaska (Sloan, 1986). The sea cucumber is a deposit feeder, consuming organic matter and associated microorganisms. Sea cucumbers can be either aggregated or solitary; some concentrations are extensive, although patch size is not documented (Boutillier et al. 1998). They are most commonly found in shallow subtidal habitats where detritus accumulates in areas with little or no current or wave action (Brumbaugh, 1980), and have been observed as deep as 249 m (Lambert, 1997). Substrate preference of adult sea cucumbers is unclear. On the central coast, Cripps and Campbell (2000) found the highest densities on boulders, cobble, and mixed hard and soft substrates. However, sea cucumbers of harvestable density are also found on soft substrates, which harvesters prefer because the animals are easy to see (pers. comm. from K. Ridgway, in Campagna and Hand, 1999).

Broadcast spawning occurs in shallow water from late spring through the summer; fertilization is external (Cameron and Fankboner, 1986). Larvae drift as plankton for between 65 and 125 days (McEuen, 1987), are dispersed by currents, then settle and develop into juvenile sea cucumbers. Juveniles hide in dense mats of filamentous red algae, algae holdfasts, under rocks or in rock crevices, and are rarely seen in the same habitat as adults (Cameron and Fankboner, 1989). Kelp greenling, hermit crab, and sea stars feed on juvenile sea cucumbers, whereas predation on adults has not been observed or sufficiently studied (Bingham and Braithwaite, 1986; Cameron and Fankboner, 1989). Sexes are separate, and no sexual dimorphism is evident (Cameron and Fankboner, 1986).

Sea cucumbers have limited mobility and may migrate. Locomotion along the bottom is achieved by body contractions with the aid of tube feet (Phillips and Boutillier, 1998). Swimming behaviour via body contractions has been observed in adults, and is likely a predation-avoidance strategy (Cameron and Fankboner, 1989). Sea cucumbers may migrate to shallow water to spawn from early April to August (Lambert, 1997). However, there were no discernable seasonal differences in density within surveyed areas in the Central Coast of BC (Cripps and Campbell, 2000). A study conducted on

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gently sloped substrates found that sea cucumbers moved an average of 3.9 m per day, and short-term movement patterns appeared to be random (Da Silva et al. 1986). seasonal migrations are likely to be area-specific; among fished areas, the amount of immigration varies from year to year (Boutillier et al. 1998). Consequently, the rate of recovery of harvested areas will differ by location, which suggests that an adaptive rotation cycle that can differ by location would be appropriate for the sea cucumber fishery.

Parameter estimates related to the productivity of sea cucumber populations are speculative, due to several unusual biological characteristics and because age cannot be determined (Phillips and Boutillier,1998). Annual fluctuations in body mass are caused by several factors: the evisceration of internal organs as a defence tactic, the resorption of visceral organs during the winter and regeneration through the spring and summer (Fankboner and Cameron, 1985), and seasonal variation in skin thickness (Fankboner and Cameron, 1988). In addition, changes in body shape when handled contribute to difficulties in measuring length (Hand and Rogers, 1999). Lack of contrast in length- or mass-frequency data further confounds the estimation of size structure of sea cucumber populations.

Thus, mortality rate, growth rate, longevity, maximum age, and ages at sexual maturity and recruitment to the sea cucumber fishery are all unknown. P. Fankboner speculatively estimates that the maximum age is 12 years (Phillips and Boutillier, 1998), whereas an Alaskan study assumes a maximum age of 14 years (Woodby et al. 1993). Maximum length is approximately 500 mm (Fisheries and Oceans Canada, 2005). Speculative estimates of the age at recruitment to the fishery range from 4 to 8 years (Fankboner and Cameron, 1988; Phillips and Boutillier, 1998). Fankboner and Cameron (1988) estimate that animals mature at >56 months (4.6 years), but age at maturity probably varies considerably throughout the geographic range of the species (Boutillier et al. 1989) due to differences in body growth rates.

1.6   Management of the Sea Cucumber Fishery

In British Columbia, sea cucumbers are harvested commercially by SCUBA diving, for the body wall and longitudinal muscles, as food products. The muscles are stripped from the body wall, and frozen for export to Japan and Taiwan; the body wall is

then processed into a dried product, called bêche-de-mer, for export to Hong Kong and Singapore, and then re-exported to Chinese consumers (Conand and Byrne, 1993).

Commercial exploitation of sea cucumbers began in British Columbia in 1971. Market development resulted in a rapid escalation in fishing effort during the 1980's which led to conservation concerns. In 1986 DFO set precautionary quotas by area and arbitrary regional quotas; however, landings and the number of licenses issued continued to increase and quota over-runs were common. The difficulty in limiting the fishery, as well as concerns about declining catch per unit effort in some areas, led to arbitrary quota reductions in 1989, license limitations in 1991, further quota reductions in 1993, and an individual quota (IQ) program in 1995 (Hand and Rogers, 1999).

Scientists suspected that sea cucumber stocks were being overfished due to anecdotal reports of stock decline (Phillips and Boutillier, 1998), combined with the animal's lack of mobility and its widespread availability to harvesters. In the absence of information on stock structure and dynamics, they recognised that localised overfishing may also lead to systematic recruitment overfishing of discrete stocks (Boutillier et al. 1998).

In 1993, two- and three-year rotation periods were initiated for the South and North Coast quota areas, respectively (Phillips and Boutillier, 1998). In 1997, an annual fishery was reinstated. Due to the lack of biological information about sea cucumbers, Boutillier et al. (1998) considered that a consistent time-series of fisheries data, without the gaps created by the rotational fishery, would enable biomass dynamic models to be used to evaluate the status of fished stocks.

In 1997, a new management plan was developed and implemented, based on a three-phase approach to dealing with developing invertebrate fisheries where data are limited (Perry et al. 1999). Based on advice from Phase (0), "Collection of Existing Information" (Boutillier et al. 1998), the fishery is now operating under Phase (1), "Fishing for Information". Under this management approach, annual quotas are based on biologically-conservative estimates of density (i.e., lower 90% confidence bound of the estimate of mean density) and harvest rate (4.2%). The commercial fishery is restricted to 25% of the total coastline, divided into several in non-contiguous areas, and a further 25% of the coastline is reserved for research purposes. Experiments are currently underway to test population responses to different proportional harvest rates ranging from 2% to 16%, with the aim of determining a sustainable harvest rate. In addition,

large-scale transect surveys are being conducted to provide biomass estimates (Hand and Rogers, 1999). Research results are to be used to develop a "biologically-based" management plan, and then the remaining 50% of the coastline will be available for harvesting in Phase (2), "Fishing for Commerce" (Boutillier et al. 1998).

However, the current management experiments on sea cucumbers assign harvest rates to treatment sites of 10 km in length. Because fishing effort is concentrated in particular spatial locations, the prescribed quota is harvested from a fraction of the site, and harvesters may fish a different part of the site from year to year (K. Ridgway, pers. comm., 2004). Due to limited mobility of sea cucumbers, the effects of harvest are likely to occur on a scale much smaller than 10 km. Thus, data collected from randomly placed survey transects and bio-samples (where 50 animals are collected and weighed) within each 10-km site may not reveal the effect of harvest in the localities targeted by harvesters. Also, population response to harvest levels will probably vary from area to area, and so even if experiments are locally conclusive, the results may not represent a safe strategy for all locations on the coast.

Harvesters, scientists and managers are considering whether to change the sea cucumber fishery to a rotational harvest. DFO manages the fishery in consultation with commercial harvesters, processors, First Nations, the B. C. Ministry of Fisheries, and the Sport Fishing Advisory Board. In addition, The Pacific Sea Cucumber Harvesters Association (PSCHA) fully funds research activities through membership fees and the sale of experimentally harvested animals (Hand and Rogers, 1999). PSCHA is interested in a rotational harvest system for economic and conservation reasons. Whereas many harvesters practise an ad hoc rotation, thus landing the larger sea cucumbers preferred by the market, some harvesters habitually fish the same areas each year, thus landing smaller animals. This decline in size brings down the average price per pound of landed sea cucumbers (K. Ridgway, pers. comm., 2004). The reduction in body size also indicates possible growth overfishing and/or recruitment overfishing. Commercial processors have also noted the substantial reduction in size of landed sea cucumbers over several years (Mike Crawford, Territory Seafoods, 203-12411 Vulcan Way, Richmond, B.C. V6V 1J7, pers. comm., 2004; Paulo Tai, Evergreen International Foodstuffs, Ltd., 1944 Franklin Street, Vancouver, B.C. V5L 1R2, pers. comm., 2004). Harvesters believe a rotational fishery will ensure adequate recovery of population abundance, larger harvested sea cucumbers, and a sustainable fishery.

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However, the lack of understanding of the productivity characteristics of sea cucumbers, and spatial and temporal variability in population dynamics and harvest rates means that the appropriate length of rotation cycle is unknown, and may vary with location. Consequently, an adaptive rotational harvest strategy may achieve higher yield and spawning stock levels than a fixed rotation cycle length that is based on current, limited knowledge.

2 MODELLING FRAMEWORK

2.1 General Overview

This section provides a brief overview of the overall modelling framework (Figure 1) and procedures to provide a context for the more detailed sections that appear later. I applied this modelling framework to the sea cucumber fishery in order to identify a robust harvest strategy (i.e., one that performs well despite uncertainty). Following the approach of de la Mare (1996), I developed an operating model that allowed for a range of scenarios covering the range of uncertainty in our understanding of sea cucumber population dynamics. Through computer simulation, one can evaluate the costs and benefits of different options (harvest strategies) ahead of time and avoid making expensive mistakes in the field.

I simulated the repeated harvest of a sea cucumber population in a single, small, commercially targeted area, and compared the long-term outcomes of alternative harvest strategies (Objectives 1 and 2). I tested each harvest strategy (described in section 2.5) under several "scenarios" of population dynamics (I define these scenarios by different possible levels of population productivity, recruitment-compensation, and inter-annual variability in recruitment; see section 2.3). For a given harvest strategy and scenario of population dynamics, I ran the model for one or more 100-year population and harvest simulations, and calculated long-term measures of catch (yield) and conservation (the performance criteria and number of simulations differed depending on the specific analysis). In each year of a population trajectory, the model calculated three sub-models (which are described in more detail later):

1. The **management procedure** simulated each harvest strategy, by applying the control rules (rules that specify what actions are required in response to particular observed values for attributes that indicate the state of the population) for the harvest strategy being tested. Attributes that provided feedback to the management system (for adaptive rotational harvest strategies) included mean body mass of individual sea cucumbers and population density. In each year of

the simulation, the area was harvested only if the harvest strategy specified that it would be harvested that year.

2. The basic **population model** calculated catches and changes in population abundance and other variables including mean body mass and population density, using the parameters for the scenario of population dynamics being tested.

3. The **observation model** simulated the data collection for population density and mean body mass. To represent potential observation error, the values predicted by the population model included random error.

For the adaptive rotational harvest strategies, the management model used the observations of average body mass and population density produced by the observation sub-model as indicators of recovery. These observations were then used as input for the control rules in the management procedure sub-model, and this process determined when the area was next harvested. For the annual and fixed rotation strategies, the management procedure did not employ these "recovery" observations, and the area was harvested on a fixed schedule.

This study includes three different analyses, one for each research objective. Starting with a deterministic analysis (Objective 1), I simulated the harvest of a sea cucumber stock in a single area, at different fixed cycle lengths (rotation periods), to determine the "optimal" cycle length under different scenarios of population dynamics, for a proportional harvest rate of 50%. This harvest rate reflects the effort-intensive nature of the fishery, and is within the range of harvest rates estimated from a spatial analysis of commercial fishery data (S. Humble, C. Hand, and W. de la Mare, In prep.). Each of the two adaptive rotational harvest strategies were simulated to determine whether they would achieve the optimal cycle length under each scenario, and also to compare the performance of adaptive versus fixed rotation strategies under deterministic conditions.

I then compared annual and adaptive rotational harvest strategies under stochastic conditions of recruitment and observation error (Objective 2), using the same scenarios of population dynamics as in the deterministic analysis. Using these results, I developed a simpler model to estimate how many insurance areas would be needed to ensure that at least one area would be available to harvest each year (Objective 3).

2.2 Population Model

The basic model I used to simulate population trajectories is a dynamic age-structured population model with stochastic components. Parameter estimates and the corresponding sources of data are listed in Table 1. The basic population model is a simple difference model reflecting the annual short fishing season, and where reproduction occurs before harvest. The model predicts biomass and harvest for a sea cucumber population of a typical harvestable density for a 1 km length of shoreline, over a 100-year period. I assumed that the results from simulating repeated harvesting of this hypothetical population represent the results that might occur for commercially vulnerable populations of sea cucumbers along the British Columbia coast.

The model includes the following characteristics for growth, maturity, recruitment and selectivity. Length at age (L_a) is calculated from the Von Bertalanffy growth equation:

(1) $\quad L_a = L_\infty * \left(1 - e^{-k*a}\right)$

where: a is age

L_∞ is the average length at the maximum age (Table 1)

k is the Von Bertalanffy growth rate (Table 1)

Mass at length (M_a) is calculated from the following equation:

(2) $\quad M_a = A * (L_a)^b$

where: A and b were estimated by fitting the above model to observed length and mass data (collected from commercially harvested sea cucumbers at two fish processing plants in Vancouver during the October 2003 fishing season; see Appendix 1).

$A = 0.0025702$
$b = 2.0$

Maturity at age is calculated from a cumulative normal distribution (ages at 50% and 95% maturity are listed in Table 1).

Recruitment (R_t), the number of individuals that enter the first age class in each year of the population trajectory, is calculated from a Beverton and Holt stock-recruitment function. In each year of the stochastic simulations, the calculated number of

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recruits is multiplied by a random number from a lognormal distribution with a mean of 1 and a coefficient of variation of 0.5, which is consistent with observed levels of recruitment variability in red sea urchins (Smith et al. 1998). A lognormal distribution has a tail that is spread to the right, thus characterising the rare but large recruitment events that occur in broadcast spawning invertebrates (Morgan et al. 2000). Thus:

(3) $$R_t = \frac{\alpha * N_t}{\beta + N_t} * \varepsilon(cv)_t$$

where: N_t is the total number of mature individuals in a given year

(4) $$\alpha = m * recK$$

(5) $$\beta = K * \left(\frac{\alpha}{recK} - 1 \right)$$

m is the recruitment multiplier parameter

$recK$ is the number of recruits at carrying capacity. This number is calculated based on an assumed unfished density of 50 cucumbers per metre shoreline (cpms, the units used in stock assessment surveys) for a 1 km length of coastline.

$\varepsilon(cv)_t$ is the lognormally distributed error term for recruitment, with:

(6) $$\mu = \frac{-\sigma^2}{2}$$

(7) $$\sigma = \sqrt{cv^2 - 1}$$

cv is the coefficient of variation for the error term.

μ and σ are the mean and standard deviation of the normal distribution from which the lognormal distribution was generated.

I assumed that the fishing selectivity as a function of age can vary, depending on the local population density and sizes of sea cucumbers. Selectivity-at-age was based on the following assumptions about fishing behaviour:

- Harvesters are more selective (select larger individuals) when density is high (K. Ridgway, pers. comm.)

- When density is high (over 40 cpms), harvesters will select only those individuals over 260 g, the size preferred by the market (the age at this mass depends on the growth rate).

- As density falls below 40 cpms, harvesters will progressively become less selective (select smaller individuals) while aiming for a "picking rate" equal to that at 40 cpms (Figure 2). Below some threshold density (about 25 cpms assuming the base-case growth rate), all individuals present are taken. These thresholds are arbitrary, based on harvester accounts of fishing behaviour, and survey estimates of density in "worthwhile" and "possibly worthwhile" areas.

- Selectivity at age is multiplied by a schedule of availability at age on the fishing grounds, because only those cucumbers present can be selected. This assumption addresses the separation in juvenile and adult habitat, as explained below.

Because juveniles and adults are largely segregated, I created a schedule of availability at age on the fishing grounds, using a cumulative normal distribution, with ages at 50% and 95% availability at 4 and 5.5 years, respectively. Because DFO survey data showed that the mean body mass of sampled sea cucumbers varied widely among locations, but the proportional size distribution had the same basic shape, I assumed that availability was not size-based but age-based. Given the fixed proportions present at age, the growth rate (which varies according to the different productivity scenarios) determines the sizes of individuals present. The availability-at-age schedule determines the proportions of each age class that are available for fishing, whereas selectivity-at-age determines the proportions that are harvested of those available.

2.3 Scenarios of Productivity, Recruitment-compensation and Recruitment Variability

Through preliminary simulations, I found that parameters defining growth, mortality, and recruitment of sea cucumbers were the most critical uncertain factors that affected the expected yield and population levels. To deal with these uncertainties, I tested the performance of alternative harvest strategies under a range of possible scenarios, each defined by a different set of values for four critical parameters (Table 2). I used an orthogonal comparison: changing the level of each critical parameter in turn while leaving the others constant. These scenarios of population dynamics include:

1. Base-case. I used the best available estimates of all parameters (from Table 1). The base-case parameter values in Table 2 can be considered to represent "medium" levels of productivity, recruitment-compensation, and recruitment variability (whereas the other scenarios are defined by departures from base-case parameter values, thus "low" and "high" levels).

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2. Low and high levels of productivity. To simulate different levels of productivity that might occur over space and time, I varied growth (k) and natural mortality (M) rates to create hypothetical populations that had the same average body mass (310 g) in an unexploited state (for the sake of comparison), but that recovered from harvest at different rates due to somatic growth, reflected by their different k-parameter values.

3. Low and high levels of recruitment-compensation (recruitment at low stock size, i.e., maximum per-capita reproductive rate). To simulate different levels of recruitment-compensation, I varied the slope of the Beverton-Holt stock-recruitment relationship at the origin by changing the "m" parameter (Equation 4). Figure 3 shows the stock-recruitment curves for the three levels of recruitment-compensation. In a weak recruitment-compensation scenario, there are few recruits when spawning stock is depleted, so the population is slow to recover after intense fishing. For strong recruitment-compensation, recruitment remains nearly constant except at very low spawning stock levels, so recovery is relatively fast after intense fishing.

4. High variability in recruitment (magnitude of unpredictable changes in recruitment over time). To simulate this scenario, the model uses a coefficient of variation of 1.0 for the random error distribution in the stock-recruitment function (equation 3). This level of variability is within the range observed for the red sea urchin (Smith et al. 1998). Recruitment variability was applicable only to the stochastic analysis of harvest strategies.

2.4 General characteristics of the simulated stock

2.4.1 Area and Density

To represent a commercially vulnerable population, I modelled a single population covering an arbitrary 1 km length of shoreline, with an unexploited density of 50 cpms. For DFO's current stock assessment surveys, density is estimated in these units to simplify the calculation of quotas for areas covering a given length of shoreline; if I had used units of cucumbers per square metre, the model predictions of density would be unchanged, in relative terms. While sea cucumbers can be found much deeper, surveys and the commercial fishery are conducted only above 18 m for safety and practical reasons. Thus, density in units of cpms is the number of animals, above 18 m

depth, per metre of shoreline. The assumption of an unexploited density of 50 cpms is at the lower end of the range of "high density" areas considered by harvesters to be commercially harvestable (Campagna and Hand, 1999). I chose to represent high density sites because they are more likely to be fished, assuming that the management goal is to prevent overfishing in these vulnerable areas, which are also likely to be important larval sources.

2.4.2 Migration and larval dispersal

The model assumes no immigration or recruitment from areas outside of the immediate harvesting locality. The degree of isolation of local populations is uncertain because the extent of migration and larval dispersal is unknown. The assumption of a closed population represents a worst-case scenario; an isolated population is more vulnerable because it is not replenished from outside sources. It is prudent to test harvest strategies under assumptions characterising intensive fishing of isolated aggregations that are separate stocks; if a harvest strategy is robust to unfavourable simulated conditions, then it should perform better if real conditions were more favourable.

2.5   Harvest Strategies

2.5.1   Harvest Rate

The model assumes that harvest occurs at a single time in each harvest year, to reflect the short (2- to 3-week) fishing season in BC. The harvest rate is defined as the proportion of the vulnerable population harvested in a given fishing season. To represent commercially targeted, heavily fished areas as occur in dive fisheries, the model assumes a high proportional harvest rate (either 50% or 75%). The same harvest rate is assumed for annual and rotational harvest (for example, the annual harvest rate is not divided by 3 for a 3-year rotation), reflecting the nature of dive fisheries: effort is always concentrated, so localised harvest rates will be similar regardless of harvest frequency. High local harvest rates are a realistic assumption: if visibility is good and algal cover sparse, virtually all sea cucumbers are removed from a given location in one pass (Boutillier et al. 1998). In addition, the intended biologically conservative harvest rates are not achieved on a local scale. A spatial analysis of data from the commercial fishery (1997 to 2004) estimated the mean harvest rate at approximately 40% of estimated

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biomass in fished areas (summing smaller lengths of shoreline fished in a given year, from <1 km to several kms each, to estimate the total length of shoreline fished and the biomass therein), with a distribution of harvest rates spread toward higher values (S. Humble, C. Hand, and W. de la Mare, In prep.). The assumption of high local harvest rates also represents the possibility that dense aggregations targeted by harvesters may be separate stocks, because the spatial scales of migration and stock boundaries are unknown. In practice, the harvest rate will depend not only on fishing behaviour but on animal mobility and distribution with depth as well.

2.5.2 Annual Harvest Strategy

To represent different levels of optimism for an annual fishery (with respect to meeting management objectives for population conservation and harvest), I evaluated two different annual harvest strategies (Table 3). In the deterministic analysis, I evaluated the first annual strategy (AFIXH), which assumes that the area is harvested annually at a proportional harvest rate of 50%. Given that an annual harvest strategy at such high harvest rates would likely perform relatively poorly under conditions of variable recruitment, for the stochastic analysis, I evaluated only the "best case" scenario for an annual fishery (MSY), which assumes that the area is harvested annually at the MSY harvest rate (assuming perfect knowledge of this rate and the ability to achieve it in practice). To calculate the MSY harvest rate for each scenario of population dynamics, I ran deterministic simulations using annual harvest rates of (2%, 4%, ...90%) and calculated the total 100-year yield for each harvest rate, generating a curve of yield versus harvest rate. For each scenario, the MSY harvest rate was taken to be that which resulted in the highest total yield over 100 years; these harvest rates are listed in Table 4.

While evaluating the performance of rotational harvest strategies versus the best-case annual harvest strategy is an interesting theoretical comparison, achieving the MSY harvest rate on a small scale (such as <1 km, for a local aggregation) is improbable in this fishery for the following reasons:

    d) It assumes perfect knowledge of the MSY harvest rate, which is not possible because population parameters used to estimate MSY are very uncertain for this species;

e) Even if we had perfect information and were able to determine the MSY rate, and quotas were calculated based on this harvest rate, it could not be achieved in practice. In experiments designed to test different harvest rates for sea cucumbers, the proportion of a treatment area that was actually fished increased proportionally with the intended harvest rate, such that harvesters only covered a small area within the low harvest-rate sites to achieve the target catch (Humble Hand and de la Mare, In prep.). This observation illustrates the fact that changing the harvest rate used to set quotas only changes the total area harvested; the proportional harvest rate in areas that are actually fished remains high.

2.5.3 Rotational Harvest Strategies

Fixed Rotational Harvest

In order to compare the performance of adaptive rotation versus the conventional strategy of rotational harvest based on a fixed cycle length, in the deterministic analysis, I simulated fixed rotation intervals of 3, 4 and 5 years, assuming a 50% proportional harvest rate in each harvest year (row 3 of Table 3).

Adaptive Rotational Harvest

The two adaptive rotational harvest strategies are summarized in rows 4 and 5 of Table 3. I simulated both strategies under a proportional harvest rate of 50% for the deterministic analysis, and either 50% or 75% for the stochastic analysis. For both adaptive harvest strategies, observations of average body mass and population density ("recovery data") are collected prior to harvesting the area, and compared to threshold levels in order to assess whether the area has recovered. The harvest control rules, which determine subsequent harvest actions based on observed recovery data, differ between the two harvest strategies as follows.

In "Harvest when ready" (HWR), recovery data are collected annually and the area is re-opened to harvest only when the average body mass AND population density have recovered to minimum thresholds (Figure 4a). In "Harvest then adjust" (HTA), the cycle length is initially 4 years, and is subsequently adjusted if necessary. The area is harvested when planned, and recovery data are collected just before or during harvest.

These data could be fishery-dependent (i.e. estimating density from CPUE, and mean mass from catch samples) or fishery-independent (i.e., estimating of density and mean mass from scientific surveys). If either mass OR density have not recovered to the respective minimum thresholds, one year is added to the next cycle length. If both mass AND density have recovered beyond the respective upper thresholds, the next cycle length is reduced by one year (Figure 4b). If mass and density estimates lie between the minimum and upper thresholds, the cycle length is not adjusted. The rationale for HTA is that it may offer a more practical option. A pre-harvest survey may not be economically feasible for the harvesters (in B.C., the PSCHA funds survey activities, and harvesters conduct surveys along with science personnel) if the area had not recovered and they could not recover the costs of travel and surveys through the sale of harvest (K. Ridgway, pers. comm.).

Mass and Density Thresholds

Because the average body mass and population density that occur naturally will depend on site conditions, the thresholds used to define recovery could, in practice, be determined specifically for each site. These thresholds could be based on survey estimates of average mass and population density prior to fishing (in areas that have not been fished for a long time, perhaps 10 years). They could also be fine-tuned over time, as more is learned about the recovery process.

However, as a starting point, I defined the threshold levels for body size as follows. The minimum threshold for average mass was 260 g (split weight, i.e., gutted); a sea cucumber of this size (about 300 mm long) is considered a desirable size for the market (P. Tai, pers. comm., 2004). Also, 263 g was the mean mass of commercially landed sea cucumbers for the Central and North Coast quota management areas in 1997 (Hand and Rogers, 1999). The model predicts that a cucumber weighing 257 g is 5 years old (assuming the base-case growth parameter estimates), which is consistent with the age of mature animals, estimated at over 4.6 years (Cameron and Fankboner, 1989). Thus, a threshold of 260 g for average mass should allow animals to spawn before the area is re-opened to harvest[1]. "Harvest then adjust" allows a decrease in cycle length (harvesting more often) only if the average mass exceeds a threshold of

[1] Because fecundity likely increases with age, using this mass threshold would likely not result in larval production as high as in unharvested populations. However, in combination with a population density threshold, this mass threshold should allow substantial recovery in population spawning biomass.

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280 g (and density exceeds the upper threshold defined below). I determined this upper mass threshold by numerical experiments with the model in which I adjusted the threshold until the harvest strategy led to an equilibrium cycle length that maximized the long-term yield at low, medium, and high levels of productivity, given a 50% harvest rate.

I chose 15 cpms as the minimum threshold for population density, the second indicator of whether an area should be harvested. This density is close to the lower 95% confidence limit for survey estimates of density in a "medium density" site that was considered "possibly worth harvesting" by divers (Campagna and Hand, 1999). "Harvest then adjust" allows a decrease in cycle length (harvesting more often) only if the density exceeds a threshold of 30 cpms. This density is close to the upper 95% confidence limit for survey estimates from the same medium density site; it also represents 60% of the unfished density assumed for the stock. Presumably, setting threshold densities to commercially harvestable levels should ensure an acceptable level of recovery. There are no published estimates of a density below which spawning success is compromised in sea cucumbers.

2.6 Observation Model

The implementation of an adaptive rotational harvest strategy will not be perfect; its performance will be affected, in part, by some level of inaccuracy in the estimates of average body mass and population density that determine future harvests. Therefore, for the stochastic analysis, the observation model simulates 'observed' values for mass and density, which are then used as input to the management procedure calculations (harvest strategy). In each year of the stock trajectory, the observation model takes the values of both average body mass and density from the population model, and multiplies them by their respective error terms, each of which is drawn randomly from a different distribution. I assume errors in mass and density observation are not correlated. For both error-terms, the model used a normal distribution with a mean of 1 (thus assuming no bias); the coefficients of variation were different between observation errors for mass and density. No observation error was applied to the annual harvest strategy; the theoretical MSY harvest rate was achieved in each scenario.

For the observation error in density, I assumed a coefficient of variation of 0.25, which is consistent with the average magnitude of experimentally-determined observation error. Campagna and Hand (1999) compared survey-estimates of density to

the actual densities measured by complete removal experiments. From these data, I found that the standard deviation of the estimates from the actual values was approximately 0.25 of the mean density for low, medium, and high density sites.

For the observation error in average body mass, I estimated the coefficient of variation using DFO survey data. Using individual body mass measurements (collected from fished and unfished areas along the B.C. coast), I calculated the mean and standard deviation of body mass in the population at 300g and 122g, respectively. The standard error (SE) for the mass estimate depends on the sample size according to the following equation:

$$SE = \frac{SD}{\sqrt{n}}$$ where: SD is the standard deviation of individual mass;

n is the sample size collected to estimate mass.

The coefficient of variation is calculated as follows:

$$CV = \frac{SE}{\mu}$$ where: μ is the mean individual mass

Given the standard deviation of individual body mass (122 g), a randomly chosen sample of 100 sea cucumbers should produce an estimate of average mass with a standard error of 12.2 g and a coefficient of variation of 0.041. Thus, I set the coefficient of variation for mass observation error at a value of 0.05. To reduce the possibility of non-random sampling, a larger sample (for example, 200 to 500 animals) would be required to ensure this level of accuracy; I assumed that such a large sample size would be feasible for a 1-km long harvest area, given that the fishing industry funds research and monitoring activities, and are interested in improving data collection for this fishery.

2.7   Deterministic Simulation Procedures

As a theoretical exercise, I used the modelling framework to compare the long-term performance of annual, fixed rotation and adaptive rotational harvest strategies under deterministic conditions (no observation error or random variation in recruitment). Although we cannot predict the level of productivity or recruitment-compensation in a given area, if an adaptive rotational harvest strategy correctly identifies the "optimal" cycle length for different unknown local conditions (by using biotic feedback indicators),

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then this strategy is a good candidate to be robust to uncertainty. To calculate the "optimal" cycle length under each scenario of population dynamics (base-case, low and high productivity, and low and strong recruitment-compensation), the model ran one 100-year trajectory for each of 9 fixed cycle lengths (harvesting at fixed schedules ranging from every year to every 9 years), at a realistically high local harvest rate of 50%. The "optimal" cycle length was taken as that with the highest cumulative yield. To determine whether the adaptive rotational harvest strategies would achieve the "optimal" cycle length under each scenario, the model ran one 100-year population trajectory for each strategy. The cycle length at equilibrium was taken to be the length of the final rotation cycle, starting with the year after the previous harvest, and ending in the year of the last harvest of the 100-year trajectory. I compared this result to the "optimal" cycle length for each scenario.

To compare the deterministic performance of annual, fixed rotational, and adaptive rotational harvest strategies, I used the model to calculate long-term levels of spawning biomass and yield for annual harvest, 3, 4, and 5-year fixed rotation periods, and the two adaptive strategies. To assess long-term performance, I ran one 100-year simulation for each harvest strategy under each scenario, and considered the results predicted for the final rotation cycle of each simulation, when the system was near equilibrium. For annual harvest strategies, the last cycle length was always 1 year. Spawning biomass was taken as the average value over the final rotation cycle, and average annual yield was the biomass yield from the final year of harvest, divided by the number of years in the final rotation cycle. By taking the average across years in the final cycle, the results represent a network of harvest areas, each at different stages of recovery.

2.8   Stochastic Simulation Procedures

Having analysed deterministically the theoretical properties of alternative harvest strategies, the next step was to compare the performance of harvest strategies in a more realistic setting of unpredictable year-to-year changes in recruitment and observation error. I used the modelling framework to simulate an annual harvest strategy (MSY) and the two adaptive rotational harvest strategies (HWR and HTA) under these stochastic conditions. For each harvest strategy under each scenario, the model ran 1000 Monte

Carlo simulations ("trials"), each consisting of a 100-year population trajectory, and calculated measures of performance from the set of 1000 results.

2.8.1 Performance Criteria

I compared the performance of alternative harvest strategies using several performance criteria related to either conservation of the sea cucumber population or economic benefits realized from the fishery. Calculations for each criterion are:

Economic Performance Criteria

a) *Long term average annual yield:* Catch in the last harvest year, divided by the final cycle length (for each trial), averaged over 1000 trials;

b) *Inter-annual variability in yield:* coefficient of variation (standard deviation divided by mean) among trials of yield in the last harvest year.

c) *Equilibrium average mass:* Starting from an unfished average mass of 310 g for all scenarios (for the purpose of comparison), the equilibrium average body mass of sea cucumbers was calculated as the average mass over the final cycle of each trial, averaged over 1000 trials.

d) *Relative proportion of large cucumbers remaining:* Relative proportion of large sea cucumbers (number of individuals over 300 g divided by total number of individuals present), averaged over the last cycle. To measure depletion, this proportion was divided by the proportion of large sea cucumbers in the unfished state (year 1), and then averaged over 1000 trials.

Performance Criteria for Biological Conservation

e) *Equilibrium spawning biomass:* Spawning biomass was averaged over the final cycle, and expressed as a proportion of the initial spawning biomass (which depends on the growth and mortality rates in each scenario); this proportion was averaged over 1000 trials.

f) *Minimum spawning biomass:* The minimum spawning biomass reached within each 100-year simulation was recorded (as a proportion of the unfished spawning biomass), and the average value over 1000 simulations was used for this performance measure.

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2.9 Simulation Procedures for Insurance Areas

Suppose several areas are harvested on an adaptive rotational basis, each area taking on a different rotation schedule according to local conditions affecting the speed of recovery after harvest. As the rotation cycles of the different areas move out of synchrony, the number of areas harvested in any given year will vary depending on the differing "recovery" stages of each primary area. It is quite possible that in certain years, no area would be open to harvesting.

Therefore, I needed to determine how many insurance, or "spare" harvest areas should be set aside in order to ensure at least one harvest opening each year when an adaptive rotational harvest strategy is employed. To answer this question, I developed a simpler model, referred to here as the "insurance" model, that used the information generated by the full management model. The insurance model was designed to simulate the harvest of a number of areas with adaptive rotation, using the population of cycle lengths from the stochastic population trajectories. The insurance model included four primary harvest areas, and up to 100 insurance areas that could be opened in the event that none of the primary areas were available for harvest. Each of the primary and insurance areas were assigned a series of 100 rotation cycle lengths, by "bootstrapping" from the set of 1000 cycle lengths (the last rotation cycle of each of 1000, 100-year simulations) that resulted from the stochastic trajectories (for a particular harvest strategy and scenario).

Using these sampled cycle lengths, the model simulated an adaptive rotational harvest strategy for the four primary harvest areas, harvesting an insurance area each year in which none of the primary areas were available for harvest. The primary harvest areas were initially harvested in a staggered manner: one was harvested in each of the first four years. After the first harvest, each primary area was harvested in rotation according to the set of re-sampled cycle lengths. After an insurance area was harvested, it was then subject to its own recovery schedule (re-sampled cycle lengths) and could not be harvested until recovered, but also was only harvested when needed. If the insurance area that was harvested first was not "ready" by the next time an insurance area was required, a second insurance area was harvested. Additional insurance areas were harvested as needed, to ensure that at least one harvest area was open each year. Rotational harvest of this multi-area system was simulated for a 100-year time period, for each of the two adaptive rotational harvest strategies under each scenario of population

dynamics. For each combination of harvest strategy, harvest rate (50% and 75%), and scenario of population dynamics, I ran 1000 simulations (trials), producing 1000 results of the total number of insurance areas that were used in each 100-year trial.

When fishery managers decide the number of insurance areas to set aside, the goal would be to avoid having no area ready to open for harvest in any given year. From simulation results, I estimate the probability of having no harvest openings, given different numbers of insurance areas set aside. The number of insurance areas that is predicted to have a near-zero probability of no harvestable areas is taken to be the maximum number of insurance areas used in a 100-year period, in any one of the 1000 trials. For each combination of harvest strategy, harvest rate (50%, 75%) and scenario of population dynamics, statistics were calculated as follows:

a) The maximum number of insurance areas used in a 100-year period, over all trials; this is the number associated with a predicted ~0% probability of no harvest openings

b) The median number of insurance areas used in a 100-year period, over all trials

c) The 95th percentile of the number of insurance areas used in a 100-year period (50th highest of 1000 trials); this is the number associated with a predicted 5% probability of no harvest openings

d) The probability of having no area available to harvest in any given year versus the number of insurance areas available.

e) the mean proportion of years in which an insurance area was used

3 RESULTS

3.1 Deterministic Comparison of Harvest Strategies

Deterministic simulations of annual, fixed, and adaptive rotational harvest strategies reveal their theoretical underlying properties, unaffected by observation error and variability in recruitment.

3.1.1 "Optimal" Rotation Cycle Length

The rotation cycle length that resulted in the highest mean annual yield from the fishery, given a 50% proportional harvest rate, depended on the scenario of population dynamics that the model assumed. Curves of yield versus harvest rate for different fixed cycle lengths represent the different population dynamics scenarios (Figures 5a through 5e). The "optimal" cycle length (that which maximized yield) differed among scenarios of population dynamics (Table 5). This result supports the idea that a fixed rotation cycle is not appropriate for all areas, given that population dynamics probably vary by location and over time.

3.1.2 Can an adaptive rotational strategy correctly identify the "optimal" rotation cycle?

Although it is impractical to accurately estimate the productivity or recruitment dynamics of a sea cucumber stock, simulation results show that, simply by using biotic feedback rules, the adaptive rotational harvest strategies resulted in the "optimal" rotation cycle length for a wide range of scenarios (Table 5) Both adaptive strategies achieved the "optimal" cycle length under base-case conditions (2 years) and under scenarios of low and high productivity (3 years and 1 year, respectively). However, under low productivity, while the final cycle length of HWR was "optimal", the cycle length varied in the pattern of 2, 3, 3, 2, 3, 3, etc., thus the average cycle length is 2.67 years, which is below the "optimal" period of 3 years. The variable cycle length was due to the assumption that harvesters are more selective (i.e., take larger animals) when density is higher. After the second 3-year recovery period (Figure 6), both mean mass

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and population density are relatively high. Because relatively larger animals are selected during harvest, the "impact" of harvest is lower and recovery to the threshold mean mass takes only 2 years. However, mean mass is only slightly above the threshold and density is relatively lower, at the time of harvest, than at the previous harvest event. Consequently, smaller animals are selected, leading to a 3-year recovery period for the following cycle.

Under a scenario of strong recruitment-compensation, both "Harvest when ready" (HWR) and "Harvest then adjust" (HTA) resulted in a cycle length of 2 years whereas the "optimal" cycle length was 1 year. This longer-than-"optimal" cycle is a result of harvest control rules designed to allow average body mass to recover to 260g; thus, some yield is sacrificed to maintain the size of sea cucumbers.

Similarly, under a scenario of weak recruitment-compensation, HTA resulted in a longer rotation cycle length (10 years) than that which maximized yield (5 years). This result was due to the harvest control rule that requires population density to recover to 15 cpms. Also, HWR resulted in an average cycle length of 6.5 years; in both strategies, some yield is sacrificed in order to maintain the density of the sea cucumber population above the recovery target. However, the cycle length of HWR alternated between 4-year and 9-year periods. In this case, the varying cycle length was due to an effect of harvest on age-structure leading to patterns of recruitment that differed between the 4-year and 9-year periods (Figure 7). When the density threshold was met and harvest occurred after 9 years, recovery occurred more quickly due to a high relative abundance of older, fecund animals and thus high recruitment in the years prior to harvest. The result was a relatively fast recovery of population density after harvest, as juveniles entered the adult habitat according to the availability-at-age schedule. In contrast, after 4 years, the density threshold was met, but most of the animals were young (and less fecund); the associated low level of recruitment prior to harvest resulted in fewer animals entering adult habitat and contributing to the recovery after harvest (thus the lower drop in density following harvest, relative to that after a 9-year recovery period, Figure 7). The "hole" in recruitment created by this relatively-greater harvest "impact" resulted in a delayed effect on population density mid-way through the cycle, and a total period of 9 years until the density threshold was again reached. Regardless of this variability, HWR reaches the cycle lengths that enable population density to recover to the target threshold for recovery.

The result that HWR and HTA exceed the "optimal" cycle length under certain scenarios indicates the biologically conservative nature of an adaptive rotational harvest strategy: the cycle length is adjusted to ensure that both population density and mean body size meet the designated targets for recovery.

3.1.3   Performance of annual, fixed and adaptive rotational harvest strategies

The long term yield and spawning biomass levels vary across annual, fixed, and adaptive rotational harvest schedules, assuming a 50% harvest rate (Figures 8 and 9, Appendix 2 (deterministic)). Consistent with longer rotation cycles, the adaptive HWR and HTA strategies generally resulted in higher spawning biomass (Figure 8) and mean annual catch (Figure 9) than annual harvest, with two exceptions. First, for a scenario of high productivity, both adaptive strategies led to annual harvest and the results were identical to the annual strategy. However, annual harvest resulted in spawning biomass below 20% of original levels in all scenarios except high productivity (Figure 8). Second, when recruitment-compensation was high, catch was slightly lower for the adaptive strategies than for the annual strategy (Figure 9), but the annual strategy resulted in lower spawning biomass. The relative results in terms of catch and spawning biomass are consistent with both HWR and HTA reaching longer-than-"optimal" cycle lengths under this scenario (Table 5).

For a given scenario, the spawning biomass increased with the fixed rotation period (Figure 8, annual and fixed rotation periods). For scenarios of high productivity, strong recruitment-compensation, and the base-case, HWR and HTA resulted in lower spawning biomass than fixed periods of 3, 4, and 5 years (Figure 8) due to shorter cycle lengths, but with higher catches (Figure 9). However, for the scenario of weak recruitment-compensation, the adaptive strategies resulted in higher spawning biomass than any of the fixed rotation-period strategies, as well as higher yields. The adaptive strategies are robust to uncertainty in population dynamics. By adjusting the rotation cycle length to meet recovery targets, these strategies provided yield comparable to or higher than the yield from any fixed rotation period, while maintaining a spawning biomass between 20% and 50% of initial levels. Recognising that an 80% decline in spawning biomass may not be acceptable, conservation performance could be easily improved by increasing the minimum threshold for recovery of population density used in

the adaptive rotational harvest strategies (I defined this threshold at only 30% of initial population density).

For the base-case, high productivity, and strong recruitment-compensation scenarios, spawning biomass (Figure 8) and catch (Figure 9) were identical between the two adaptive rotational harvest strategies, due to identical cycle lengths. However, under low productivity, HTA resulted in higher spawning biomass and slightly higher catch than HWR. This result is due to the stage at which the 100-year simulation ended within the latter strategy 's variable cycle-length pattern: ending on the 3-year cycle that occurred just after a 2-year cycle (Figure 6). In this final rotation cycle (from which results are calculated), relatively low population density on average resulted in lower yield and spawning biomass; average results over the final three cycles may be higher. As it stands, HTA resulted in both higher spawning biomass and catch than HWR under a scenario of low productivity.

Similarly, under weak recruitment-compensation, HTA resulted in higher spawning biomass than HWR, but lower catch, due to HWR's shorter cycle length. Catch was higher for HWR for this scenario because the cycle length was 3.5 years shorter on average than that of HTA. In comparison, for low productivity, HWR's cycle length was only 0.33 years shorter on average, and catch was lower due to the stage within the pattern of variable cycle lengths at which the final cycle occurred.

3.2 Stochastic Comparison of Harvest Strategies

In the deterministic analysis, the adaptive rotational harvest strategies resulted in higher yield than fixed rotational harvest strategies across a range of scenarios of population dynamics, and higher spawning biomass under a scenario of weak recruitment-compensation. Thus, fixed rotational harvest strategies were excluded from this next step of comparison of strategies under realistic, stochastic conditions. From the stochastic simulations, Under most scenarios, the adaptive strategies performed similar to, or better than, annual harvesting at the MSY harvest rate specific to each scenario. (Figures 10 – 15, Appendix 3).

3.2.1   Long term yield and inter-annual variability in yield

Performance of alternative strategies in terms of yield (harvest) is shown in row (a) of Figures 10 through 15 for scenarios of base-case, low and high productivity, and

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weak and strong recruitment-compensation, respectively. For all scenarios, HWR and HTA resulted in similar or higher mean annual harvest, at both proportional harvest rates of 50% (column 1) and 75% (column 2), than annual harvest at the MSY harvest rate, which assumed perfect knowledge and implementation of the MSY rate specific to each scenario of population dynamics.

Under a scenario of high inter-annual variability in recruitment, the yield advantage of HWR over MSY is most pronounced (Figure 15a), even though MSY assumed a much lower harvest rate (26%). The reason for lower harvest in the annual strategy was that, due to great variation in recruitment and thus population density among years, a 26% proportional harvest rate more frequently compromised the ability of the population to recover than it would under less variable conditions. In contrast, HWR required the population to recover to set thresholds, thus resulting in higher harvest (Figure 15a), but a highly variable cycle length (Figure 15e).

Under all scenarios, mean harvest was higher for HWR than HTA (row a), due to the shorter mean cycle length of HWR (row e); these relative results held true for both the 50% harvest rate (left column) and the 75% harvest rate (right column). Within each scenario, mean harvest of the adaptive strategies differed little between 50% and 75% proportional harvest rates because both strategies reached a longer cycle length at the higher harvest rate in order to meet recovery targets for mass and/ or density.

Variability in yield is illustrated by the range of the distribution of harvest results among simulations (row (a) of Figures 10 through 15). For most scenarios, the adaptive rotational harvest strategies resulted in higher inter-annual variability in harvest than the annual harvest strategies, as exemplified in the base-case scenario (Figure 10a). However, under a scenario of high recruitment variability (Figure 15a), harvest was more variable than in the base-case, for the adaptive and annual harvest strategies.

Comparing the two adaptive rotational harvest strategies reveals a trade-off between yield and variability in yield. Mean annual harvest was greater for HWR than for HTA, for all scenarios of population dynamics, as exemplified in the base-case scenario (Figure 10a). The harvest advantage of HWR over HTA, like its advantage over MSY, is most pronounced for high recruitment variability (Figure 15a). Here, the average cycle length for HWR was 3.4 years (Figure 15e), with more than double the harvest of the less flexible HTA (which harvested less frequently at an average cycle length of 6.3 years). While harvest was higher in HWR, it was also more variable than that of HTA in

all scenarios. Higher inter-annual variability in harvest for HWR was a result of the more variable cycle length for this harvest strategy.

3.2.2 Mean Individual Body Mass

The conservation and economic advantage of the adaptive rotational harvest strategies over annual harvest in terms of mean individual body mass of sea cucumbers is clearest under scenarios of low productivity and strong recruitment-compensation. Results are shown in terms of mean body mass at equilibrium and can be compared to the initial, unfished mean body mass of 310g assumed in the model.

Under a scenario of low productivity (slow-growing sea cucumbers), HWR and HTA resulted in a mean body mass close to 260g (Figure 11b) at a 50% harvest rate (column 1) and slightly lower (245 to 255 g) at a 75% harvest rate (column 2). In contrast, MSY resulted in a mean mass of 240 g, with a lower range of values, despite the relatively low harvest rate of 22% for this scenario. Mean mass results for MSY also ranged to below 200 g, while the minimum value for mean mass was substantially higher for the HWR and HTA. More strikingly, under a scenario of strong recruitment-compensation (if numbers recovery quickly after harvest), HWR and HTA again maintained the mean body mass close to 260 g, while MSY resulted in mean body size reduction to approximately 200 g (Figure 14 (b)), due to the high MSY harvest rate (90%) in this scenario. Under all scenarios, adaptive rotational harvest strategies resulted in a mean body size of approximately 260g or higher, due to harvest control rules that adjusted the cycle length so that mean body mass of individual sea cucumbers met the target threshold of 260g.

3.2.3 Proportion of "large" sea cucumbers remaining

The adaptive rotational harvest strategies showed an even greater advantage over annual harvest in terms of the relative proportion of "large" sea cucumbers (300 g or more) in the population than in terms of mean body mass. As with mean body mass, this advantage was most clear under scenarios of low productivity and strong recruitment-compensation. Results are shown in terms of the proportion of large animals in the population as a fraction of the initial, unfished proportion of large animals.

Under a scenario of low productivity, the mean relative proportion of "large" sea cucumbers was greater for HWR and HTA than for MSY (Figure 11c) at an annual

harvest rate of 22%. Under strong recruitment-compensation (Figure 14c), the MSY harvest rate was 90%, which in comparison to the former scenario, resulted in a far lower proportion of large animals relative to that of the adaptive strategies. Also, the advantage of HWR and HTA over annual harvest was greater for this performance criterion (Figure 14c) than for average body mass (Figure 14b). Thus, compared to annual harvest, the longer rotation cycle of the adaptive strategies allowed for not only larger sea cucumbers on average but a far greater proportion of large sea cucumbers in the population. This result represents an economic advantage in terms of potential product price per lb because larger sea cucumbers are favoured by the market, as well as a conservation advantage because there are more animals of spawning size in the population.

3.2.4   Spawning stock biomass

The adaptive rotational harvest strategies resulted in similar or higher spawning stock biomass levels compared to annual harvest at the MSY harvest rate, for most scenarios. While HWR and HTA resulted in equilibrium levels of spawning stock biomass at over 20% of unfished levels for most scenarios (Figures 10d 11d, 12d, 14d, and 15d) the exception was weak recruitment-compensation (Figure 13d). This scenario assumed such a low recruitment rate (at low stock size) that, for a 75% proportional harvest rate, a frequent result among simulations was that HTA did not increase the cycle length quickly enough for the population to recover within the 100-year simulation. At this harvest rate, HWR resulted in higher spawning biomass than HTA (column 2), although the relative performance was reversed at a 50% harvest rate (column 1). In contrast to the spawning biomass results of the adaptive strategies, which assumed high harvest rates, MSY led to depletion below 20% of original spawning stock biomass levels under scenarios of low productivity (Figure 11d) and recruitment-compensation (13d), and high variability in recruitment (15d), despite low harvest rates (22%, 10%, and 26%, respectively).

Consistent with longer rotation cycle lengths and lower harvests, HTA resulted in higher spawning stock biomass levels than HWR for most scenarios of population dynamics with the exception of weak recruitment-compensation when combined with a 75% harvest rate.

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3.2.5   Comparison of Harvest Strategy Performance across Criteria

The low productivity scenario (Figure 11) best illustrates the advantages of the adaptive strategies relative to annual harvest, in terms of conservation and economic criteria. HWR and HTA resulted in similar or higher harvest (a) than MSY, but with higher mean body mass (b), higher proportion of large animals in the population (c), and larger spawning biomass (d). Under scenarios of base-case (Figure 10), high productivity (Figure 12), and low resilience (Figure 13), MSY resulted in mean mass, proportion large, and spawning biomass levels closer to those of the adaptive strategies than in the other scenarios. However, the annual strategy assumed that the MSY harvest rate could be achieved in practice, while the adaptive rotational harvest strategies assumed relatively high harvest rates that are more realistic for the commercial dive fishery.

Within each scenario, (Figures 10 to 15, respectively), the relative performance of harvest strategies was similar between 75% and 50% proportional harvest rates (columns 1 and 2, respectively). For example, in the low productivity scenario (Figure 11), the relative harvest levels among harvest strategies (row a) at a 75% harvest rate was similar to those at a 50% harvest rate. Likewise, the relative performance among harvest strategies, in terms of each other criterion in turn (rows b through e), differed little between harvest rates. The only result that changed was the cycle lengths; both HWR and HTA adjusted to a longer average cycle length when the harvest rate was higher. This adaptive property allowed the conservation and economic performance of these harvest strategies to be relatively unaffected by uncertainty in the harvest rate.

3.3   Harvest Insurance Areas

Given that a deterministic analysis revealed theoretical advantages of adaptive rotational harvest strategies over fixed rotation and annual harvest strategies, and a stochastic analysis showed promising performance in terms of economic benefit and population conservation, further exploration into the practical application of an adaptive strategy is warranted. Thus, I looked at a hypothetical situation where four primary areas are designated for adaptive rotational harvest, and one area must be harvested each year to support the sea cucumber fishing industry. Because rotation cycle lengths will vary by area and by year, one would expect that in some years, none of the four primary areas will be "ready" for harvest. Managers and harvesters would like to avoid this situation at all cost because it would result in zero fishing opportunities in some years.

Thus, some number of secondary harvest areas, or "insurance" areas must be available to ensure that there is always at least one area available for harvest.

The number of insurance areas that is associated with a less than 0.1% chance of no harvestable areas (probability = 0.001) is the maximum number of insurance areas used in a 100-year period in any of the 1000 simulations. To explain, this number of insurance areas ensured at least one harvestable area every year for all 1000 simulations; the probability that more insurance areas would be required is less than 1/1000. This maximum number varied according to the scenario of population dynamics considered. In the base-case scenario, given a 50% proportional harvest rate, the maximum number of insurance areas used was 3 for HWR, and 4 for HTA (Figure 16a); these numbers increased by 1 for a 75% harvest rate (Figure 16b). The highest numbers of insurance areas were used under a scenario of weak recruitment-compensation: at a 50% proportional harvest rate, HTA used a maximum number of 15 (Figure 16a), but at a 75% harvest rate, HWR used a greater number, at 16 (Figure 16b). Appendix 4 lists the full results of insurance model simulations.

Because a 75% proportional harvest rate resulted in longer rotation cycles, on average, than a 50% harvest rate, the maximum number of insurance areas used also increased with the harvest rate within each scenario, as can be seen in comparing Figure 16a and 16b. Under most scenarios of population dynamics, and at both harvest rates tested, HWR used fewer insurance areas than HTA. This difference is due to HWR's shorter cycle length on average. Similarly, the proportion of years in which an insurance area was used (Appendix 4) was less for HWR than for HTA. However, under a scenario of weak recruitment-compensation, the cycle length of HWR was much more variable than that of HTA (Figure 13e) relative to other scenarios, leading to the result that HWR used more insurance areas than HTA in that case.

As you increase the number of insurance areas set aside, you reduce the probability of no harvestable areas in any given year; however, this probability also depends on the harvest strategy, proportional harvest rate, and scenario of population dynamics. For HWR, at a 50% harvest rate, Figure 17 illustrates the probability of no harvestable areas for different numbers of insurance areas set aside. A probability of no harvestable areas of less than 0.001 is associated with the maximum number of insurance areas used by the model, under a given scenario of population dynamics. Figure 18 shows these results for HTA at a 50% harvest rate; because the strategy

required more insurance areas in general, the probability curves are shifted further to the right than in HWR (Figure 17). In other words, for a given probability of no harvestable areas that managers might choose as acceptable (for example, 0.05), the number of insurance areas required is greater for HTA, within each scenario. These general results were similar for a 75% proportional harvest rate, but with greater numbers of insurance areas required due to the longer cycle lengths of both adaptive strategies.

4 DISCUSSION

Because population dynamics of sea cucumbers are poorly understood and likely to vary both spatially and temporally, not one of the scenarios of population dynamics I simulated is "correct"; to estimate with any level of certainty the population characteristics of a given area is impractical. Therefore, a harvest strategy that performs relatively well under a range of scenarios is the most robust to that uncertainty. By using biotic feedback to determine the appropriate level of harvest, the adaptive rotational harvest strategy adheres to the "precautionary approach" based on objective, measurable criteria.

My results showed that the adaptive rotational harvest strategies adjusted the cycle length to suit a range of scenarios of population dynamics. The deterministic analysis showed that, at a realistic local harvest rate of 50%, simply by monitoring recovery in body mass and population density, the adaptive strategies identified the economically "optimal" cycle length for each scenario, except in scenarios where a long cycle was required to meet conservation constraints. In contrast, annual harvest at 50% performed poorly in terms of yield and conservation for most scenarios.

The stochastic analysis showed that the adaptive strategies prevented undesirable levels of depletion of the mean body mass of animals, proportion of large animals in the population, and spawning biomass, while allowing for high local harvest rates of 50% and 75%. The adaptive rotational harvest strategies generally resulted in similar or higher yield, and often better conservation performance, than even the most optimistic case for an annual fishery where the MSY harvest rate is exactly achieved. Although both "Harvest when ready" and "Harvest then adjust" were robust to most types of uncertainty, HTA (as implemented here) was not robust to very weak recruitment-compensation and a high harvest rate.

In addition to adapting to different scenarios of population dynamics, the result that the adaptive strategies compensated for different local harvest rates by adjusting the rotation cycle length in order to meet recovery targets is important, because localised harvest rates are difficult to control and can be very high in the sea cucumber fishery.

The two adaptive strategies represent a trade off between harvest, temporal stability, and conservation: HWR resulted in higher but more variable harvest than HTA, and with lower spawning biomass. The insurance area analysis showed that between-year variability in harvest under adaptive rotational harvest strategies can be mitigated by employing a number of insurance areas, depending on the desired level of precaution against a shortage of areas available to harvest.

In light of uncertainty, the result that adaptive rotational harvest strategies generally performed better than annual harvest under a range of scenarios implies that these strategies are more appropriate for the sea cucumber fishery. These general conclusions have implications for similar fisheries for sedentary species where the rate of recovery from harvest might vary spatially and temporally, and where localised harvest rates are high due to fishing methods that require effort concentration, such as SCUBA diving.

Like this study, other modelling studies of rotational fishing converge on the result that increasing the rotation period allows higher spawning density (Pfister, 1996; Myers et al. 2000; Zhang and Campbell, 2002). Botsford et al. (1993) state that for broadcast spawning invertebrates, "Rotating spatial harvest could result in greater recruitment by concentrating breeding stock into aggregations where spawning success is maximized".

However, these same studies differ on the question of whether rotational fishing can provide higher yields than annual fishing. I found that yield was maximised at rotation periods greater than 1 year in all scenarios of population dynamics except high productivity and recruitment-compensation, and was positively related to the harvest rate. Similarly, Myers et al. (2000) found that yield from the American sea scallop fishery would be maximized at longer rotation cycles as fishing mortality increased. Lai and Bradbury (1998) found that, over a wide range of harvest rates for the red sea urchin, mean annual yield increased with cycle length, and that these increases were greater at higher harvest rates. Conversely, other studies predicted lower yields for rotational, as opposed to annual, harvest (Pfister and Bradbury, 1996; Botsford, 1993). The likely reason for the difference is that, for the red sea urchin, these authors assumed both high growth rates, and relatively low harvest rates (ranging from below 25% to 40%) fitted to size frequency and population census data. These studies did not explore higher harvest rates, which might occur on a small scale in dive fisheries. While my deterministic results

for a high-productivity scenario indicate higher yields under annual harvest in this range of harvest rates, I found that yield is maximized at longer rotation periods if harvest rates are higher.

Zhang and Campbell (2002) predicted that, to maintain the spawning stock biomass at a given target level, the proportional exploitation rate required in rotational fishing is lower than in annual fishing, and concluded that yield must also be lower. In comparing rotation schemes, they standardised the exploitation rates for rotation fisheries to the exploitation rate for a 1-year rotation (annual) fishery by dividing them by the number of years of rotation (in other words, a 30% exploitation rate for a 3-year rotation fishery is equivalent to 10% for an annual fishery). Results of my study disagree with their assumption that lower standardised exploitation rates in rotational fishing would imply lower yields than annual fishing. The deterministic analysis predicted that, for some scenarios, fishing at longer rotation cycles would result in higher yields than annual fishing over a range of exploitation rates, often below the standardized annual equivalent. Similarly, a modelling study of geoduck clams (Breen, 1992) predicted that longer rotation cycles would result in decreased yield; however, the model assumed very low harvest rates, standardising rotational harvest to the annual exploitation rate (e.g. three times the annual harvest rate for a three year rotation). While managers might assume this harvest rate structure when calculating catch limits, if effort is concentrated, escapement as a proportion of the population in commercially attractive fishing areas will be similar regardless of the number of years between harvest events. For such fisheries, comparing rotational harvest at high exploitation rates with annual harvest at lower exploitation rates is largely theoretical, because localised harvest rates are likely to be high regardless of harvest frequency.

In addition to higher yields, Lai and Bradbury (1998) also found that inter-annual variability in yield decreased with increasing rotation cycle length. This result indicates not only an advantage of rotational over annual fishing, but a trade-off between yield and yield variability when comparing strategies of fixed rotation period versus adaptive rotation. While the latter strategy could potentially provide higher yields via its ability to shorten the rotation cycle under favourable conditions, this flexibility is likely associated with more variable yield than a strategy of fixed rotation period. My results cannot be directly compared with these because I did not compare fixed-rotation with adaptive rotation strategies in my stochastic analysis.

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4.1 Comparison of Harvest Strategies

An annual harvest strategy may pose serious conservation concerns in "favourite" fishing locations where localized harvest rates are high. Under deterministic conditions, annual harvest at a 50% harvest rate compared favourably with rotational harvest, as long as productivity was high. However, annual harvest at 50% was not robust to low productivity or recruitment-compensation, resulting in low-to-negligible harvest. This result was due to local population collapse, as evidenced by low-to-negligible spawning biomass. Even if recruitment-compensation was high, annual harvest resulted in low spawning biomass.

In the stochastic analysis, even the most optimistic annual harvest strategy (MSY), which assumed managers had perfect knowledge and were able to achieve the MSY harvest rate, was not robust to unfavourable conditions. Under a scenario of weak recruitment-compensation, this strategy failed even at a relatively low harvest rate (10%); low spawning biomass was likely a result of recruitment-overfishing. Annual MSY was also not robust to high variability in recruitment: spawning biomass and harvest were far lower than in the base-case. This result was caused by a higher frequency of weak recruitment events under this scenario, leading to periods of low population abundance. Consequently, annual harvest at a theoretical MSY harvest rate of 26% produced a higher probability of over-harvest than under conditions of less variable recruitment.

In contrast, HWR is robust to uncertainty in population dynamics, as shown by reasonable harvest and conservation performance under adverse scenarios. The strategy's good performance in terms of spawning biomass and sea cucumber average body mass, under scenarios of low productivity and recruitment-compensation, result from harvest control rules that do not allow any harvest before the population recovers to target thresholds for population density and average body mass. This strategy's high harvest performance relative to other harvest strategies, particularly under high variability in recruitment, results from an annual monitoring scheme that allows the fishery to take advantage of strong recruitment events that have sped population recovery.

If localised harvest rates are as high as 75%, HTA is robust to uncertainty in productivity, but not to weak recruitment-compensation. Low spawning biomass and harvest levels under this scenario highlight a flaw in the design of this particular harvest

strategy as tested. Unlike HWR, there is no annual monitoring of population density or average body mass to rule out harvest before recovery targets are met. The trade-off for the more industry-acceptable and lower-cost attribute of harvesting areas when planned (and then adjusting the rotation cycle length if needed) is the chance of harvesting before the population has recovered. The weak recruitment-compensation scenario assumes very low recruitment levels at low stock abundance and, at a 50% harvest rate, requires an average of 10 years (the cycle length achieved by HWR) to meet recovery targets. However, as implemented in this study, HTA starts with a 4-year rotation and only lengthens the cycle by one year at a time (each time the population assessment, carried out at the time of harvest, reveals a shortfall in recovery of population density). This harvest control rule allows the population to be depleted even as the cycle length is adjusted. A simple solution would be to change the control rules: increase the rotation cycle by more than one year, depending on the magnitude of the recovery shortfall. However, I did not simulate this improved strategy.

In comparing the relative performance of the two adaptive rotational harvest strategies, two trade-offs are apparent. The first is between harvest and conservation. HWR had consistently higher mean annual harvest than HTA, but HTA had higher spawning biomass, except under weak recruitment-compensation, in which case HTA resulted in very low spawning biomass. This comparison differs from the deterministic results, wherein the two adaptive strategies showed identical cycle lengths and harvests. Lower harvest for HTA was due to a longer mean cycle length than HWR under stochastic recruitment. Longer rotation cycles reflect the former strategy's less flexible nature, which results from its different control rules. While HWR allows re-harvest as soon as recovery targets for body mass and population density are met, HTA (as implemented here) can only adjust the cycle length by 1 year at a time; it cannot jump from a 6-year cycle to a 2-year cycle, for example. Consequently, the cycle length in HTA was not only shorter, but less variable across years. Higher variability in the rotation cycle length for HWR resulted in higher inter-annual variability in harvest, presenting a second trade-off: that between harvest and harvest stability. While HWR provides more harvest, HTA provides consistently more stable harvest, as well as higher spawning biomass.

That the performance of both adaptive rotational strategies was changed little by different harvest rates is a significant result because the harvest rate is not easily

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regulated in the sea cucumber fishery, and is likely to vary both spatially and temporally. Thus, simply by using feedback from the population, an adaptive rotational harvest strategy can automatically adjust to a rotation period that is appropriate for the harvest rate that occurs in a particular area at a particular time.

4.2 Limitations

Although this analysis considered many key features of the sea cucumber population and fishery, there are still factors that have not been included, as with any model. For instance, I did not account for harvesters' self regulating behaviour; they tend to avoid fishing in low-density areas. The annual harvest model assumed that the harvest area would be harvested every year even if density had been severely depleted. While harvesters generally move on to another area if the density is lower than is economically worthwhile, low density areas are fished where the harvester has no prior knowledge of density in the area. Such would be the case with a new license holder, or an experienced license holder exploring new harvest areas (K. Ridgway, pers. comm.). To account for this possibility, and to represent potential fishing behaviour if market demand were to increase dramatically, I did not assume any density threshold below which harvesting would cease. This assumption may have resulted in unrealistically low predictions of spawning biomass for an annual harvest strategy.

Another factor omitted from this model was movement of sea cucumbers. To represent the possibility that local populations can be small and isolated, I assumed no migration between harvest areas. Because I simulated the harvest of only one area for the deterministic and stochastic analyses, this assumption meant that there was no immigration into or out of the area. Assuming no immigration may have resulted in underestimated animal size, spawning biomass and harvest. Without knowing the densities of adjacent areas relative to fished areas before and after harvest, one cannot infer the net direction of movement. If there is net immigration into the harvested area, the localized harvest rate would be lower, and recovery in density and body size faster, because the harvest would affect a larger area than that actually fished by divers. For example, harvesters may remove 50% of the population in a 1km length of shoreline, but depending on the extent of migration, the effective harvest rate might be 25% over 2km of shoreline. Conversely, assuming no emigration from the simulated area may have resulted in overestimated densities (because emigration would reduce population

density). Thus, on a larger scale than each km of coastline, the omission of immigration and emigration should balance out to no net effect or bias of results here. The rank order of management options for each performance criterion will not change. Likewise, omission of migration between the multiple simulated areas in the insurance analysis should not affect the results.

Another reason that harvest rate may be lower than I have assumed is natural refuge with depth. The fact that sea cucumbers are known to occur below harvestable depth implies that some proportion of the population may not be harvested during the fishing season. Because vertical migration has been observed in relation to spawning, some degree of mixing between deep and shallow sea cucumbers occurs, so refuge with depth will limit the harvest rate on a population inhabiting a given length of shoreline that is harvested, provided that there is suitable habitat at depth. If harvest rates are lower than I have assumed, the conservation performance of harvest strategies will be better than suggested by these results, and the rotation period required to meet recovery targets will be shorter. Nonetheless, the deterministic analysis showed that for a given harvest rate, the adaptive rotational harvest strategies identified the cycle length that maximized harvest within recovery constraints. Lower harvest rates would simply result in the adaptive strategies identifying shorter cycle lengths.

Implicit in my stock-recruitment relationship for the small simulated population is the assumption that larval dispersal and recruitment are local (i.e. recruitment is entirely from larvae produced and settled within the harvest area). Although subpopulations of marine invertebrates are linked by larval dispersal (Botsford et al. 1994), this link is likely weaker for sea cucumbers than sea urchins. Sea urchins have been the focus of much of the literature on larval dispersal, and are distributed in more exposed, high-current areas. While sea cucumbers tend to be found in areas of moderate current, harvesters target only protected inlets, channels, and bays, where currents are low, and harvesters can find relatively larger animals, which are preferred by the market (K. Ridgway, pers. comm.). Thus, local harvested populations of sea cucumbers in low-current areas likely have a smaller spatial scale of larval dispersal than for urchins. Still, the assumption of total retention of larvae in the harvest area may overestimate recruitment levels. Yet, I also assumed no settlement of larvae from external sources, which may positively affect recruitment, balancing out the effect of larval drift from the area; there should be no net effect on the results of my analyses. Because the scenario of weak recruitment-

compensation (very low recruitment after intensive harvest) is based on the unrealistic assumption that recruitment is ultra-sensitive to depletion of local spawning population, this scenario is an unlikely extreme. However, the goal is to predict whether a harvest strategy would be robust to possible adverse scenarios; if so, its performance could only improve if the true state of nature is more forgiving.

Although HTA is not robust to weak recruitment-compensation and a 75% harvest rate, the combination of these two scenarios in nature is unlikely. The occurrence of sea cucumbers below diving limits (whereas fishing generally occurs above 15 m depth) provides a natural refuge that limits the harvest rate. This effect would, however, require there to be enough suitable habitat below fishing depths to support a substantial number of animals coast-wide, and that these animals would migrate vertically, but these hypotheses are not well-documented. Also, while recruitment dynamics of sea cucumbers have not been studied, larval dispersal on a larger scale than that of targeted aggregations would make recruitment less sensitive to local stock size than the weak recruitment-compensation scenario assumes.

The spatial scale of this study is limited. For the deterministic and stochastic analyses, I simulated each alternative harvest strategy on a population within a single area. I assumed that the results from simulating repeated harvesting of this single area would represent the results that might occur for a network of areas harvested under each strategy (in other words, for the exploited population of sea cucumbers along the British Columbia coast). This assumption is reasonable, given that I simulated a range of scenarios of population dynamics that might occur in different areas, thus evaluating harvest strategies in light of uncertainty. Nonetheless, a multi-area model would allow the comparison of harvest strategies under different assumptions about migration, stock-recruitment dynamics, and how sub-populations are linked by larval dispersal. This spatial analysis is yet to be done.

4.3   Management implications

Given anecdotal evidence of decline in body size of sea cucumbers in some areas that are fished annually, rotational harvest is an attractive option for addressing this conservation concern. This simulation study predicts that increased rotation cycle length will lead to substantially larger sea cucumbers and higher spawning biomass, and higher yields for a 3-year rotation than annual harvest except under high productivity and

strong recruitment-compensation, where annual harvest yields more. An advantage of spatial rotation is that area closures would be more easily enforced than attempting to reduce localized harvest rates through diluting fishing effort in dive fisheries, where economic feasibility depends on concentration of effort. In other words, it would be easier to manage for recovery after intensive harvest than to attempt to reduce the intensity of harvest. For example, it would be extremely difficult to force vessels to travel further during the fishing season and cover shorter distances at each stop, in order to prevent intensive harvest of large areas, or to force divers to pick only one out of every five animals they encounter. My results show that rotational harvest improves the probability of recovery if harvest rates are high. However, the choice between strategies of fixed versus adaptive rotation cycle depends on management objectives. A fixed rotation cycle of 4 years, for example, will not conserve spawning biomass if harvest rate is over 50% and productivity or recruitment-compensation is low.

In addition to better performance in terms of yield and conservation under adverse scenarios, adaptive rotational harvest strategies could potentially lower management costs. The increased cost of spatially intensive management might be more than offset by lower stock assessment costs. Instead of a quota system based on estimated stock abundance, a system of adaptive rotational harvest can be managed by area closures. Small-scale surveys to measure the pre-harvest population density and average animal mass and to estimate the degree of recovery of these attributes after harvest, replaces elaborate, large scale stock assessment. The cost of enforcing spatial closures need not be prohibitive if non-compliance is suspected. Spatial closures in Australia (Queensland Government, 2005) are managed through live GPS monitoring of commercial vessels using a satellite-linked vessel monitoring system during the fishing season, so that vessel entry into a closed area is always detected. Harvesters working in this system prefer this type of regulation to one based on trust. Each vessel operator knows that no one else is fishing in closed areas, because detection and penalties are certain.

For the sea cucumber fishery in B.C., a system of individual vessel quotas works well for harvesters and management. How an adaptive rotation could be applied while retaining the quota system is a question managers may wish to pursue. In effect, quota limitation within a system of spatial rotation would likely create reserves if the prescribed

harvest rate is low, because only a portion of the area would be harvested to meet quota limits.

Whether fishery-dependent data could be used to monitor recovery of sea cucumber populations is another important management question, because small-scale scientific surveys performed prior to harvest in each spatial management unit might be cost-prohibitive, depending on the sample size required for an acceptable level of accuracy. A subsample of harvested sea cucumbers may suffice to estimate average mass. However, because harvest intensity and size selectivity varies among harvesters and between years and aggregation dynamics are also not understood for this species, using data on catch-per unit effort (number caught in a given area in a given time spent fishing) would probably not provide a reliable index of density. Overestimation of the average mass is possible where harvesters are more size-selective, but this behaviour would result in harvesters leaving more animals behind than they would otherwise, and would still work in favour of conservation. Also, misreporting of diving time is common because harvesters find it impractical to adhere to insurance-related regulations on time limits for diving. These regulations create expectations that divers find unrealistic. The use of fishery-dependent data thus requires careful study and, possibly creative approaches to ensure that harvesters could provide data with the required level of accuracy and precision.

The choice of fishing unit size represents a trade-off between better conservation, yield, and feasibility. Because little is known about the spatial scale and rate of migration of animals, it will be difficult to determine the appropriate size of fishing units. In general, smaller areas will be more homogeneous in terms of productivity and recruitment-compensation (due to more complete population mixing via migration) and thus recovery measurements more precise, so that the rotation cycle determined by the adaptive strategy will be appropriate for the whole area. Currently, quota management units for this fishery are on the scale of several hundred km of shoreline. Adaptive rotation units might, for example, be limited to several kms each. Harvesters may endorse a system of smaller area rotation because, under an adaptive rotational harvest system, greater long term yields can be obtained in productive areas when they are harvested more often, while slowly-recovering areas are harvested less often. The overall yield in this case would be substantially greater than if larger areas (for example, each 1/3 of a quota-management unit) were fished on longer rotation periods.

Smaller areas also serve precautionary management objectives concerning conservation. By managing smaller spatial units, overfishing in isolated and unproductive areas is prevented, because slower recovery within these areas leads to a longer cycle length. In contrast, if these areas have attractive commercial density and are managed within a larger spatial unit, they will be harvested on a shorter cycle determined by faster overall recovery in the management unit, which can result in relatively greater depletion of these less productive areas over time.

However, spatial management units that are too small may be cost-prohibitive, and difficult to coordinate. Larger areas may be more feasible, but care must be taken to avoid over-fishing less productive smaller areas within the larger area. For this reason, recovery measurements should be taken in areas where the harvest is concentrated, so that measurements from the slowest recovering areas identify a more conservative rotation cycle for the whole spatial unit.

Consultation with the fishing industry will be imperative in management planning for rotational harvest. In mapping out spatial fishing units, harvesters can point out high density areas ("hot spots" for fishing), which should also be detectable through spatial analysis of commercial logbook data which references harvest locations. This information, combined with survey data, could be used to delineate spatial units for harvest areas containing similar harvestable biomass. Harvesters can thus help ensure that yield is stable from one year to the next. In addition, they can quantify constraints regarding travel costs and accessibility to ports, which can be used to define a minimum feasible area. Harvesters have expressed concern that a system of small, widespread areas being harvested simultaneously would make it infeasible for buyers to pick up the landed product, as it would require travel to many different ports. This problem serves as a strong argument for a strategy of fixed rotation, where the entire fishing fleet moves to a different general area each year. Whether the potential for increased yield from adaptive rotational harvest would outweigh these concerns might be determined by future market conditions.

While unused insurance areas would serve as spawning stock reserves (at least temporarily), establishing permanent reserves would be an additional step towards precautionary management. These reserves would ideally consist of high density areas located between harvest areas on a relatively small scale; because larval dispersal distance is poorly known, this arrangement would increase the chance of providing

sources of recruitment to fished areas. How large these reserves should be is a difficult question. Whether the population in a reserve retains enough larvae to sustain itself depends on the width of the area relative to larval dispersal distance (Botsford et al. 2001). Because migration is limited in sea cucumbers, larval dispersal would be the constraining factor in determining a minimum effective size. As a management issue, reserves may become more important as market conditions for sea cucumbers improve, and harvesters find it worthwhile to fish areas of lower density.

4.4　Relevance to other species

Adaptive rotational harvest has the potential to work well as a management strategy for other fisheries for sedentary species such as clams, urchins, geoducks, and possibly certain species of groundfish. Adaptive rotation is particularly useful as a conservation mechanism where effort is concentrated and there is concern for serial depletion. Because it uses harvest control rules that ensure population recovery after harvest, this strategy provides a management tool that adheres to the "precautionary approach" based on objective, measurable criteria. Such a strategy would be ideal for fisheries in less-developed countries, where there is often little funding for stock assessment, to prevent sequential depletion and collapse of sedentary fisheries.

4.5　Future Research

Yield and spawning biomass predicted for fixed rotation-period strategies were sensitive to the proportional harvest rate, and HTA allowed severe depletion with a 75% harvest rate. Therefore research to estimate the range of localized harvest rates in the sea cucumber fishery could help in ruling out unrealistically low and/or high predictions of the performance measures for alternative harvest strategies and narrow the number of insurance areas needed for adaptive rotation strategies. Field studies could provide estimates of proportional harvest rates more precisely than those estimated through spatial analysis of fishery data. For example, surveys conducted before and after harvest could effectively estimate the proportion that is left behind by harvesters (either via size selection or harvesters not detecting animals). If a larger area than that harvested were also surveyed, the spatial pattern of change in population density may allow estimation of the size of the area affected relative to that harvested (thus pointing to the spatial extent of migration) and the actual harvest rate within the affected area. Remotely

operated video (ROV) equipment could be used to supplement these dive-surveys in order to estimate the proportion of the population distributed below harvested depths and to quantify the extent that this depth-refuge limits the harvest rate (because of post-harvest vertical migration). ROV surveys could also be used to assess the extent of vertical migration from depth and the associated effect on the localised harvest rate. Better estimates of the proportion of the population that escapes harvest could be obtained via field studies designed to quantify natural refugia. Comparing the density of sea cucumbers in areas that are targeted with unfished-areas would increase understanding of the extent to which natural refugia could develop through self-regulating fishing behaviour.

Given the failure of HTA to conserve spawning biomass under a scenario of weak recruitment-compensation and high harvest rate, research on stock-recruitment dynamics, in addition to realised harvest rates, would facilitate a decision regarding if and how the control rules need to be adjusted to guard against unacceptable depletion. Monitoring the recovery of population density after intensive harvest, and taking measurements of the length or mass of individual re-colonized animals, would improve understanding of recovery mechanisms. For example, if most of the animals are small, recruitment is the main mechanism; if most are large, immigration dominates. Trying this harvest experiment on different spatial scales could help to quantify the effect of the size of fishing units on population recovery. Another factor affecting recovery is the degree of isolation of aggregations; a harvest experiment could reveal the difference in recovery between areas with, and without, surrounding aggregations of sea cucumbers. However, because replication is required, such an experiment may not be feasible if areas with these characteristics are difficult to find. Better understanding of recruitment-compensation would also help managers to narrow the number of insurance areas needed to ensure that, in each year, a sufficient number of areas can be harvested, so as to provide more stable catch levels.

Another research question that would be useful in planning for an adaptive rotational harvest system is: how accurate are fishery-dependent versus fishery-independent measures of the recovery of population density and animal size? Estimates from different methods of data collection can be tested against more intensive scientific surveying, to determine how much information would be lost in choosing less expensive methods.

Finally, a spatially explicit model including multiple harvest areas could be used to answer several important questions. First, harvesters and processors could provide input for an economic model component to determine the size and spatial arrangement of harvest areas that would a) minimize travel cost, b) steadily provide landed product to each processing plant over the fishing season, and c) provide stable yield to the industry from year to year, given estimated population densities. Second, an economic analysis could account for survey and associated travel costs in assessing how often insurance areas as well as primary harvest areas should be re-surveyed in a "harvest when ready" strategy, or whether "harvest then adjust" is more cost-effective. Because individual vessel quotas are the preferred allocation method for this fishery, another modelling extension could evaluate the performance of a quota-based system in combination with an adaptive rotational harvest system.

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TABLES

Table 1: Population parameters used in the operating model

Parameter	Value	Source
Lifespan (t_{max})	12 years[2]	Speculative estimate of maximum age by P. Fankboner (Phillips and Boutillier, 1998)
Natural mortality (M) (annual)	0.37*	Boutillier et al. (1998) estimate M using the Hoenig (1983) model: $\ln(M) = 1.44 - 0.982\ \ln(t_{max})$
Length at maximum age (L_∞)	500mm	Maximum length is estimated at 500m (Fisheries and Oceans website); I assume this is close to length at max. age.
Age at 50% maturity	5.5 years	Mature animals are >4.6 years (Cameron and Fankboner, 1989); Individuals reach sexual maturity at 5-6 years (Fisheries and Oceans website)
Age at 95% maturity	7 years	
Age at 50% selectivity	5 years	Speculative estimates of the age at recruitment to the fishery range from 4 to 8 years (Boutillier et al. 1989).
Age at 95% selectivity	7 years	
Von Bertalanffy growth rate	0.20*	Found numerically to meet assumption of average commercial mass in an unfished state = 330 g, given selectivity at age. (some areas have higher average mass, so this growth rate may be an underestimate)
Interannual variability in recruitment (coefficient of variation)	0.5*	Recruitment variability observed for red sea urchins: 0.5 to 1.0 (Smith et al. 1998)

* these values are varied to represent the different scenarios of population dynamics described in section 2.3

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[2] The population model does not have a "plus" age class, but carries forward the survivors of age 12 into the same age class for the next year (i.e., the maximum age class is "12 plus").

Table 2: Parameter values used in the model to characterise different scenarios of productivity, recruitment-compensation, and interannual variability in recruitment. For each scenario (row), the values of parameters changed from base-case values are shown in bold font.

Scenario		Von Bertalanffy growth rate	Natural Mortality rate	Recruitment "m" parameter	Coefficient of variation in recruitment
Base-case		0.20	0.37	1.3	0.5
Productivity	low	**0.16**	**0.20**	1.3	0.5
	high	**0.26**	**0.73**	1.3	0.5
Recruitment-compensation	weak	0.20	0.37	**3.0**	0.5
	strong	0.20	0.37	**1.05**	0.5
Recruitment variability	high	0.20	0.37	1.3	**1.0**

Table 3: Alternative Harvest Strategies

HARVEST STRATEGY	CONTROL RULES	FEATURES
AFIXH: harvest every year	Harvest every year (50% harvest rate*)	• Represents fishing behaviour if market value is high: worthwhile to harvest even low density areas
MSY: harvest every year at MSY % harvest rate	Harvest every year (MSY harvest rate*: specific to productivity / recruitment-compensation scenario)	• Best-case scenario for an annual harvest • Assumes perfect knowledge of life history parameters at each site, and appropriate effort dispersal
Fixed rotation (FR): 3,4, and 5-years	Harvest every 3, 4, or 5 years (50% harvest rate*)	• Rotation cycle length remains constant
"Harvest when ready" (HWR): Harvest when average body mass and population density have recovered	Harvest only in years when: Avg mass>260g AND Density> 15cpm (Figure 4a) (50% or 75% harvest rate*)	• Requires annual monitoring • Cycle length for each area is most variable
"Harvest then adjust" (HTA): Start at cycle length = 4 years, harvest when planned, and then adjust cycle length if appropriate (based on estimates of density and average mass from data collected prior to harvest	Extend cycle length if: Avg mass<260 g OR Density < 15 cpm Shorten cycle length if: Avg mass > 280 g AND Density >30 cpms (Figure 4b) (50% or 75% harvest rate*)	• Areas are harvested when due • Avoids wasted travel cost to remote sites • Monitor individual masses and population density only in harvest years (prior to harvest)

* Harvest rates are proportional, defining the proportion of the vulnerable population that is harvested in each harvest year. Only the stochastic analyses (Objectives 2 and 3) tested 75% harvest rates.

Table 4: Proportional MSY harvest rate calculated for scenarios of low, medium, and high productivity and numerical-recovery.

Scenario		MSY harvest rate
Base-case		0.26
Productivity	Low	0.22
	High	0.48
Recruitment-compensation	Low	0.10
	High	0.90

Table 5: Cycle lengths achieved by adaptive rotational harvest strategies, compared to economically "optimal" cycle lengths.

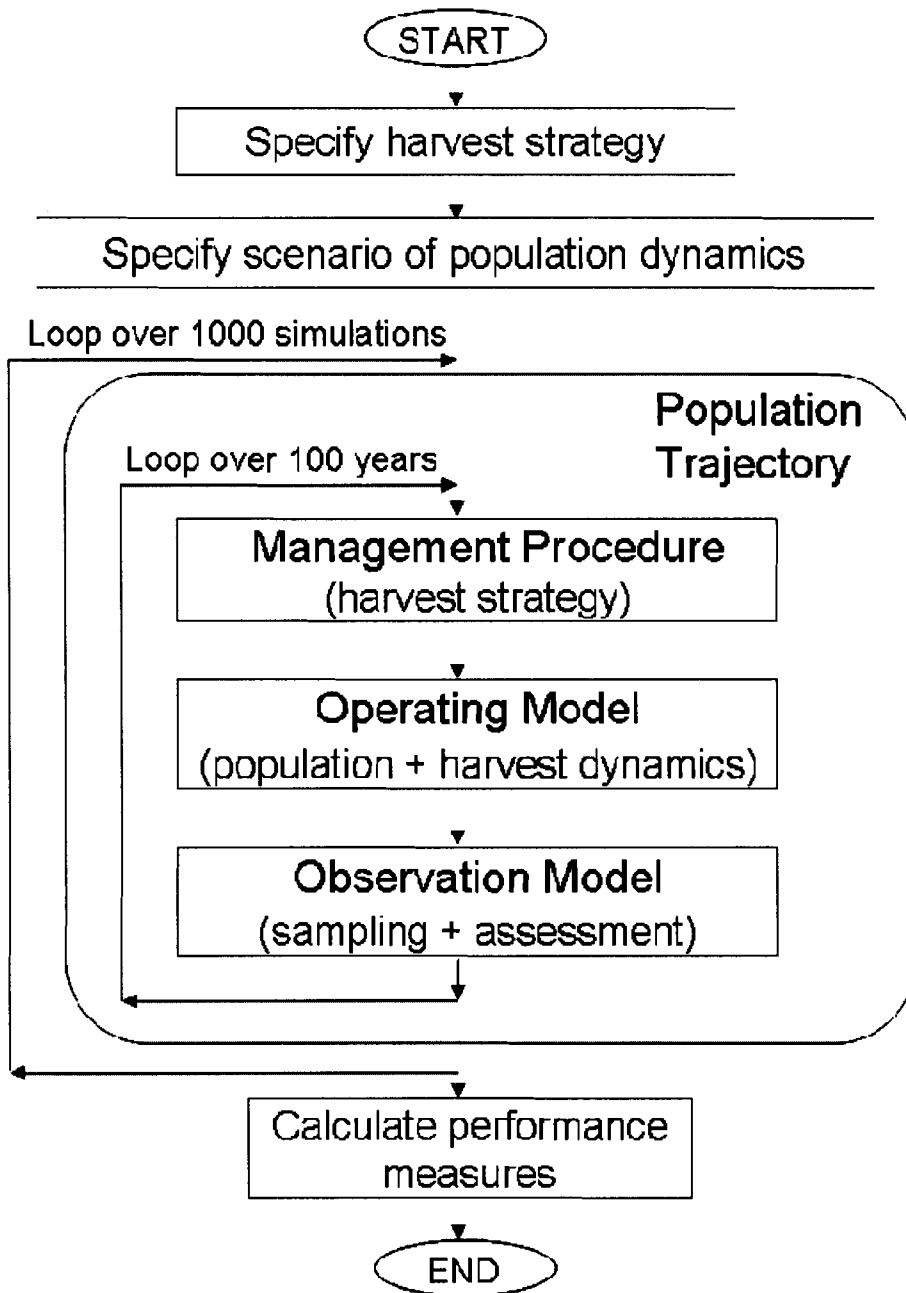| Scenario		"Optimal" cycle length (years)	Cycle length achieved (years)	
			Harvest when ready	Harvest then adjust
base case		2	2	2
productivity	low	3	2,3,3,2,3,3...	3
	high	1	1	1
recruitment	low	5	4,9,4,9...	10
compensation	high	1	2	2

FIGURES

Figure 1: Simulation modelling framework used for evaluating harvest strategies. For the deterministic analysis, only one simulation was performed for each combination of harvest strategy and scenario of population dynamics.

Figure 2: Selectivity as a function of age, at population densities of 40 cpms (dash-dotted line), 30 cpms (dashed line), and 25 cpms (dotted line). Availability of sea cucumbers as a function of age is shown by the curve furthest to the left (solid line).
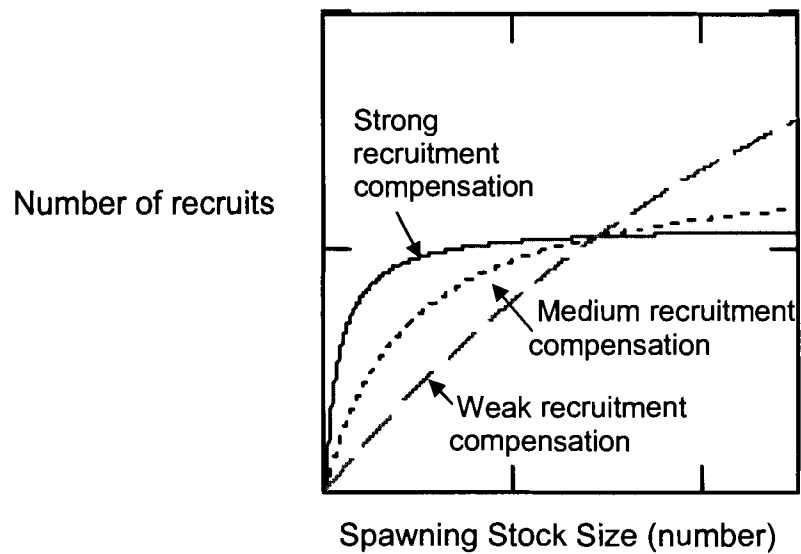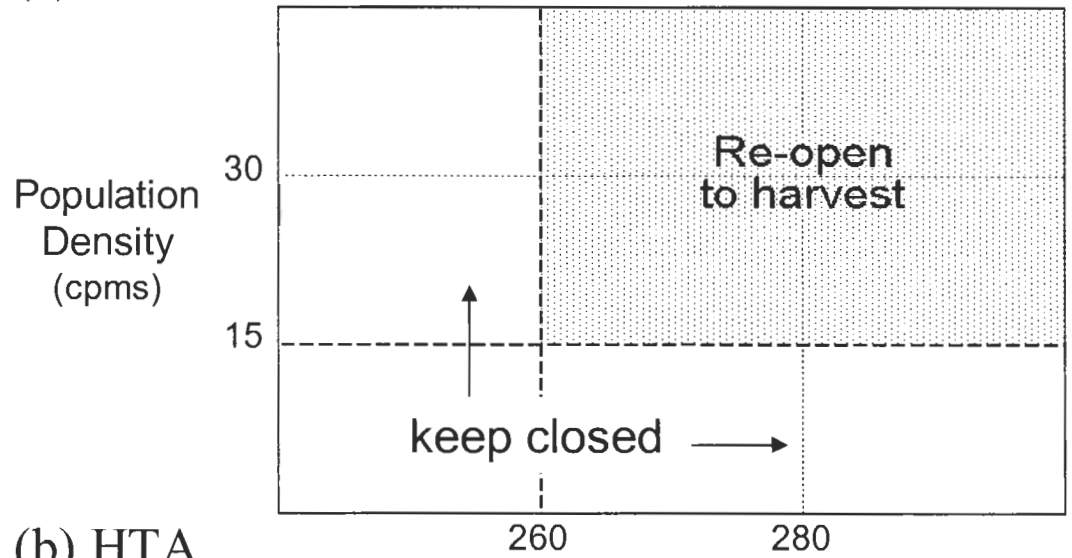

Figure 3: High, medium and low levels of recruitment-compensation (recruitment "m" parameter = 1.05, 1.3 and 4.0, respectively) as a function of spawning stock size.
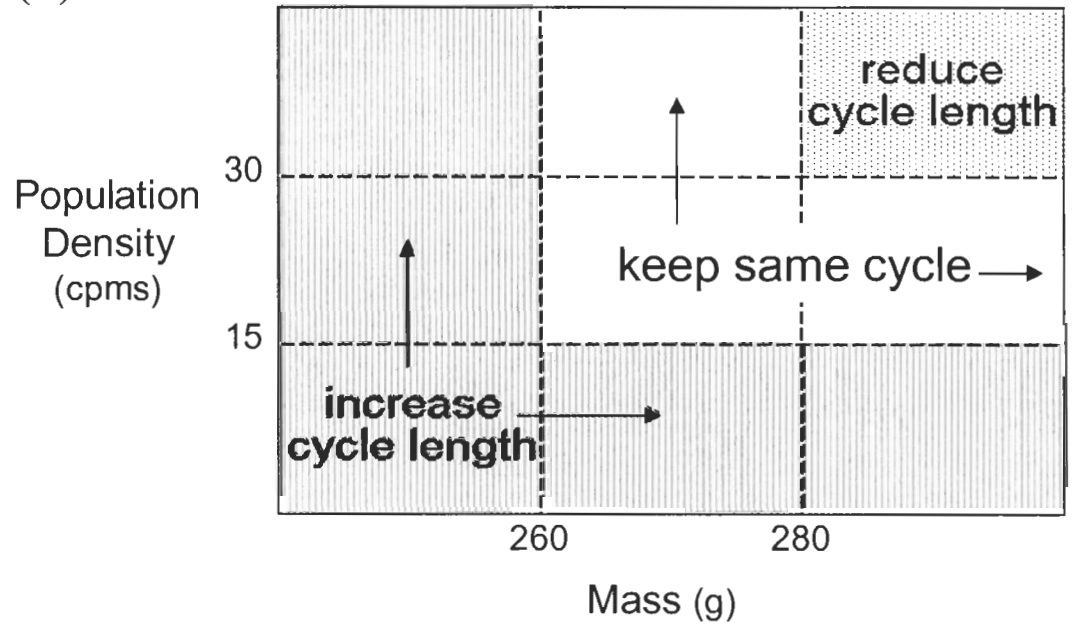
Figure 4: Harvest control rules for adaptive rotational harvest strategies (a) harvest when ready (HWR) and (b) harvest then adjust (HTA).
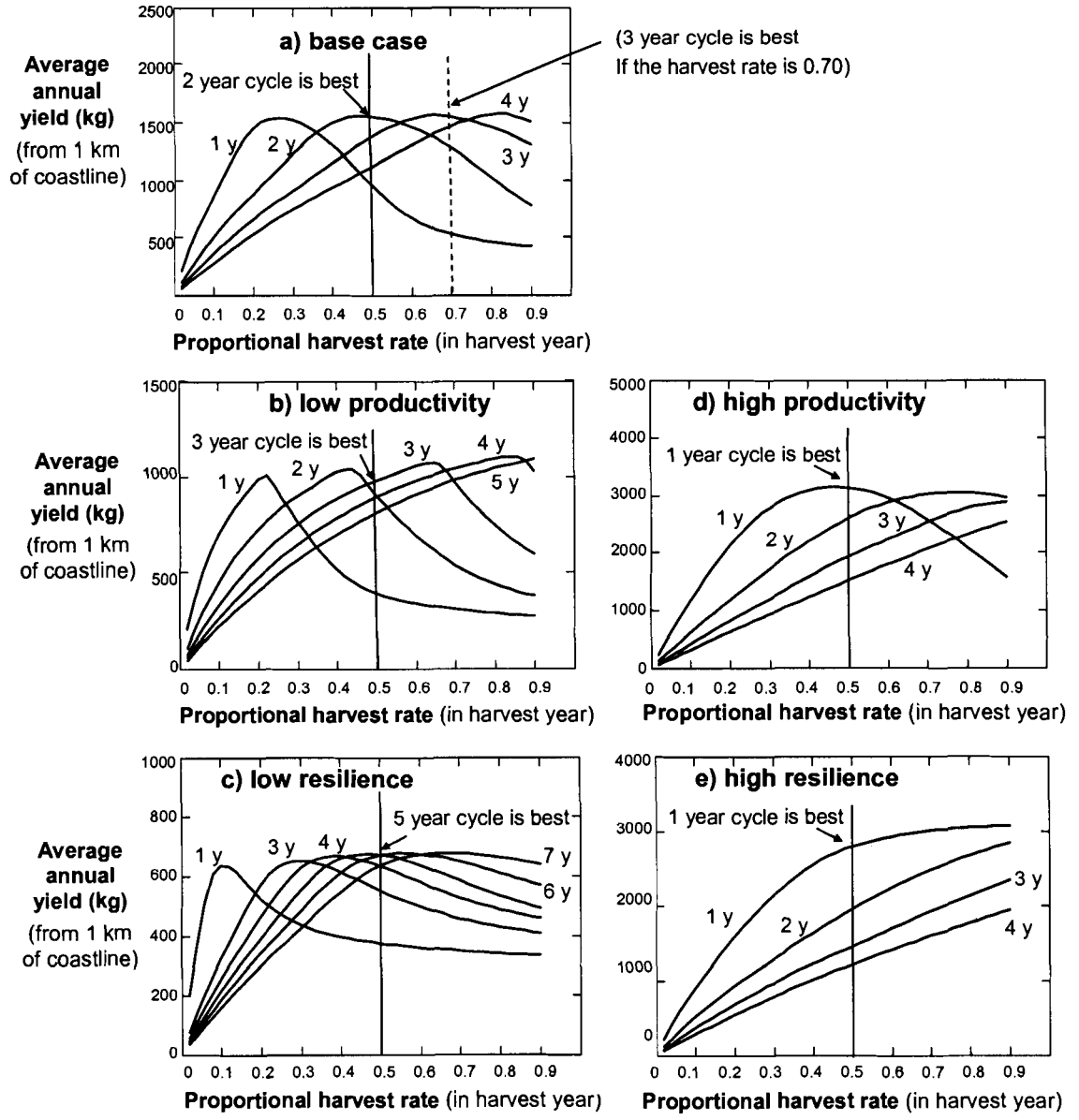
Figure 5: Deterministic predictions of 100-year yield vs. proportional harvest rate, for different cycle lengths, under scenarios of a) base-case, b) low productivity, c) high productivity, d) weak recruitment-compensation, and e) strong recruitment-compensation. If the harvest rate is 50% (as assumed for deterministic simulations), the "best" cycle is that with the highest yield at a 50% harvest rate. If the harvest rate is 70% for example, a longer cycle would maximize yield.
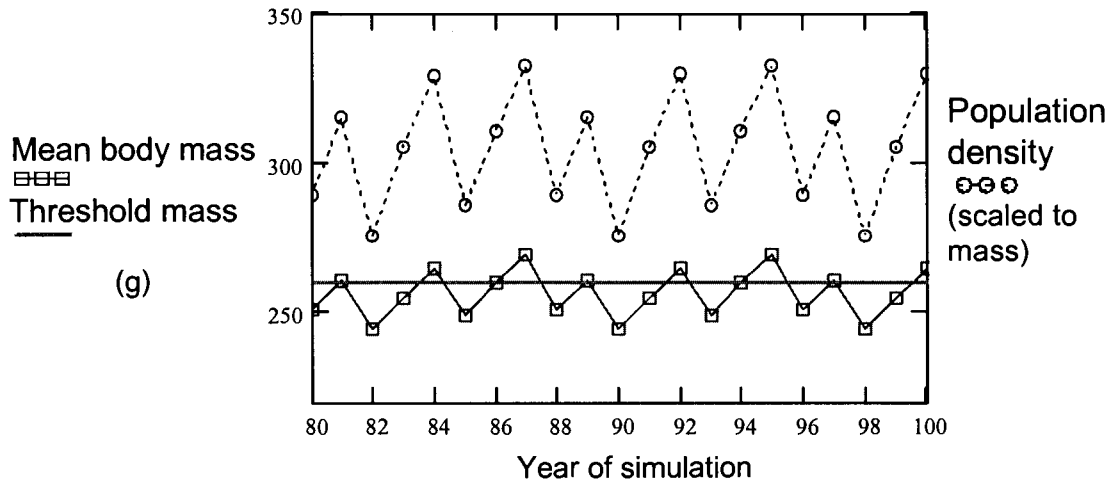
Figure 6: Change in body mass (dotted line) over time for "Harvest when ready" under a scenario of low productivity (deterministic simulation). The solid horizontal line indicates the minimum threshold for body mass (260 g) and the dashed line indicates population density.
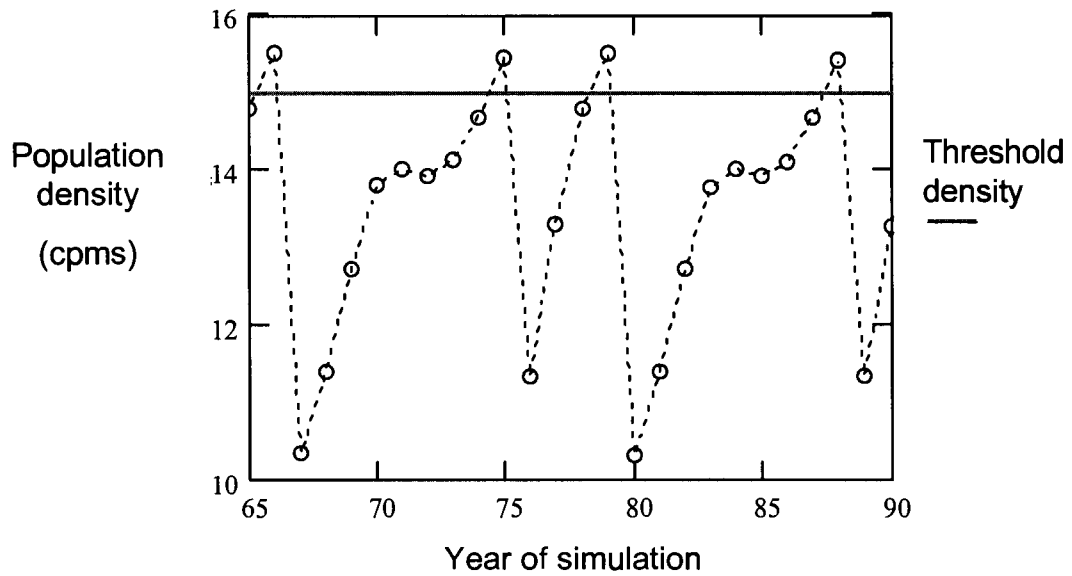
Figure 7: Change in density over time for "Harvest when ready" under a scenario of weak recruitment-compensation (deterministic simulation). Solid horizontal line indicates the minimum threshold for density (15 cpms).
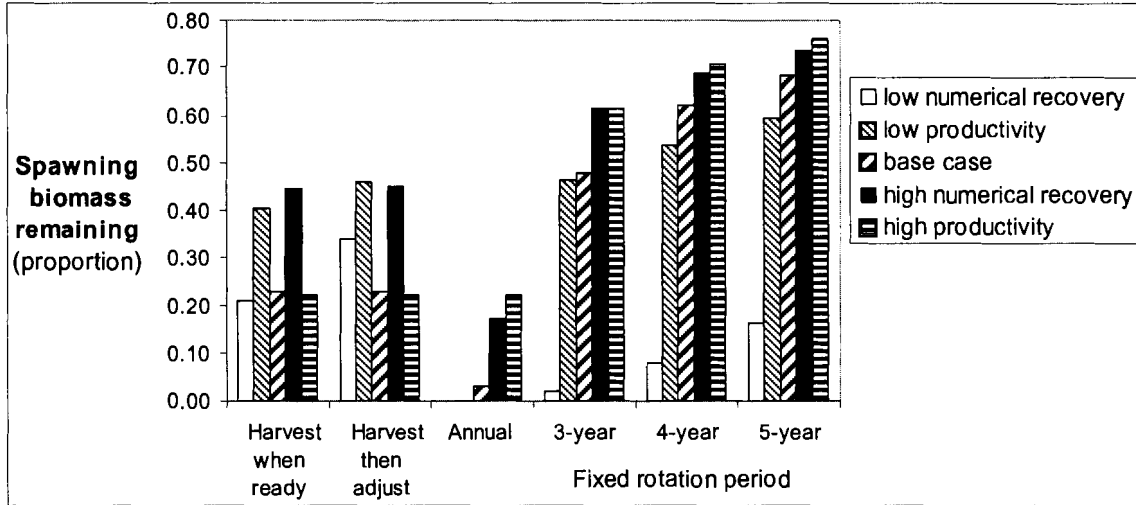
Figure 8: Mean spawning biomass, expressed as a proportion of the unfished spawning biomass, resulting from alternative harvest strategies under each scenario of population dynamics (Deterministic Simulations).
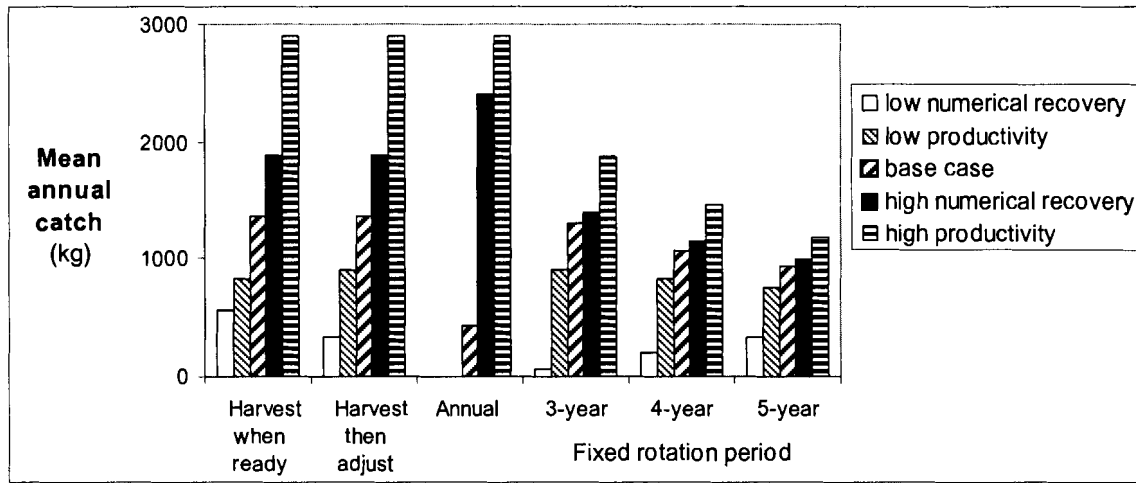
Figure 9: Mean annual catch resulting from alternative harvest strategies under each scenario of population dynamics (Deterministic Simulations).

50% harvest rate   **75% harvest rate**

(a) Harvest (kg)

(b) Mean mass (g)

(c) Proportion large

(d) Spawning biomass (scaled to K)

(e) Mean cycle length (years)
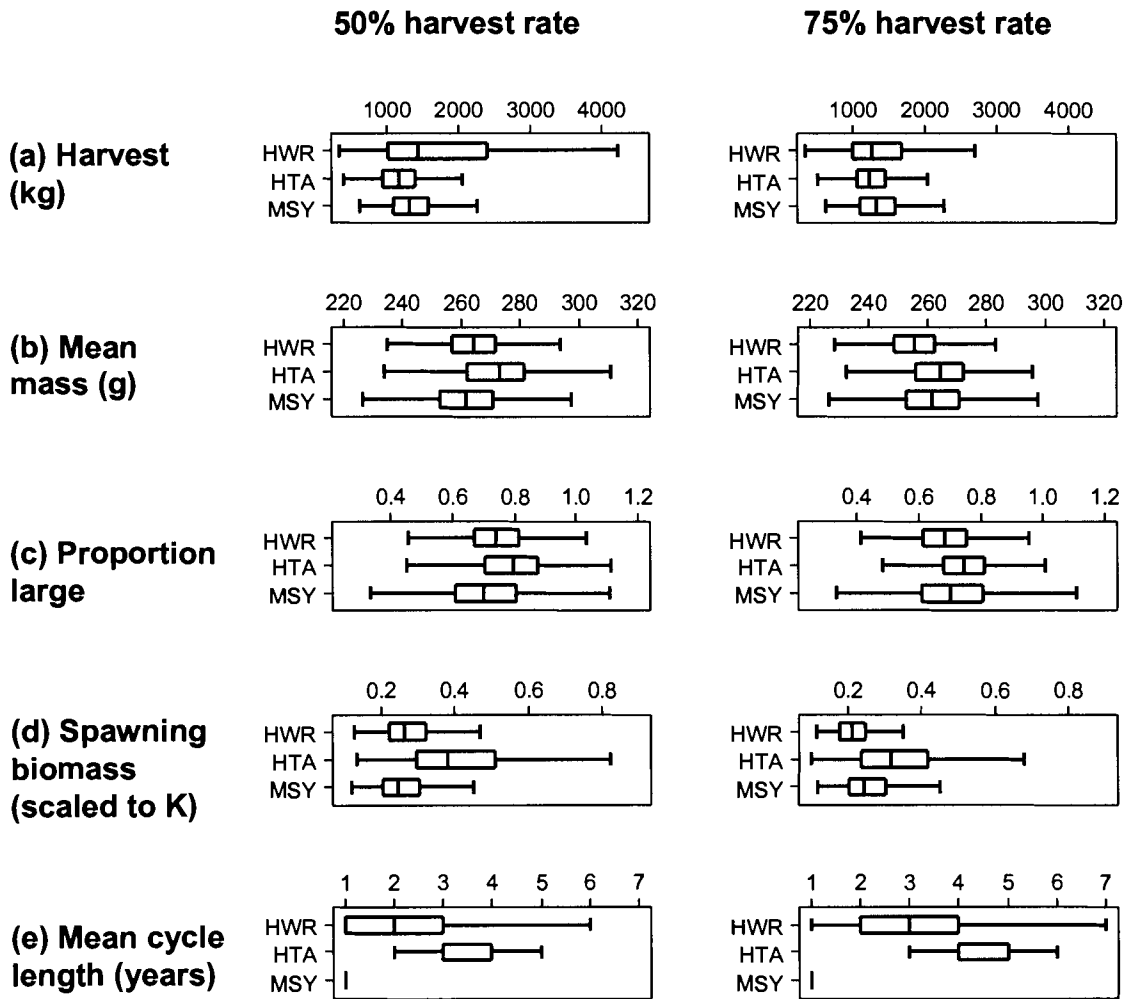
Figure 10: Stochastic simulation results for the **base-case** scenario (medium productivity, recruitment-compensation, and variability in recruitment). Columns 1 and 2 represent 50% and 75% harvest rates for the adaptive strategies, however the MSY results are identical between columns because the harvest rate is constant at 26% for this scenario.

Figure 11: Stochastic simulation results for the **low productivity** scenario. the MSY results are identical between columns because the harvest rate is constant at 22% for this scenario.
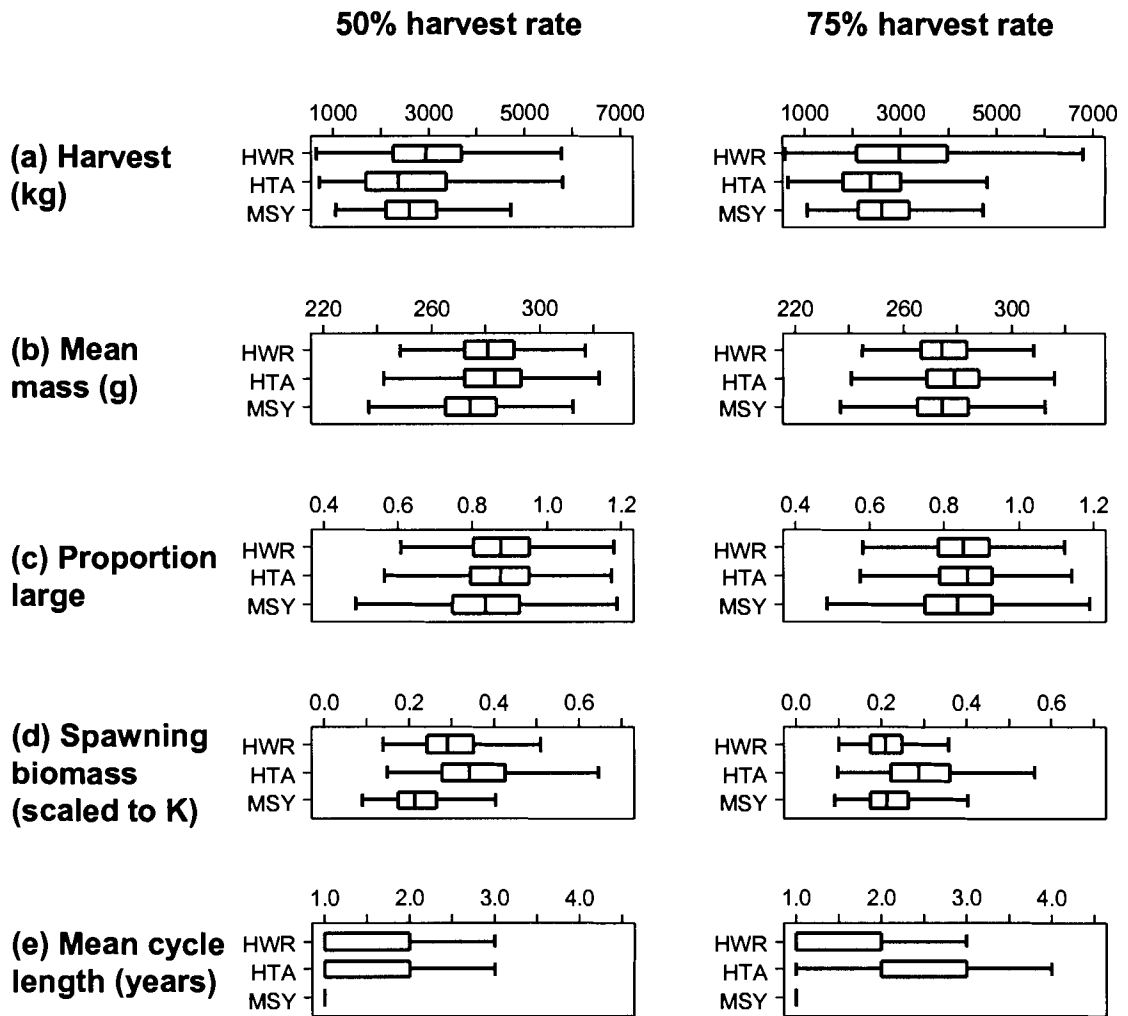
Figure 12: Stochastic simulation results for the **high productivity** scenario. the MSY results are identical between columns because the harvest rate is constant at 48% for this scenario.

50% harvest rate　　　　　　**75% harvest rate**

(a) Harvest (kg)

(b) Mean mass (g)

(c) Proportion large

(d) Spawning biomass (scaled to K)

(e) Mean cycle length (years)
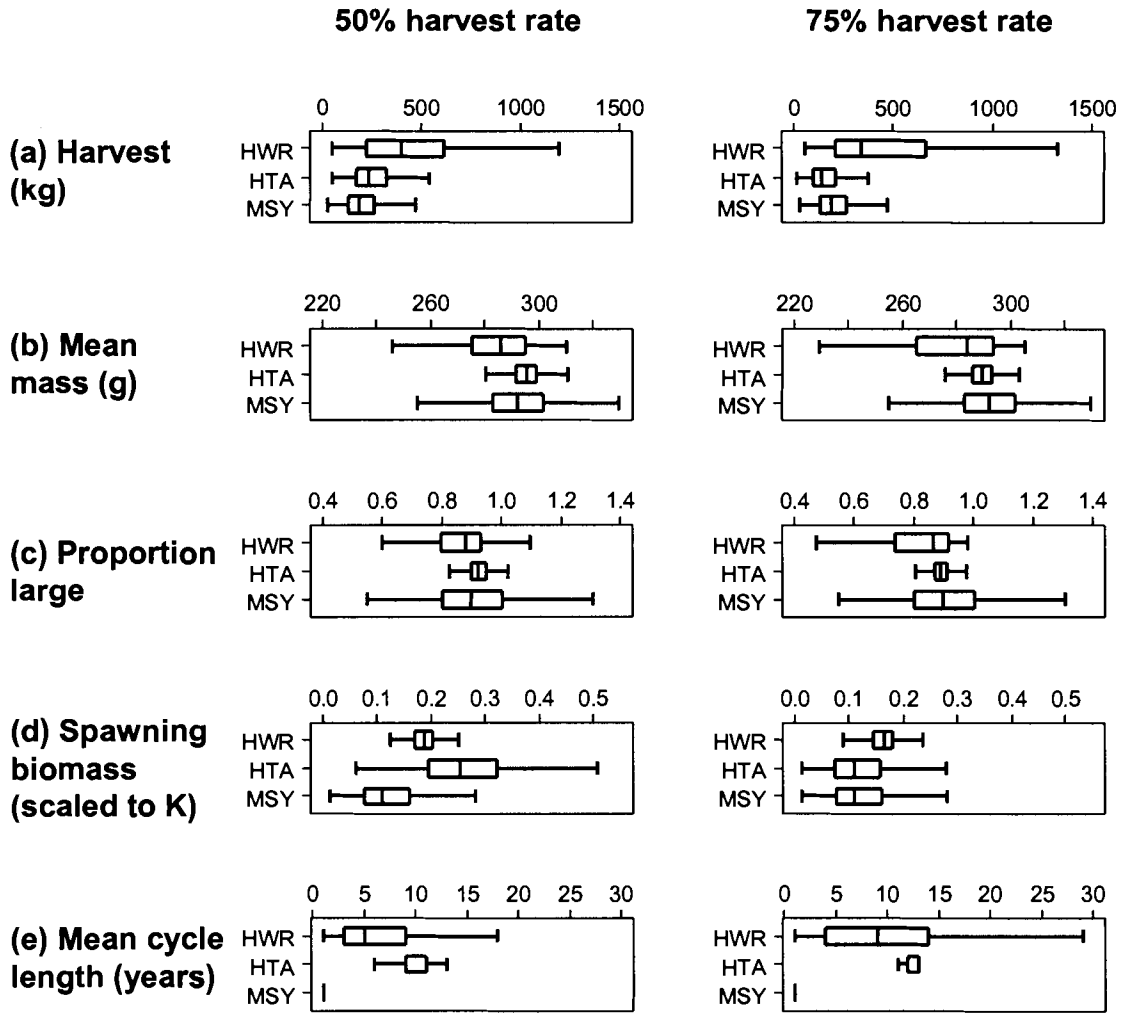
Figure 13: Stochastic simulation results for the **weak recruitment-compensation scenario**. The MSY results are identical between columns because the harvest rate is constant at 10% for this scenario.
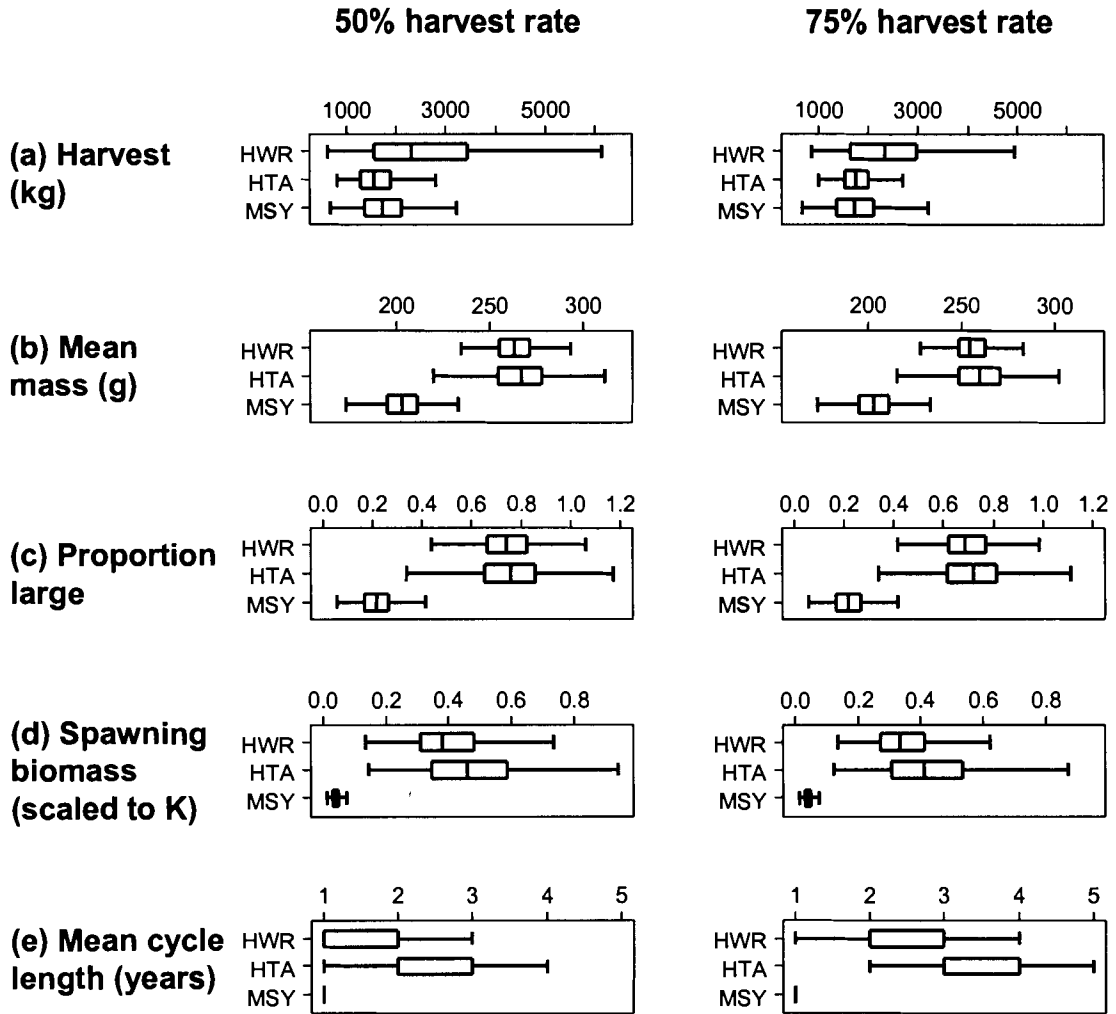
Figure 14: Stochastic simulation results for the **strong recruitment-compensation scenario**. The MSY results are identical between columns because the harvest rate is constant at 90% for this scenario.

50% harvest rate   **75% harvest rate**

(a) Harvest (kg)

(b) Mean mass (g)

(c) Proportion large

(d) Spawning biomass (scaled to K)
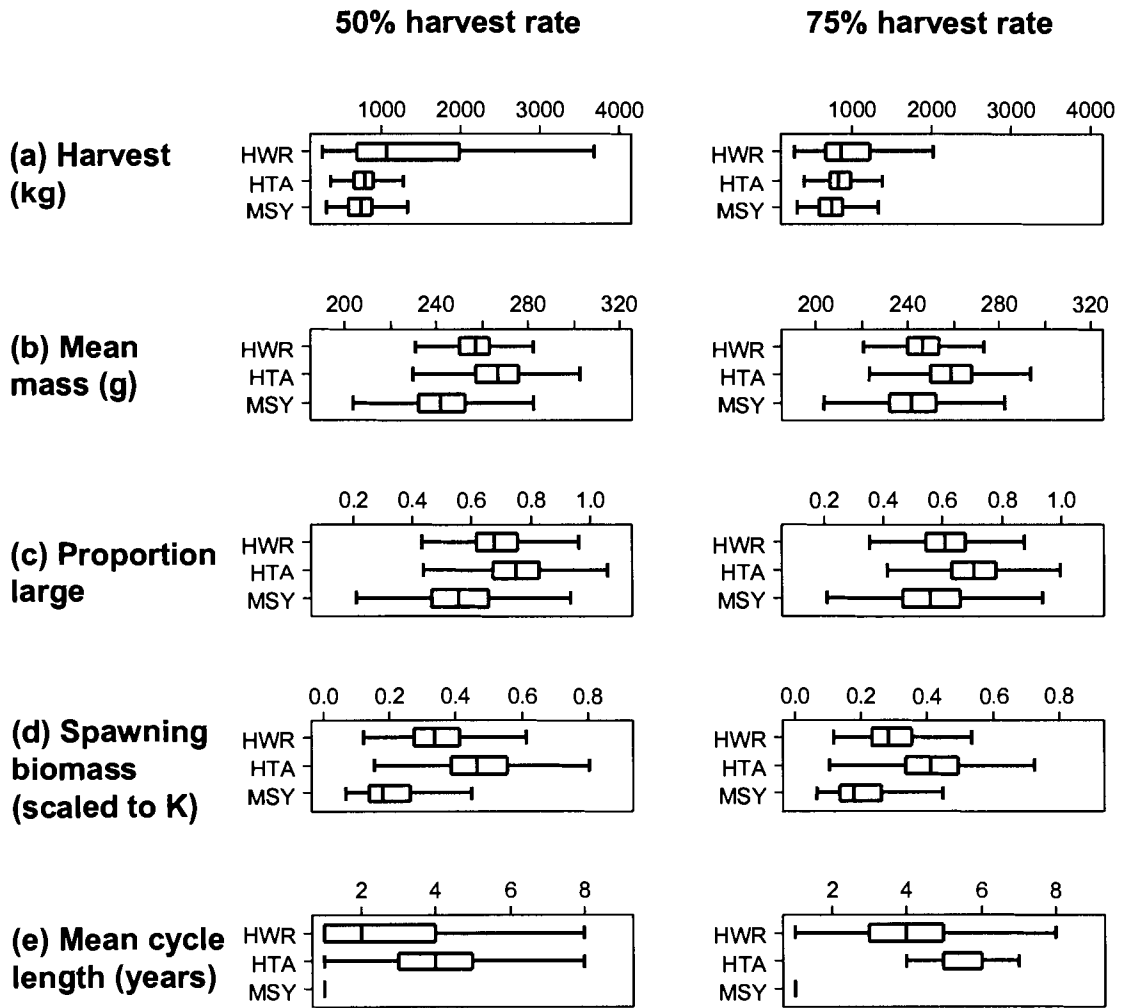
(e) Mean cycle length (years)
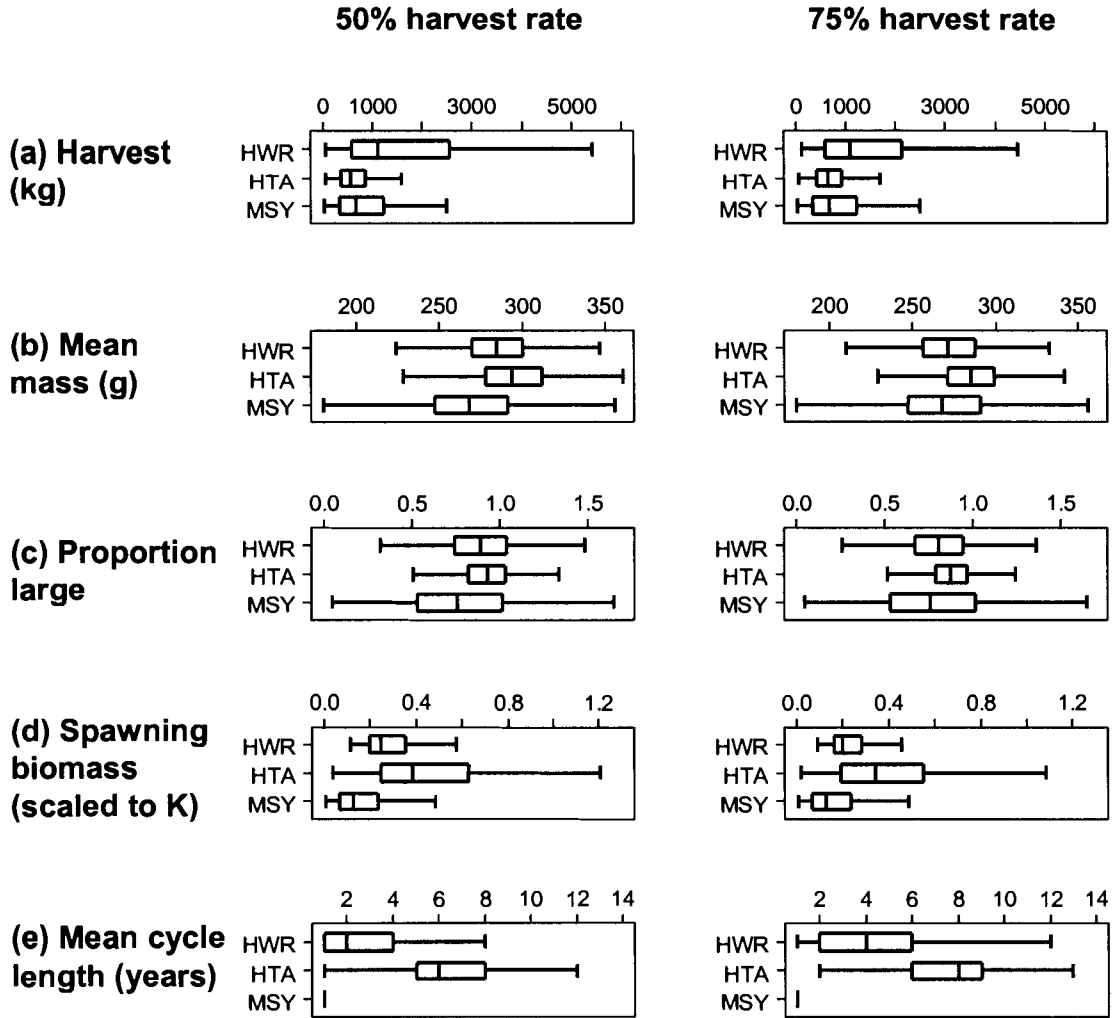
Figure 15: Stochastic simulation results for the **high recruitment variability** scenario. The MSY results are identical between columns because the harvest rate is constant at 26% for this scenario.

(a) 50% proportional harvest rate

Low numerical recovery

High recruitment variability

Low productivity

Base-case

High numerical recovery

High productivity

☐ Harvest when ready
☒ Harvest then adjust

0 2 4 6 8 10 12 14 16 18

(b) 75% proportional harvest rate

Low numerical recovery

High recruitment variability

Low productivity

Base-case

High numerical recovery

High productivity

☐ Harvest when ready
☒ Harvest then adjust

0 2 4 6 8 10 12 14 16 18
Maximum number of insurance areas used

Figure 16: Maximum number of insurance areas required by adaptive rotational harvest strategies, under each scenario of population dynamics, given proportional harvest rates of (a) 50% and (b) 75%.

74
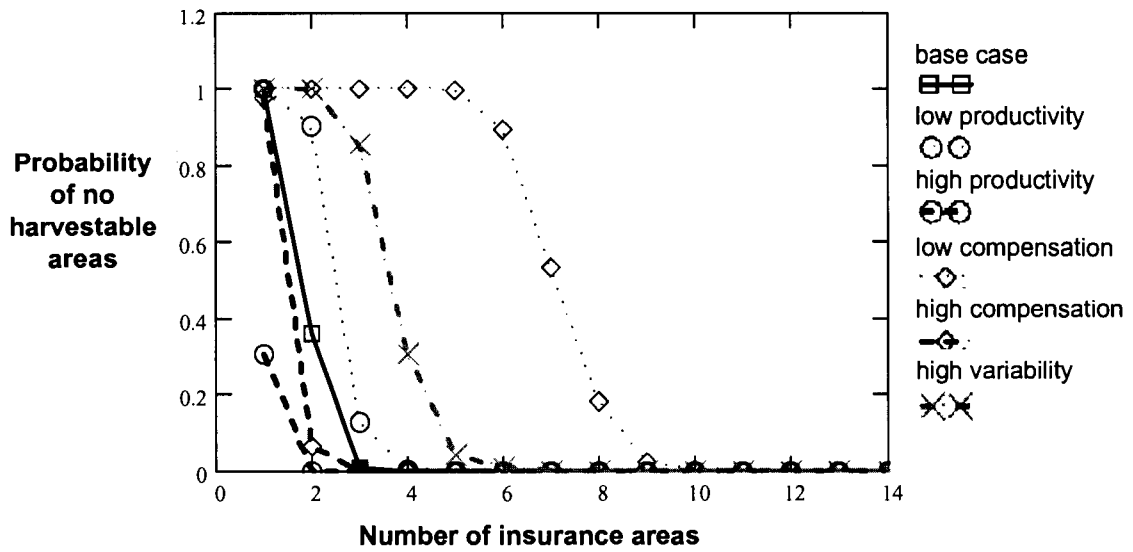
Figure 17: The probability of no harvest areas being available to harvest in any given year, as a function of the number of insurance areas available, for a strategy of "**Harvest when ready**".
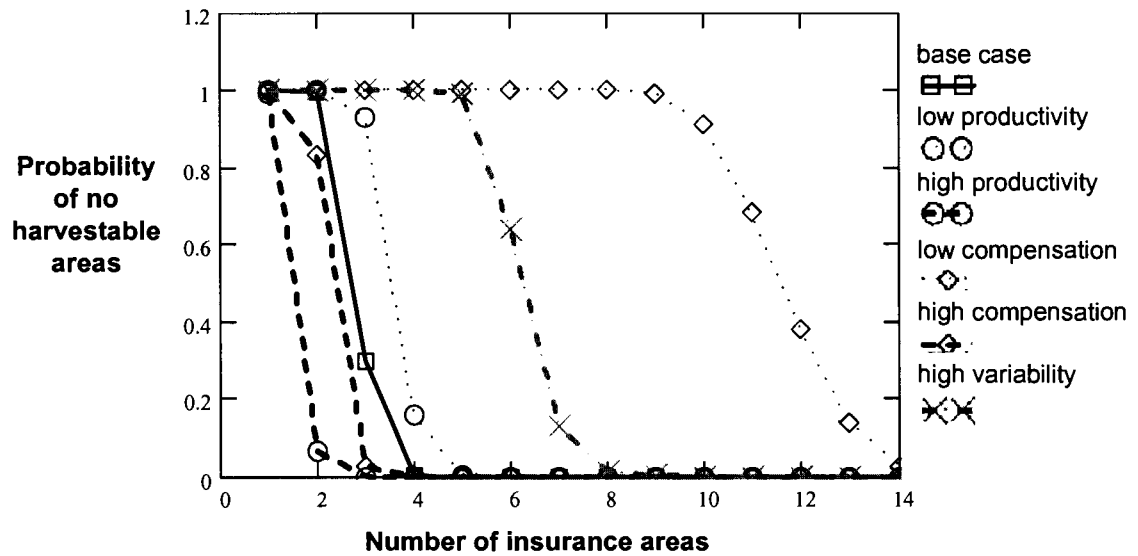
Figure 18: The probability of no harvest areas being available to harvest in any given year, as a function of the number of insurance areas available, for a strategy of "**Harvest then adjust**".

APPENDIX 1: MASS AT LENGTH RELATIONSHIP

Because the relation between body mass and length is not documented for adult sea cucumbers, I collected data from the commercial fishery in order to estimate parameters of this relationship:

$M = A * L^b$ where: M is sea cucumber mass (g);

L is sea cucumber length (mm);

A and b are the parameters to be estimated.

Methods

On October 24 and 25, 2003, an assistant and I measured length and mass of a sample of sea cucumbers from five commercial vessels, at two seafood processing plants in Vancouver, B.C. (Evergreen International Foodstuffs Ltd. and Territory Seafoods). Cucumbers had been split (eviscerated) at sea. We haphazardly sampled 30 sea cucumbers from a plastic cage from each vessel, sampling 150 sea cucumbers in total. Because smaller cucumbers may sink to the bottom and samples were collected from the top of each cage, the average size of sampled animals may have been larger than the landed average size.

We measured the approximate length (to the nearest cm) by laying each cucumber on a metal rule and straightening without stretching it; length measurements may have been accurate to within 5cm, but were rough estimates only, due to the highly variable shape of the animals. We weighed each cucumber to the nearest gram using an electronic balance with a tray, and recorded whether cucumbers were still firm (i.e. relatively tense and slightly moving) versus flaccid and stretched out long.

To fit the mass-length model to the data, I used only the measurements from the "firm" sea cucumbers (89 in total), to reduce the variability among length measurements and avoid biasing the length due to longer, flaccid sea cucumbers. On October 24th, the sea cucumbers sampled at the processing plant had been landed approximately three days earlier and were flaccid, so I excluded them from this analysis; on October 25th, the

processing plant had cucumbers that been landed the day before, and I included all but one of the samples in the analysis. I estimated the parameters of the mass-length model by solving for the values of A and b which resulted in the minimum sum of squared errors between observed and predicted mass, given the measured lengths.

I used an arbitrary constraint of 2.0 for the minimum value of the b parameter. The reason for this constraint is that the original fitted estimate of b was approximately 1.5; a value of 3 would represent isometric growth (constant ratio of diameter to length), whereas a value of 1 represents a constant diameter. Based on my observations of living sea cucumbers while SCUBA diving with commercial divers, larger sea cucumbers appear to be thinner in proportion to length than smaller sea cucumbers, but this difference is not very pronounced. Thus, I speculated that 1.5 was an underestimate of the b parameter, due to the fact that the sea cucumbers were eviscerated. An underestimation would result if larger sea cucumbers had increased viscera mass as a proportion of total body mass; however, there are no data to support this assumption.

An overestimation of the b parameter would overestimate population productivity due to body growth, but it would not in change the relative performance of harvest strategies. I evaluated alternative harvest strategies under three different levels of productivity by varying growth (von Bertalanffy "k") parameter of the age-length relationship, and the natural mortality parameter, to account for the uncertainty in productivity. Overestimation of the b parameter would affect each set of results equally, and thus would not affect the conclusions.

Results

Appendix 1 Figure 1 shows the individual length and mass measurements (diamond symbols) and the predicted relationship between length and mass (smooth line). The slightly more "concave up" shape of the fitted line, as compared with the data, is a result of the minimum constraint of 2.0 for the b parameter. Given $b = 2.0$, the fitted value for $A = 0.00257$.
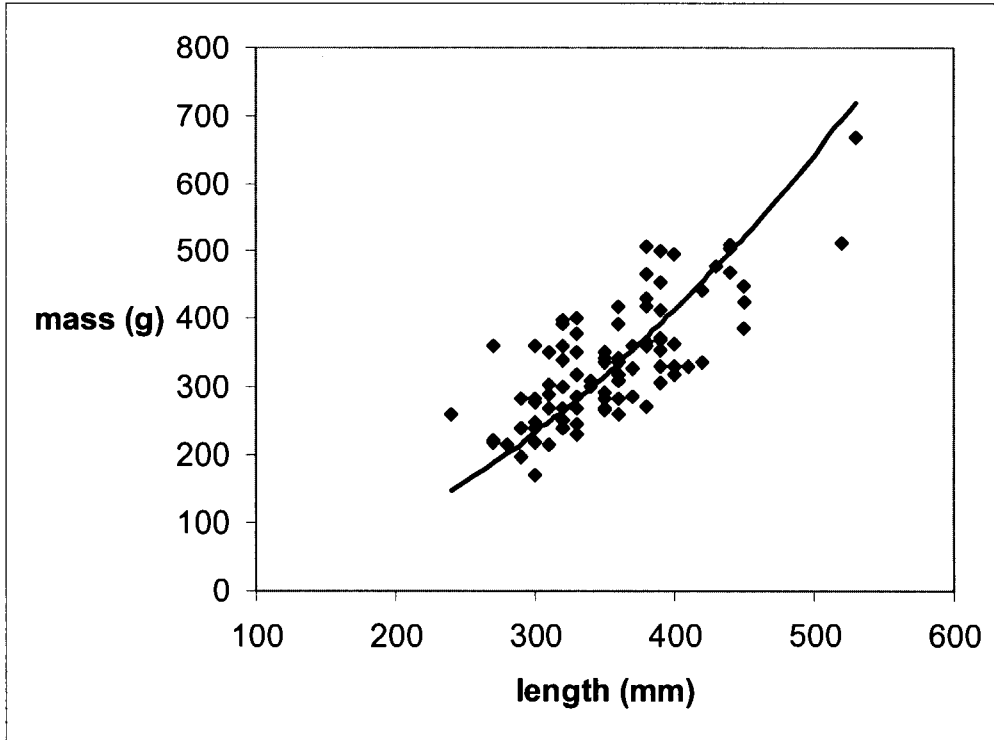
Figure 19: Sea cucumber mass versus length. Observed values are represented by dots, and predicted values by a line.

APPENDIX 2. DETERMINISTIC RESULTS

Scenario		Performance Measure (at equilibrium)	HARVEST STRATEGY		50% harvest rate			
			Harvest when ready	Harvest then adjust	Annual	3-year	4-year	5-year
base case		Mean annual yield	1373	1373	434	1315	1069	925
		Spawning stock biomass	0.23	0.23	0.03	0.478	0.62	0.68
productivity	low	Mean annual yield	830	901	2	901	823	748
		Spawning stock biomass	0.41	0.46	0.00	0.46	0.54	0.59
	high	Mean annual yield	2897	2897	2897	1876	1460	1193
		Spawning stock biomass	0.22	0.22	0.22	0.62	0.71	0.76
resilience	low	Mean annual yield	562	333	0	70	208	339
		Spawning stock biomass	0.21	0.34	0.00	0.02	0.08	0.16
	high	Mean annual yield	1883	1883	2399	1399	1156	990
		Spawning stock biomass	0.45	0.45	0.17	0.61	0.69	0.74

APPENDIX 3: STOCHASTIC RESULTS

Scenario		Measure (at equilibrium)	HARVEST STRATEGY				
			AMSY	HWR	HTA	HWR	HTA
			MSY harvest rate*	*50% harvest rate*		*75% harvest rate*	
Base case		Mean annual yield at equilibrium	1346	1755	1275	1565	1281
		CV of yield at equilibrium	0.23	0.529	0.39	0.614	0.26
		mean body mass at equilibrium	262	264	272	256	264
		mean prtn of cucs>300g	0.72	0.75	0.79	0.69	0.74
		mean SB (prtn of original)	0.26	0.28	0.42	0.23	0.34
		5th %ile of min SB (prtn of original)	0.16	0.18	0.22	0.15	0.17
		Mean cycle length at equilibrium	1.0	2.2	3.2	3.4	4.3
		CV of cycle length at equilibrium	0.00	0.552	0.32	0.421	0.23
Productivity	low	Mean annual yield at equilibrium	745	1246	809	1072	862
		CV of yield at equilibrium	0.27	0.57	0.28	0.59	0.24
		mean body mass at equilibrium	242.6	256.8	266.3	246.6	258.1
		mean prtn of cucs>300g	0.57	0.69	0.75	0.62	0.70
		mean SB (prtn of original)	0	0	0	0	0
		5th %ile of min SB (prtn of original)	0	0	0	0	0
		Mean cycle length at equilibrium	1.0	3	4	4	5
		CV of cycle length at equilibrium	0.00	0.59	0.26	0.42	0.21
	high	Mean annual yield at equilibrium	2721	3012	2621	3147	2574
		CV of yield at equilibrium	0.31	0.37	0.45	0.45	0.42
		mean body mass at equilibrium	274.4	281.5	282.4	275.5	278.2
		mean prtn of cucs>300g	0.84	0.88	0.87	0.86	0.85
		mean SB (prtn of original)	0	0	0	0	0
		5th %ile of min SB (prtn of original)	0	0	0	0	0
		Mean cycle length at equilibrium	1.0	1	2	2	3
		CV of cycle length at equilibrium	0.00	0.43	0.45	0.50	0.37
Recruitment Compensation	weak	Mean annual yield at equilibrium	368	488	263	454	169
		CV of yield at equilibrium	0.44	0.76	0.49	0.69	0.62
		mean body mass at equilibrium	290.5	284.5	295.3	279.3	289.5
		mean prtn of cucs>300g	0.90	0.86	0.92	0.82	0.89
		mean SB (prtn of original)	0	0	0	0	0
		5th %ile of min SB (prtn of original)	0	0	0	0	0
		Mean cycle length at equilibrium	1.0	7	10	10	12
		CV of cycle length at equilibrium	0.00	0.75	0.16	0.69	0.06
	strong	Mean annual yield at equilibrium	1795	2470	1683	2668	1829
		CV of yield at equilibrium	0.34	0.44	0.36	0.52	0.26
		mean body mass at equilibrium	203.0	263.7	266.3	255.5	259.6
		mean prtn of cucs>300g	0.22	0.76	0.75	0.70	0.72
		mean SB (prtn of original)	0	0	0	0	0
		5th %ile of min SB (prtn of original)	0	0	0	0	0
		Mean cycle length at equilibrium	1.0	2	3	3	3
		CV of cycle length at equilibrium	0.00	0.57	0.35	0.49	0.26
Recruitment Variability	high	Mean annual yield at equilibrium	917	1707	706	1813	772
		CV of yield at equilibrium	1.04	0.93	0.81	1.09	0.89
		mean body mass at equilibrium	267.5	284.4	294.6	272.0	286.4
		mean prtn of cucs>300g	0.78	0.92	0.93	0.84	0.88
		mean SB (prtn of original)	0	0	1	0	0
		5th %ile of min SB (prtn of original)	0	0	0	0	0
		Mean cycle length at equilibrium	1.0	3	6	5	8
		CV of cycle length at equilibrium	0.00	0.97	0.34	0.85	0.27

APPENDIX 4. INSURANCE AREA STATISTICS

Harvest Strategy	Harvest Rate	Scenario	Base case	Productivity		Numerical Recovery		Stochasticity
				Low	High	Low	High	High
Harvest when ready	50%	MedNI	1	2	0	7	1	3
		MaxNI	3	4	1	10	2	6
		5NI	1	1	1	1	1	1
		proptime	0.08	0.14	0.00	0.49	0.04	0.24
	75%	MedNI	3	3	1	10.5	2	5
		MaxNI	4	5	2	16	4	9
		5NI	1	1	1	1	1	1
		proptime	0.24	0.31	0.03	0.64	0.13	0.38
Harvest then adjust	50%	MedNI	2	3	1	11	2	6
		MaxNI	4	5	2	15	3	8
		5NI	1	1	1	1	1	1
		proptime	0.21	0.30	0.04	0.64	0.14	0.48
	75%	MedNI	3	4	2	11	2	8
		MaxNI	5	6	3	15	4	11
		5NI	1	1	1	1	1	1
		proptime	0.33	0.42	0.14	0.66	0.24	0.57

MedNI   - median number of insurance areas used

MaxNI   - maximum number of insurance areas used (probability ≤ 0.01 of no harvest openings)