ABSTRACT

BROOKS, ELIZABETH NICOLE. Dynamics and Management of Sub-divided Populations. (Under the direction of Kenneth H. Pollock).

Multi-site Leslie matrices for sub-divided populations are explored with respect to optimization of management goals and transient dynamics associated with implementing actions to achieve those goals. The management goals explored were minimizing the cost associated with controlling a pest species (Yellow Legged Herring gull, *Larus cachinnans*), and maximizing the yield from a commercially valuable species (Artco-Norwegian cod, *Gadus morhua*). Transient dynamics were evaluated for a representative r- and K-selected species, and time to convergence was compared between one-site versus multi-site models, and for different migration patterns, migration levels, and proportion of the population migrating.

In a density-independent model for the Yellow Legged Herring Gull, the most efficient control technique was to focus management actions on the better quality sites, because breeders at high quality sites had higher expected life-time reproductive values. The amount of harvest required to maintain equilibrium was a function of site quality and the balance between immigration and emigration—cost (and effort) increased as dispersal favored better quality sites. Given a choice between destroying eggs or culling adult breeders, culling required ten times less effort per-capita and would be the optimal strategy as long as per-capita culling cost is no more than ten times greater than the per-egg destruction cost.

A density-dependent model of Arcto-Norwegian cod revealed that the theoretical yield was maximized from harvesting age 6 individuals. If only the minimum age harvested could be controlled, then the constrained yield was maximized from harvesting ages five and older. Yields were compared between a reserve model with 25% of fishing area closed and a no-reserve model. Yields in the reserve model exceeded the non-reserve model when transfer rates out of the reserve were higher, when higher fecundity was realized in the reserve (which could result from improved habitat quality), and when fishing rates in the non-reserve model were 1.5 and 2.0 times the optimal level.

In both a density-independent and a density-dependent context, I showed that the optimal strategy could be determined from inspection of elements of the left eigenvector (i.e. reproductive value) divided by a vector of age specific harvest value (or cost of control action, in the case of a pest species). The maximum sustained yield was obtained when the age class with the smallest ratio was harvested; the minimum cost comes from removing individuals with the largest ratio. In one-site models, the optimal strategy involved the harvest of no more than two age classes, where the second (younger) age class had the second smallest ratio (for maximization) or largest ratio (for minimization). However, in multi-site models, the presence of migration permitted the replenishment of age classes beyond the one fully exploited in a harvested site, and thus the optimal strategy could involve the harvest of more than two age classes.

Optimal solutions to the above models corresponded to equilibrium conditions. However, the amount of time between the implementation of a management action and the attainment of equilibrium can be great. Analysis of transient dynamics revealed that the time to convergence is affected by many factors. I defined convergence as the time

when a measured population growth rate (and the growth rate in all subsequent years) was within 1% of the asymptotic growth rate (corresponding to equilibrium for a given action). Comparing single-site versus multi-site models, the multi-site models converged more slowly. Multi-site models that incorporated low levels of migration and migration in only the first age class (as opposed to migration in all age classes) converged slowest. Models for the longer-lived K-selected species generally converged more slowly than the short-lived r-selected species, although for some migration patterns (particularly when emigration out of the site receiving a management action exceeded immigration into that site) models for both species converged quickly.

Dynamics and Management of Sub-divided Populations

by

Elizabeth N. Brooks

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Biomathematics

in the

GRADUATE SCHOOL

at

NORTH CAROLINA STATE UNIVERSITY

2000

_____   _____

Dr. Kenneth H. Pollock   Dr. George R. Hess
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Dr. Joseph E. Hightower   Dr. Theodore R. Simons

To my mother, Brenda M. Brooks,

to my father, Kenneth F. Brooks (5 April 1938 – 22 April 2000),

to my brother, Jeffrey J. Brooks,

and to my sister, Colleen N. Brooks.

Biography

Elizabeth Nicole Brooks was raised in Pittsburgh, Pennsylvania. She attended Washington and Jefferson College in Washington, Pennsylvania, double majoring in mathematics and biology. She graduated with a Bachelor of Arts in May of 1994 and enrolled in the Biomathematics Program at North Carolina State University in Raleigh, North Carolina in August 1994. She defended her Master's of Biomathematics in September 1996. She was awarded a Chateaubriand Fellowship and from December 1998 to December 1999 she worked in the biometry laboratory of Dr. Jean-Dominique Lebreton in Montpellier, France and attained a masterful command of "franglais." She defended her PhD in Biomathematics 15 December 2000, and will begin a post-doc at the Cooperative Institute for Marine and Atmospheric Studies at the Rosensteil School of Marine and Atmospheric Studies, University of Miami. She looks forward to challenging research opportunities and is eager to add "spanglish" to her arsenal of foreign language assault skills. Miami promises to be an interesting environment, though she fears she may find the climate perspirationally challenging.

Acknowledgements

> A box bird trying to box a button bird found himself buttoned in his own box and said, "I have learned about buttons." The button bird unbuttoned the box bird and smiled, "You have nobody to thank but yourself and me."
>
> -Carl Sandburg
> in: <u>Fables, Foibles, and Foobles</u>

As for me, I've got plenty of people to thank…

Thanks to my committee for convening late in the semester; to George Hess for working with me in the Preparing the Professoriate Program; Joe Hightower for offering such a cool applied course (Quantitative Fisheries Management)—all I will ever need to know about Excel I learned in that class; and Ted Simons for agreeing to sign on to my committee rather late in the game. Special thanks to Ken Pollock for his mentoring and for providing funding for my graduate education with Research Assistantships that allowed me to participate in some very interesting work. As an advisor, he was sensitive, encouraging, and gave me the freedom to pursue topics that interested me. Also, an excellent sportsman with **annoyingly** consistent strokes! I hope we will have more opportunities for collaboration and tennis in the future. Also, thanks to Steve Ellner, an excellent teacher and excellent role model—always exemplifying what Biomathematics can be.

Thanks to the teachers I have had over the years, many of whom were not just teachers but were friends, as well.

Thanks to family and friends, especially my cohort in the Biomathematics Program and "honorary" statistics students that were *nearly* cool enough to have been a part of Biomath. Thanks also to Tom Kepler and family for hosting some "intellectually stimulating" BMA gatherings. Many thanks to Ann Ethridge, tender of the flock, Mother Goose to all, and occasional whip-cracker.

Thanks to Terry Byron and Nalin Dayabhai, the (former) dynamic duo of departmental computing, whose generosity and patience were greatly appreciated. Thanks also to the friendly faculty and staff in the Department of Statistics.

Special thanks to the Equipe Biometrie for making me feel welcome in beautiful Montpellier, and especially Jean-Dominique Lebreton for accepting me into his laboratory and finding the time to work with me.

Thanks to all the musicians for making the interminably long hours in front of my computer more pleasant: Miles Davis, Duke Ellington, John Coltrane, Lester Young, Thelonious Monk, Charlie Parker, Dizzy Gillespie, Ella Fitzgerald, Billie Holiday, Cannonball Adderley, Charles Mingus, Art Blakey, Charlie Haden, Bela Fleck, Cassandra Wilson, Us3, Wynton Marsalis, Sam Cooke, Ray Charles, James Brown, Marvin Gaye, and good ol' JT.

Thanks to Carl Sandburg, who wrote one of the funniest collections of "poems" that I read this year. Here are two more from <u>Fables, Foibles and Foobles</u> that still make me laugh:

> A Fly, a Flea, and a Floohoo talked about books and reading.
> The Fly said he reads two books a day and forgets one.
> The Flea said he reads two books a day and forgets both.
> The Floohoo said he opens two books every day and starts to
> read, "Then I shut 'em up and lock 'em away because if I didn't
> I would read 'em and if I read 'em I would read 'em and weep.

A Fly, a Flea, and a Flitwit talked about books and how to appreciate them.

The Fly said, "When I read a book I tell you that book gets appreciation, on every page from me it gets appreciation."

The Flea did a little thinking. "When I read a book I just read it because if I appreciate and appreciate I get a little headache over my left ear."

The Flitwit shook one bleem and then another bleem out of his head and said, "When I read a book I like lickerish and the more books the more lickerish and what I appreciate is the lickerish."

And now an *Ode to Raleigh*:

<div align="center">

The Weather is hot.
Hot. Hot. Hot.
The Weather is like that.
Whether you like it or not.
Not. Not. Not.

</div>

Thanks to my Soulmate for his encouragement and humor.

One more…

<div align="center">

Last but not least,
I'd like to thank yeast.

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Contents

List of Tables

Chapter 2

Chapter 3

Chapter 4

List of Figures

Chapter 2

Chapter 3

Chapter 4

Chapter 1: Introduction

1 What it be

Perhaps the simplest, and most straightforward way of introducing this thesis is to deconstruct the title: "Dynamics and Management of Sub-divided Populations." I'll start at the end and work my way backwards.

1.1 "Connect the dots…"

The sub-divided aspect of populations is at the core of this thesis. Some populations are naturally disjoint due to the geographic separation of their habitat (fish on coral reefs, insects on patchily distributed vegetation, e.g.). Other populations have become disjoint due to man fragmenting (via harvesting, supplanting, or otherwise destroying) their habitat (spotted owl, e.g.). The spatial separation does not always imply isolation, however, as many times "local" populations are linked by individuals changing sites.

Throughout this thesis, I model populations that exhibit a spatial structure and which are connected by migrating individuals within various age classes. In some cases, I examine high levels of migration (as high as 75%) and other populations with possibly very low exchange of individuals (5%). The amount of movement, and the direction of movement will be seen to have significant consequences for the model dynamics.

When speaking of sub-divided populations, one generally imagines sub-populations that inhabit geographically distinct habitats. However, this need not be the case. A species may inhabit contiguous habitat, with only a fraction experiencing different mortality forces as a result of managers "sub-dividing" the area into an

exploitable portion (hunting and fishing are permissible) and a reserve portion (closed to all hunting and fishing). An example of this can be found in Chapter 3 in my model for Arcto-Norwegian cod (*Gadus morhua*).

Regardless of the nature of spatial separation, all populations are modeled by a multi-site Leslie matrix. All models are deterministic and density-independent except for the Atlantic cod, which incorporates density-dependent survival into the first age class. These models are employed for a variety of purposes, from estimating the best way to reduce a pest population, to maximizing harvest of a commercially valuable species, to studying the expected transient dynamics following a perturbation in one of the life history parameters. All of the modeling questions are united by the fact that they attempt to address potential management issues for sub-divided populations.

1.2 "Speaking of management…"

This brings us to the second keyword in the thesis title: "management." The recognition that populations are not discrete closed systems has important implications. First, the amount of influx/outflow of individuals at different sites influences the dynamics of the whole system. More importantly, applying a management action at one site can cause changes beyond the treated site. This strongly suggests that a wider approach be considered and potential repercussions be examined beyond the immediate stated goal. A useful way to evaluate potential outcomes and risks is with models.

Population management in practice, population management in theory, and population modeling overlap in their intentions but not necessarily in their implementation. One reason for this is that extrinsic social and political factors cannot easily be included in scientific models, yet they are a significant component of the

decision-making process that governs management action. Cost or value, by nature a quantifiable factor, can be incorporated into theory and models. Ideally, management decisions are guided solely by respect for what is best for a given population, however, the reality is that economics often determines the scope of potential actions. A natural course of action is to ask what is the best we can do given a specific set of economic constraints. This can be addressed by using optimization theory.

The first two modeling endeavors approach the optimization problem from opposite points of view: minimization of cost associated with a management action for a pest species, and maximization of value from harvesting a commercially valuable species. A new optimization methodology, which is biologically intuitive and straightforward to calculate from matrix models, is derived to solve these two problems. The final modeling endeavor examines the transient effects on a population following an action that lowers a vital rate (survival or fecundity) at one site (this could result from the application of a control measure to one site or it could be due to an environmental event).

1.3 "At last, the beginning…"

Many populations exhibit spatial structure and are connected by the movement of individuals, and this needs to be taken into account when planning courses of management action. Therefore, we need a mathematical way of evaluating the result of implementing the planned action. Transient analysis looks at the initial dynamics following perturbation of a system formerly at equilibrium. In the last modeling section, I examine transient dynamics and measure the amount of time required for convergence to asymptotic values. I compare this for two species with very different life-histories (a short-lived, r-selected species and a long-lived K-selected species). This exploration

reveals general patterns and emphasizes the importance of accounting for spatial structure of, and migration between, sub-populations.

Chapter 2: Optimizing removals to control a metapopulation:

Application to the Yellow Legged Herring Gull (*Larus cachinnans*)

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Abstract: The standard one-site harvest maximization problem is extended to consider minimizing the cost associated with removing individuals from an annually increasing "nuisance" or "pest" population exhibiting spatial structure (i.e. a metapopulation). We investigate the problem using a linear, deterministic, multi-site matrix. A new approach for estimating the optimal harvest strategy based on sensitivity analysis, rather than linear programming is presented. We show that the optimum stage class(es) to harvest can be determined from stage/site specific reproductive values (i.e. the components of the left eigenvector), weighted by stage/site specific harvest costs. The amount of harvest that should be directed at the determined stage(s) can be estimated from sensitivities. This method is illustrated for a Mediterranean gull, the Yellow Legged Herring Gull (*Larus cachinnans*). Results obtained from the sensitivity analysis method (both a "one-step" approximation and an iterative Newton-Raphson algorithm) are compared with linear programming solutions. As expected, the iterative sensitivity method yields the same solutions as linear programming, while the "one-step" approximation underestimates the level of harvest. Several constrained optimizations are investigated to address spatial limitations and difficulties associated with age-determination.

Key words: Optimal harvesting; Leslie Matrix; Metapopulation; sensitivity analysis; Larus cachinnans *; spatially structured populations; bird pests.*

1.0 INTRODUCTION

The idea that population dynamics results can be used to understand the effect of additional mortality induced by man in exploited populations can be traced back to Baranov (1918) (in Vilim 1977). More recently, the effect of harvesting was investigated using matrix models: Usher (1966; 1969a-b) considered the problem of maximizing harvest, constrained to be proportional to a stable size structure. Lefkovitch (1967) evaluated the effect of a given removal strategy on population growth rate, but did not address yield maximization. Beddington and Taylor (1973) and Rorres and Fair (1975) demonstrated analytically that the optimum unconstrained harvesting strategy involved at most two age classes, by partial removal of one age class and complete removal of a second (older) age class. This type of optimization problem can be solved easily by linear programming, and the maximum yield is then obtained when harvesting occurs after reproduction, as shown by Doubleday (1975). The bimodal nature of the optimal solution is explained by the fact that complete harvest of an age class in a one-site model reduces the maximum age, thus eliminating the possibility of harvesting additional age classes beyond the fully exploited class (Rorres 1976; Reed 1980). It results from the "Fundamental Existence Theorem" of linear programming theory (Getz and Haight 1989). Getz and Haight (1989) summarize the methodology for linear, linear-stochastic, and non-linear matrix models (both age- and stage-structured) and provide numerous applications of optimal harvesting theory.

Despite the variety of applications, optimal harvesting has been studied and applied most frequently from the point of view of maximizing the harvest from an exploited population (either in terms of number or overall value when prices/costs differ

between classes). The opposite problem of minimizing the harvest or its cost for a maximal effect on population size or growth rate, typical in population management (see e.g. Coulson 1991), has been addressed rarely (see Harwood 1978 in a grey seal population) and never in an optimization context.

Additionally, harvesting studies of populations exhibiting both spatial and age (or stage) structure have been infrequent. Tuck and Possingham (1994) modelled a two-site hypothetical fish metapopulation by two finite difference equations, and used dynamic programming to investigate the optimal harvest strategy. They compared yield estimates from their spatial model to two different non-spatial models, and concluded that yields are maximized when spatial structure and site productivity are taken into account, as the "non-spatial" approaches underestimated allowable harvest in this case. McCullough (1996), without using quantitative models, concluded that metapopulations do not provide much promise for profitable or sustainable harvesting due to the sensitivity of "sink" populations to over-harvesting. However, he restricted his analysis to the typical "source-sink" case, where "sinks" have non-zero extinction probabilities. In such a particular case, harvesting sinks would tend to increase the occurrence of local extinctions, thereby reducing the likelihood of achieving a sustainable harvest. There is thus a clear need for a general theory of optimal harvesting in metapopulations, in the broad sense of a set of sub-populations interconnected by dispersal.

Here, we extend the traditional one-site harvest optimization problem in two directions. First, to a minimization context, where it is desired to minimize the cost needed to control an overabundant or "nuisance" species—i.e. we will consider minimizing the cost of "removals" rather than maximizing the yield of harvests. Second,

the standard one-site problem will be extended to a metapopulation setting, via multi-site matrix models (Le Bras 1971; Rogers 1974; Lebreton 1996).

We use an explicit approach to the harvesting problem based on sensitivity analysis, where reproductive values play a central role (Caswell 1989). Since the reproductive values can be viewed as the relative contribution of an individual to the ultimate growth of the population, this approach will provide an intuitive interpretation of the optimal solution in terms of life history traits. A connection between optimal harvesting and reproductive value had first been suggested by McArthur (1969). He speculated that maximal harvest by a predator would come from removing individuals with the smallest reproductive value. Law (1979) concluded that this point was valid only when reproductive values were calculated under harvesting.

Previous studies have approached optimal harvesting (primarily in a fisheries context) by using linear programming (Rorres 1976; Getz and Haight 1989, and references therein), dynamic programming (Walters 1975; Hilborn 1976; Mangel 1985), graphical techniques (Hilborn 1985; Hightower and Lenarz 1989), or by simulating various alternative strategies and comparing the resulting yields (Ricker 1958; Hilborn 1979; Jensen 1996). Some of these techniques are reviewed in Hilborn and Walters (1992). These methods are all strictly numeric or theoretical in their approach and can be computationally complex. Also, the simulation approach can be inefficient if there are very many competing strategies to simulate. In contrast, our method is very straight-forward and has direct biological interpretation. It is perfectly suited to age/stage structured populations represented by matrix models because the calculations require

only eigenvectors and sensitivities which are easily calculated with any linear algebra software.

Our work was motivated by concern over the rapid growth in the western Mediterranean of Yellow Legged Herring Gull (*Larus cachinnans*, YLHG hereafter) populations. The control of similarly growing populations took place in Spain, on the Mediterranean coast north of Barcelona (Bosch et al. 2000) and in Portugal north of Lisbon (Berlengas islands) (Morais et al. 1998). In both cases, population control was done by culling breeding adults on a large colony. In France some local culling took place to protect sensitive waterbird colonies in the Camargue and some egging took place on islands off Marseilles (N. Sadoul, pers. comm**.**). In such a context, models can be of great help in assessing the validity of various empirical actions (Benton and Grant 1999). However, as in many population management or conservation biology issues, the available data do not make it possible to build a specific model, based for instance on documented estimates of dispersal between existing colonies. It thus seems unavoidable to address this type of problem with a theoretical model and to provide general principles. Therefore, we apply multi-site harvest optimization to a hypothetical YLHG population and compare the results from various techniques (sensitivity analysis, linear programming).

1.1 The Yellow Legged Herring Gull

In the Western Mediterranean, the YLHG is the most abundant sea bird species and has been present since at least 1859 (Vidal et al. 1998a). Due to an increase in the amount of human-produced garbage, which is concentrated in large, open land-fills, and an increase in the amount and availability of offal from fisheries, a rapid growth in gull

populations of 5-15% per year has been observed over the last several decades (Vidal et Bonnet 1997; Vidal et al. 1998b). This species (as well as other large gulls) is considered to be a pest due to the great variety of damage it causes: collision with aircraft, pollution and fouling due to feces, decline of more desirable indigenous bird species due to predation and/or loss of space, and vegetative and agricultural degradation (Murton and Westwood 1976; Coulson 1991; Feare 1991; Cezilly et al. 1993; Cadiou 1997; Vidal et al. 1998a; Vidal et al. 1998b). In roof-nesting urban colonies, there is both noise and fecal pollution, as well as damage to roofing (Cadiou 1997).

The YLHG is an undesirable presence in the Mediterranean, but it is a protected species (Spaans et al. 1991; Cezilly et al. 1993). Partial eradication to prevent further population increases is an acceptable management objective. The existence of several possible control actions ("egging"—the destruction of eggs, and "culling"—the killing of adults) which differ in cost and efficacy necessitates an examination of which harvest strategy can achieve the greatest impact on population growth while incurring the least cost. Lacking per-capita costs for each action, we optimize total effort (proportion of individuals removed from the population) needed to stabilize population growth. However, since the unconstrained "optimal" action is not always tractable, we will also investigate several constrained optimizations.

2.0 MODELLING AND OPTIMIZATION TECHNIQUE

2.1 The Multi-site Matrix

Our approach is based on matrix models, generalized to several sites. For simplicity, we consider birth pulse populations with a time step of one year. We account for the following events between censusing periods: survival/stage transition,

reproduction, and survival from harvest (given by the matrices G, R, and (I-H), respectively). The overall transitions of individuals within the year are obtained by multiplying these three component matrices in the appropriate order (Table 1). In the standard one-site Leslie or Lefkovitch matrix, all entries in the component matrices are scalar with rows and columns corresponding to stage classes. By comparison, entries in a multi-site matrix are stage- and site-specific. We choose to nest sites within stage classes (though one could also nest stage within sites—see Caswell 1989; Lebreton 1996). Thus, the multi-site component matrices have entries that are themselves matrices (i.e. "sub-matrices", see Table 1).

Harvest will be minimized when it occurs before reproduction, i.e. after individuals have already experienced annual mortality (Doubleday 1975). Our multisite matrix, M, corresponding to a pre-birth census, is M=(I-H)*G*R. By pre-birth census we mean that individuals are counted just prior to reproducing. This form of the model was our choice and is not a requirement for the method we introduce later.

For a metapopulation with p distinct sites and n stage classes (stages 1, 2, …, n), the population vector, N, has dimension np x 1, with elements $N_{\text{stage, site}}$ (elements are grouped into n stages, and then indexed according to the p sites). In general, we have

$$N(t+1) = MN(t) = (I-H)GRN(t) \ . \qquad (1)$$

The function of each component matrix can be understood by examining the result of pre-multiplying the vector N first by R, then by G, and then by (I-H). R is a matrix whose first row contains p x p sub-matrices, R_i, (i=1,2,…,n) representing stage/site-specific reproduction. These are generally assumed to be diagonal, with entries $r_{i,j}$ (i=stage, j=site), so that any migration occurring after birth is incorporated into the first year

survival/dispersal sub-matrix ($G_{1,0}$) (Lebreton 1996). The remainder of R is diagonal with p x p identity matrices, I_k (k=1, 2, …,n). Thus, R has dimension $(n+1)p$ x np. Pre-multiplying N by R maps the np x 1 vector N to an $(n+1)p$ x 1 vector, which now contains the "zero" stage class (i.e. newborns) as well as the original stage classes 1,2,…,n. The validity of this is that we are assuming a birth-pulse, where reproduction occurs as one very brief event per time step.

The matrix G is composed of p x p sub-matrices $G_{i,j}$, containing information about transitions from stage j to i. We consider the simplest case where individuals grow at most by a single stage-class per time step, i.e. either i=j or i=j+1. For $G_{i,j}$, with i=j, we have the survival/dispersal of individuals who remain in the same stage-class for a given time step ; when i=j+1, then we have the survival/dispersal of individuals who grow into the next stage class in a given time step. G maps the $(n+1)p$ stage classes (0, 1, 2, …, n) to np stage classes (1, 2, …, n), so G has dimension np x $(n+1)p$. Thus, there will be a sub-matrix $G_{n,n}$ which represents survival/dispersal of individuals in the last stage-class (an "absorbing" class). Entries in $G_{i,j}$ will be of the form $g_{k,l}^{i,j}$ where the superscripts denote transition from stage j to i (matching those on $G_{i,j}$). The subscripts denote migration from site l to site k, and so diagonal elements of $G_{i,j}$ indicate individuals censused in the same site at times t and (t+1), while off-diagonal elements represent migration during this time interval.

For generality, we have not separated the processes of survival, dispersal and growth. This could be done by specifying separate stage/site-specific matrices for each process and multiplying them in the appropriate order for a given time-step. However,

parameter estimates for each process would then be required (see Hestbeck et al. 1991, e.g.).

Lastly, we premultiply by (I-H). H is a diagonal matrix composed of p x p sub-matrices, H_i (i=1,2,…,n), which are also diagonal. Each H_i contains elements of the form $h_{i,j}$, which give the proportion harvested in site j for stage i. We denote as h the vector containing the diagonal elements of H. The dimension of H (and thus I) is np x np, so pre-multiplying N by (I-H) returns the np x 1 vector of individuals that survived or escaped harvesting in the present time step.

By direct multiplication of the harvest and stage transition matrices ((I-H)G), we are assuming an additive structure among mortality forces. If in fact harvest mortality lessens population pressures and risks associated with interspecific competition, or if the timing of harvest affects seasonal mortality by reducing density and lowering vulnerability to climatic or habitat limitations, then a more compensatory relationship might be expected (Anderson and Burnham 1976; Koko and Lindstrom 1998). Among large gull populations, we have no evidence for compensatory mortality, and thus we assume parsimoniously that harvesting mortality is additive to natural mortality.

For a population with a single annual birth pulse, under mild conditions of connectivity between sites, the matrix M will have a single dominant eigenvalue which is real and positive (Lebreton 1996). Following the notation of Caswell (1989), λ, the dominant eigenvalue of matrix M, gives the annual growth rate of a population. In a metapopulation context, λ represents the overall multiplication rate of the system (Lebreton 1996). **w**, the right eigenvector of M associated with λ, gives the stable

stage/site structure; **v** is the associated left eigenvector and gives reproductive values per stage and per site (Lebreton 1996).

2.2 Derivation of Sensitivity Analysis Method

This optimization problem deals with identifying a method of reducing population growth for the smallest total cost. Thus, we are assuming that there is more than one management option, and that removal costs vary according to population stage class.

For an unharvested population with growth rate $\lambda^* > 1.0$, we seek a harvest strategy that will maintain the population at a predetermined size (i.e. achieve a population growth rate after harvesting equal to 1.0). Recall that the vector h contains the diagonal elements of the harvest matrix, H. The total cost associated with a given harvest strategy ($T_{COST(h)}$) is defined to be:

$$T_{COST(h)} = \sum_{i,j} c_{i,j} h_{i,j} x_{i,j} X \qquad (2).$$

$c_{i,j}$ is the per-capita stage- and site-specific harvest cost, $h_{i,j}$ is the proportion harvested in each stage/site, $x_{i,j}$ is the proportion of individuals in stage class *i* in site *j* at equilibrium, and X is the total equilibrium population size. The optimum strategy is found by solving:

$$\min_{h>0} T_{COST(h)} \qquad (3)$$

such that

$$N(t+1) = (I - H)GRN(t) = N(t). \qquad (4)$$

We begin our derivation by considering the sensitivity of population growth rate to harvest of any given stage/site class, $h_{i,j}$. The sensitivity of λ to an entry $m_{i,j}$ in matrix

M is $\dfrac{\partial \lambda}{\partial m_{i,j}} = \dfrac{v_i w_j}{<vw>}$ (Caswell 1989), where <vw> gives the scalar product of vectors v

and w. When $m_{i,j}$ is a function of a lower level parameter, θ, the sensitivity of λ to θ is, by the chain-rule (e.g., p127 in Caswell 1989) :

$$\frac{\partial \lambda}{\partial \theta} = \sum_{i,j} \frac{\partial \lambda}{\partial m_{i,j}} \frac{\partial m_{i,j}}{\partial \theta}. \qquad (5)$$

Applying (5) to our matrix, M, we have:

$$\frac{\partial \lambda}{\partial h_{i,j}} = \frac{-v_{i,j} \sum_{k=1}^{p} (w_{i-1,k} g_{j,k}^{i,i-1} + w_{i,k} g_{j,k}^{i,i})}{<vw>} \qquad (6).$$

The eigenvectors v and w are indexed in the same manner as the population vector, N. Now, if λ were a linear function of $h_{i,j}$, then we would have

$$\frac{\Delta \lambda}{\Delta h} = \frac{\partial \lambda}{\partial h} \qquad (7).$$

$\lambda(h_{i,j})$ being non-linear, (7) is in general a first order approximation. However, if we consider $\dfrac{\partial^2 \lambda}{\partial h_{i,j}^2}$, we will find that the sensitivity of $h_{i,j}$ diminishes as $h_{i,j} \rightarrow 1.0$, i.e. as there are fewer survivors in the harvested stage (see Kirkland and Neumann 1994, Caswell 1996 for discussions of the second derivative of matrix entries with respect to λ). Thus, for at least some portion of the interval [1.0, λ^*], we will find the approximation to be quite satisfactory. We will discuss later a method that will converge on the exact $h_{i,j}$.

Given that (7) is an approximation, we have

$$\frac{\Delta \lambda}{\Delta h_{i,j}} \approx \frac{-v_{i,j} \sum_{k=1}^{p} (w_{i-1,k} g_{j,k}^{i,i-1} + w_{i,k} g_{j,k}^{i,i})}{<vw>} \qquad (8).$$

In (8), $\Delta\lambda = \lambda^*-1.0$ and $\Delta h_{i,j} = 0 - h_{i,j} = -h_{i,j}$. We scale the eigenvectors so that $<vw> = 1.0$. From $Mw=\lambda w$, the term inside the summation is equal to $w_{i,j}$ (after some algebra and using p.102 in Caswell 1989).

Introducing these simplifications into (8) and rearranging terms, we get the following estimate of $h_{i,j}$:

$$\hat{h}_{i,j} = \frac{\Delta\lambda}{v_{i,j}w_{i,j}} \quad (9).$$

With this estimate, the cost associated with harvesting stage i in site j, by substitution into (2), is:

$$\hat{T}_{COST(h_{i,j})} = \frac{\Delta\lambda}{\left(v_{i,j}/c_{i,j}\right)}X \quad (10).$$

Notice that $x_{i,j} = w_{i,j}$ when $\lambda=1.0$, and so the cost is a function of "surplus individuals" ($\Delta\lambda X$) and the ratio of reproductive value to removal cost for the given stage/site class.

From examination of (10), it is clear that the minimum cost for maintaining a fixed population size (equations 3 and 4) will be achieved by harvesting the stage/site class with the largest reproductive value to harvest cost ratio. Once this class is determined, the amount that needs to be harvested can be estimated from (9). Also from (9), we see that the amount of harvest needed to attain equilibrium is inversely proportional to the sensitivity of survival in the harvested class. Since the larger a parameter's sensitivity the greater its effect on λ, we expect that the optimal harvesting solution will be associated with large sensitivities. However, sensitivity depends in part on the proportion of individuals in a given class (an element of the right eigenvector) and

should not be used alone as a criterion for determining harvest strategies because it may not always indicate the stage/site category with the greatest per-capita reproductive value.

Of course, it is always possible that the stage class selected for harvesting can be completely removed without reducing λ to 1.0. When this happens, one selects the stage class with the second largest reproductive value:harvest cost ratio for additional harvest. This procedure can be repeated until $\lambda=1.0$ is achieved. In the one-site age-structured case, at most two age-classes will be harvested in the optimal solution because the complete harvest of one age-class also eliminates all older individuals (Rorres 1976; Reed 1980; Getz and Haight 1989). However, in a multi-site context, the complete harvest of an age class in a given site does not necessarily eliminate all older individuals since there is the possibility of immigration from other sites. Thus, the two age class result found in earlier papers is particular to the one-site case.

2.3 Iterative estimation of harvest

Our estimate, $\hat{h}_{i,j}$, essentially comes from taking one "step" from λ^{*} in the unharvested population using the slope (sensitivity) at that point (see Fig. 1a). As noted previously, $\lambda(\,h_{i,j})$ is concave, so the estimate will be biased low for large $\Delta\lambda$. This problem can be overcome by using an iterative approach to estimating $h_{i,j}$, such as the Newton-Raphson method (Fig. 1b):

$$\hat{h}_{i,j}^{(n+1)} \approx \frac{\lambda_{obj} - \lambda(\hat{h}_{i,j}^{(n)})}{\left[\partial\lambda/\partial\hat{h}_{i,j}\right]_{h_{i,j}^{(n)}}} + \hat{h}_{i,j}^{(n)} \qquad (11).$$

λ_{obj} , the objective function value, is equal to 1.0 since we want to maintain the population at a constant level. This method estimates $h_{i,j}$ iteratively by using the slope $(\frac{\partial \lambda}{\partial \hat{h}_{i,j}^{(n)}})$ at each successive point and finding the intersection with the line $\lambda=1$. Under mild assumptions, the process converges, i.e. $\hat{h}_{i,j}^{\infty} = h_{i,j}$ (see, e.g. Fletcher 1987).

2.4 Constrained Harvesting

It may often be the case that the optimal harvest strategy cannot be implemented, possibly stages cannot be targeted exclusively (e.g., if age cannot be exactly determined in the field) or perhaps some sites present logistical difficulties. In these cases, one compromises the optimal strategy for a more tractable solution. Suppose, for instance, that the optimal strategy is to harvest z% of stage i in site j ($h_{i,j} = z$). However, if one cannot separate classes i-1,i, and i+1 in the field, then we must find a new h that will reduce λ^* to 1.0. This new h is estimated by taking a linear combination of the sensitivities of λ to harvest in those classes as follows:

$$\Delta\lambda \approx \sum \left(\Delta h_{i-1,j} \frac{\partial \lambda}{\partial h_{i-1,j}} + \Delta h_{i,j} \frac{\partial \lambda}{\partial h_{i,j}} + \Delta h_{i+1,j} \frac{\partial \lambda}{\partial h_{i+1,j}} \right) \quad (12).$$

Next, introducing the constraint $h = h_{i-1,j} = h_{i,j} = h_{i+1,j}$, we have:

$$\Delta\lambda \approx -h \sum \left(\frac{\partial \lambda}{\partial h_{i-1,j}} + \frac{\partial \lambda}{\partial h_{i,j}} + \frac{\partial \lambda}{\partial h_{i+1,j}} \right) \quad (13),$$

and finally:

$$\hat{h} = \frac{-\Delta\lambda}{\sum \left(\frac{\partial \lambda}{\partial h_{i-1,j}} + \frac{\partial \lambda}{\partial h_{i,j}} + \frac{\partial \lambda}{\partial h_{i+1,j}} \right)} \quad (14).$$

In the denominator, the sensitivities are calculated as in (6), and will be negative. As in the unconstrained optimization problem, $\hat{h}$ can be estimated iteratively by slight modification to (11).

One may easily check that the results in this section hold for more general stage-structured multisite matrices, as well as for the age-structured Leslie matrix, which is a special reduced form of stage-structured models. As an illustration, in the YLHG example we will consider classes based on site, age and breeding status (breeder/non breeder) rather than site and age only.

3.0 THE YLHG MODEL

3.1 Model structure

We consider a two-site matrix with age classes one through six. Ages four, five, and six are partitioned into breeders (B) and non-breeders (NB), giving a total of nine categories (Table 2). We designate the two sites as "GOOD" or "POOR", in reference to the relative reproductive success attained by birds breeding there. One can imagine the difference in fecundity derives from differences in quality of the sites—in access to a food source or reduced exposure to nest predation, for example. We assume the sex-ratio is 1:1 (Migot 1992), and model only the female segment of the population.

We assume no migration occurs among reproductive adults, because they generally show high site fidelity and often return to the same territory in the same colony year after year (Tinbergen 1953; Yesou 1991). Since it is well known that philopatry is not 100%, and has been reported as low as 30% for the Herring Gull, a close relative (Parsons and Duncan 1978; Coulson 1991; Wanless et al. 1996), the breeding colonies

may be considered as sub-populations which are connected predominantly by recruitment dispersal. A general movement pattern seems to be a wide dispersal of first-year birds, an even greater dispersal by second-year birds, followed by a contraction in dispersal from the third year on (Parsons and Duncan 1978). Our model incorporates dispersal into the first two age classes.

We will present a one-site model in addition to the two-site case to serve as a point of comparison. The single site corresponds to the GOOD site in the metapopulation, and we will use results from this model to illustrate the consequences if one ignores spatial structure and focuses control actions only on the most productive site.

3.2 Types and costs of harvesting

The costs associated with each type of management action depend on the life stages to which they are applied. We recognize the following three stages: eggs; breeding adults; juveniles and non-breeding adults. Breeding adults are killed by placing a narcotic bait in the nest, and three visits are required to kill both members of a breeding pair and then to collect the carcasses (N. Sadoul, pers. comm.). Eggs are destroyed by application of an oil-based spray which inhibits hatching or by injection with water (Wanless et al. 1996). Juveniles and non-breeders, which have no established territory, are very difficult to reach--presumably "untouchable". No estimate of per-capita costs are available, but we know *a priori* that culling is more costly than egging.

In the examples which follow, we report not the total cost associated with a culling or egging operation (T_{COST}), but rather the proportion of each age/site class which must be removed ($h_{i,j}$ in eq.1) and also a total "effort", calculated as $T_{EFFORT} = \sum_{i,j} h_{i,j} x_{i,j}$,

needed to bring the population to equilibrium. The total cost of any control action could be calculated from this if one obtains an estimate of both age/site-specific cost and total population size at equilibrium ($c_{i,j}$ and X in eq. 1). Thus, despite the fact that we lack an estimate of costs associated with each action, we can compare $\hat{h}$ and T_{EFFORT} for culling versus egging to determine how intense the action must be in each case.

3.3 Parameter Estimates

Long-term individual data are lacking for the YLHG in the Western Mediterranean, so our parameter estimates are taken from the literature on Herring Gulls (*Larus argentatus*, HG hereafter), a closely related species. Large-scale population studies have been carried out on the HG on the Isle of May, Scotland (Chabrzyk and Coulson 1976; Duncan 1978; Coulson et al. 1982) and also Treberon Island, France (Migot 1987; Pons and Migot 1995). Survival is lowest in the first year of life, with estimates ranging from 0.55 to 0.83 (Migot 1987; Lebreton et al. 1995). Beyond the first-year, survival is greater (estimates range from 0.8 to 0.935 per year) and does not appear to vary with age (Chabrzyk and Coulson 1976; Duncan 1978; Lebreton et al. 1995; Pons and Migot 1995; Wanless et al. 1996). We use survival probabilities of 0.7 for first-year survival of 0.89 for the second-year and beyond. We selected these values because they were contained in the majority of published confidence intervals.

Recruitment into the breeding segment of the population is graduated, with first time breeding occuring in 14% of 4-year old birds, 69% of 5 year olds, and 92% of 6 year olds (Chabrzyk and Coulson 1976). All birds over the age of 6 are considered to be fully recruited. The average clutch size is 3 eggs, and the average number of fledged chicks per nest ranges from 0.68 to 1.88 or more (Parsons 1975; Camberlain and Flote 1978; Kilpi

1989; Pons and Migot 1995; Bosch and Sol 1998). Thus, each breeding couple produces on average 0.34 to 0.94 female offspring per breeding season. We arbitrarily assume values of 0.75 and 0.55 for the annual production of female fledglings in the GOOD and POOR site, respectively.

To evaluate the effects of differences in recruitment between the GOOD and POOR site, we assume equal dispersal (emigration=immigration=0.5) of young from both sites in the first year, and explore 3 different scenarios for second year dispersal: (a) equal dispersal of 0.5 from both sites in the second year; (b) 0.7 emigrate from the POOR site, 0.35 emigrate from the GOOD site; (c) 0.7 emigrate from the GOOD site, 0.35 emigrate from the POOR site. These scenarios encompass the limit of the range of estimated dispersal (Coulson 1991).

3.4 Optimizations

For both one- and two-site models, we perform two separate optimizations for adult culls. The first optimization is unconstrained, while in the second we constrain the optimal solution to involve all breeding adults. The constrained optimizations are motivated by the fact that exact age determination may be impossible in the field, so one may be forced to apply culling to all breeders (either on one or both sites for the two-site model) rather than a particular age class of breeders. For this case, we estimate one parameter, $\hat{h}_{breeders}$, by taking a linear combination of sensitivities to harvest of each breeding age class (as outlined in section 2.4).

In all egging scenarios, we estimate the proportion of clutches that would need to be destroyed ($\hat{h}_{clutches}$) to bring the population to equilibrium. For the metapopulation, we estimate $\hat{h}_{clutches}$ by either focusing on clutches in the good site first and then, if

necessary, estimating additional egging needed on the poor site, or we estimate $\hat{h}_{clutches}$ assuming that egging is done equally on both sites.

Finally, we compare results between the three methods already described: the standard linear programming technique (LP), the one-step approximation using sensitivity results (1step), and a Newton-Raphson iterative estimate using sensitivities (NR). Our programs were written with MATLAB®, and we used the function, **lp**, from MATLAB® to obtain LP solutions.

4.0 RESULTS

4.1 One-site example with adult culls

For the unconstrained optimization, both LP and NR gave identical results: harvest 22.67% of 6^+ breeders (see Table 3a). The 1step approximation underestimates the amount of necessary harvest by 10% (20.40% of 6^+ breeders), resulting in a slightly lower estimate of total effort. Because as expected LP and NR converge to the same solution, we report only 1step and NR results in all subsequent tables.

In the constrained optimization (Table 3b), the NR method predicted that 17.49% of the breeding population would need to be killed (and at only a slightly higher relative cost than if only 6^+ breeders were targeted). The 1step method underestimated the amount of necessary harvest by 5.5%.

In both one-site examples, using the one-step approximation would result in an increasing annual population (less than 1% for both the unconstrained and constrained case).

4.2 Multi-site example with adult culls

The estimated amount of harvest and effort for all three dispersal scenarios for the unconstrained optimization is given in Tables 4a-c. The one-step approximation underestimates in the two cases with unequal second year dispersal. For cases (a) and (c), when migration out of the GOOD site is greater than or equal to migration into the GOOD site, the harvesting strategy involves a complete harvest of all breeders on the GOOD site and a partial harvest on the POOR site of 6^+ breeders. The least costly case is (c), because more birds migrate to the POOR site, where fecundity is lower, and consequently the population growth rate is the lowest. The 6^+ breeders in the GOOD site have the greatest reproductive value, and so in case (b), where more birds immigrate into the GOOD site, we see that the population can be regulated simply by harvesting this age class. However, (b) is the most costly case because population growth rate is highest ($\lambda = 1.0929$).

We explored two constrained scenarios (distinguished by superscripts 1 and 2 in Tables 5a-c). In the first, we estimated the proportion of all breeders (on both sites) that would need to be killed. In the second, we assumed all breeders on the GOOD site were killed and estimate the additional proportion of breeders on the POOR site that would need to be killed (for case (b) we estimated only the proportion of breeders to be killed on the GOOD site since a total harvest of breeders there reduced λ below 1.0). For the case with equal second year dispersal, (a), there was no difference between the constrained and unconstrained model estimates of effort for culling a proportion of all breeders on the POOR site or just 6^+ breeders in the POOR site. For the other constrained scenarios, the estimated effort is greater due to the fact that the most fecund individuals cannot be

isolated with certainty and so the culling effort must be applied across several ages and/or sites.

Cost and harvest strategy differ depending on the pattern of dispersal. As more birds migrate into the GOOD site, there is a greater proportion of breeders in the population attaining high reproductive success. This increases both the population growth rate and management costs needed to maintain equilibrium

We looked at the consequences of applying solutions derived for the one-site model to the GOOD site in the metapopulation model. Depending on which migration pattern is assumed, harvesting 22.67% of 6+ breeders or 17.49% of all breeders on the GOOD site yields λ's ranging from 1.0321 to 1.0543, all of which indicate an increasing population. Clearly, recognizing spatial dynamics is necessary to achieve management objectives.

4.3 Egging results

For a one-site model, we would need to destroy 65.76% of clutches to achieve a stable annual population, while a multi-site model requires a 100% clutch destruction in the good site and some additional egging in the poor site (except for case b, Table 6a). Assuming egging is performed equally at both sites (Table 6b), between 52% - 63% of clutches need to be destroyed, depending on dispersal. As expected, the estimated effort for this constrained scenario is slightly higher due to the fact that some efficiency is lost by not focusing more intensely on the good site.

Comparing the control effort expended for culling versus egging, we find that egging requires the destruction of 6-7 times as many clutches as breeding couples (i.e. approximately 10 times as many eggs as adults).

5.0 DISCUSSION

Our general approach confirms the role of reproductive values in determining optimal harvesting strategies (MacArthur 1969; Law 1979) An intuitive criterion for determining which age classes to harvest is based on inspection of $v_{i,j}/c_{i,j}$ values. In particular, costs are minimized by harvesting the stage class with the greatest $v_{i,j}/c_{i,j}$ value. Furthermore, we demonstrate that the amount of harvest required for the selected stage classes can be determined by sensitivity analysis, and is inversely proportional to the sensitivity of survival in the selected stage class. This approach provides a link between a standard form of analysis for matrix models—sensitivity analysis—and a standard application of matrix models—harvest optimization.

The iterative NR technique converges to the same solutions as linear programming. The 1step method provides a good approximation, only slightly underestimating the true harvest. However, when the true harvest required is large, the estimate is particularly low. In general, $\lambda(h_{i,j})$ is a concave function on the interval [0,1], and the non-linearity increases with $\Delta\lambda$, leading to a negative bias in harvest estimates. A parameter's sensitivity, which gives the first derivative with respect to λ, is only valid in a small neighborhood, and making large extrapolations can be expected to produce biased predictions (Caswell 1996 ; Benton and Grant 1999).

By inclusion of spatial structure in the matrix models, we demonstrated how the pattern of dispersal affects the optimal harvesting strategy. First, the optimal solution is no longer limited to the harvest of only two age classes. Although in our models dispersal was limited to the first two age classes, we still obtained solutions involving more than two classes because breeding recruitment was graduated and thus non-breeding adults

escaped the cull. Second, when sites differ in quality (such as higher survival or fecundity), the most efficient technique is to focus control actions on the better quality site (cf Defos du Rau 1995). If effort cannot be targeted directly at specific age classes (due to practical limitations), then applying control measures to age classes other than the most productive increases the amount of effort and cost that needs to be expended. However, except possibly for commercially raised animals where ages are known exactly, it will generally not be possible to precisely target the age classes identified in the optimal solution.

The amount of harvest required to maintain equilibrium is a function of site quality and the balance between immigration and emigration—both λ and T_{EFFORT} increase as dispersal favors more productive sites. However, one should not isolate productive sites and manage them as closed populations, as we demonstrated by evaluating the effects of implementing one-site harvest strategies to a metapopulation. In our example, this led to an annually increasing system ($\lambda > 1.0$ for all dispersal scenarios). The reason for this is that both our GOOD and POOR sites, when examined separately, had positive growth rates. Therefore, growth on the POOR site, which was not subjected to harvesting, more than compensated for the reduction in numbers on the GOOD site.

By comparing the estimates of per-capita culling and egging effort needed to prevent the population from increasing, we see that culling requires nearly ten times less effort per-capita. Thus, the optimal solution will be to cull breeding adults as long as the per-capita culling cost is no more than 10 times greater than the per-egg cost of egging. This difference in effort can be explained by the great difference in sensitivity of λ to adult survival versus newborn survival. Among long-lived species, we find a consistent

trend of a much higher sensitivity to survival than to fecundity (Lebreton and Clobert 1991).

While the most effective treatment appears to be the culling of breeding adults, we have not modelled any secondary effects such an action might induce. As has been observed on the Isle of May (Coulson et al. 1982), initial cullings remove the oldest individuals and also reduce colony density, which seems to facilitate recruitment of younger first-time breeders. This is a negative side-effect, particularly if young breeders achieve the same reproductive success as experienced adults as some observations have suggested (Coulson et al. 1982; Kilpi 1989; Annett and Pierotti 1999). However, studies of other long-lived sea birds have suggested that birds defer recruitment to an older age because of a reproduction cost which lowers survival when the first breeding attempt is too young (Wooller and Coulson 1977; Pyle et al. 1991; Pyle et al. 1997). Thus, if culling facilitates the recruitment of younger breeders, this is perhaps mitigated by a consequent reduction in survival.

Culling could also impact dispersal recruitment. Several authors have suggested that birds must first receive a positive stimulus before selecting a breeding site (Chabrzyk and Coulson 1976; Duncan 1978). Potential recruits witnessing a cull may be discouraged from recruiting to that site the following year, and thus culling could reduce breeding populations at that site further than anticipated while potentially shifting the problem to another site. Bosch et al. (2000) found some evidence of this after heavy culling on the Medes Islands, Spain. The overall effect on λ would depend on the quality of the site where recruitment eventually occurs—if it is a colony with lower fecundity

than the one culled, λ will be decreased further; if it is to a colony with higher fecundity, then λ will not be decreased as much as anticipated.

The possible effect of density on reproductive success (Kilpi 1989) or recruitment (Chabrzyk and Coulson 1976; Duncan 1978) are also not taken into account here. One may argue that a vigorous culling regimen may maintain the populations below a level where density effects occur. On the other hand, one may also reduce the population to a point where it is *released* from density effects that may have already been present, which could allow acceleration or deceleration in recruitment rates and in population growth rates.

A caution about the interpretation of our results--the optimal solutions are obtained from an equilibrium perspective. This means that we solve for the solution which yields the optimal equilibrium age/site structure (the culling of which is least expensive). This is mathematically convenient, but ignores two points: transient effects will be observed when the optimal solution is applied to a non-equilibrium population structure; also, it does not consider the "optimal trajectory" for reaching the optimal solution. These shortcomings were pointed out by Harley and Manson (1981), who added additional constraints to the optimization problem so that a smooth approach to the optimal solution was found.

Previous culling actions were performed on HG colonies under the assumption that individual colonies represented closed populations (Coulson 1991). However, it is well known that there is much exchange between colonies, and as even our simplified models reveal, the rates of exchange have important implications for the management of a metapopulation. We believe that the specification of a management action will depend

on a solid understanding of which colonies are interacting, and measurement of fecundity, survival, and dispersal at the colony-level. The best way to gain this understanding will be through the analysis of resightings and recoveries, and so we emphasize the importance of continuing the banding of both chicks and breeding adults.

ACKNOWLEDGEMENTS

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Table 1: Notation and format of component matrices (R, G, H), and sub-matrices (R_i, $G_{i,j}$, and H_i) in a pre-birth census multi-site matrix , $M = (I-H) \times G \times R$.

$$
R = \begin{bmatrix} R_1 & . & . & . & R_n \\ I_1 & 0 & . & . & 0 \\ 0 & . & 0 & . & . \\ . & 0 & . & 0 & . \\ . & . & 0 & . & 0 \\ 0 & . & . & 0 & I_n \end{bmatrix} \text{, where } R_i = \begin{bmatrix} r_{i,1} & 0 & . & 0 \\ 0 & . & . & . \\ . & . & . & 0 \\ 0 & . & 0 & r_{i,p} \end{bmatrix},
$$

and I_i is the *p* x *p* identity matrix;

$$
G = \begin{bmatrix} G_{1,0} & G_{1,1} & 0 & . & . & 0 \\ 0 & G_{2,1} & G_{2,2} & . & . & . \\ . & . & . & . & 0 & . \\ . & . & 0 & G_{n-1,n-2} & G_{n-1,n-1} & 0 \\ 0 & . & . & 0 & G_{n,n-1} & G_{n,n} \end{bmatrix} \text{, where } G_{i,j} = \begin{bmatrix} g_{1,1}^{i,j} & . & . & . & g_{1,p}^{i,j} \\ . & . & . & . & . \\ g_{k,1}^{i,j} & . & g_{k,l}^{i,j} & . & g_{k,p}^{i,j} \\ . & . & . & . & . \\ g_{p,1}^{i,j} & . & . & . & g_{p,p}^{i,j} \end{bmatrix};
$$

$$
H = \begin{bmatrix} H_1 & 0 & 0 & 0 \\ 0 & . & 0 & 0 \\ 0 & 0 & . & 0 \\ 0 & 0 & 0 & H_n \end{bmatrix} \text{, where } H_i = \begin{bmatrix} h_{i,1} & 0 & . & 0 \\ 0 & . & . & . \\ . & . & . & 0 \\ 0 & . & 0 & h_{i,p} \end{bmatrix};
$$

$$
M = \begin{bmatrix} (I-H_1)(R_1 G_{1,0} + G_{1,1}) & (I-H_1)(R_2 G_{1,0}) & . & . & (I-H_1)(R_n G_{1,0}) \\ (I-H_2)G_{2,1} & (I-H_2)G_{2,2} & 0 & . & 0 \\ 0 & (I-H_3)G_{3,2} & (I-H_3)G_{3,3} & 0 & . \\ . & 0 & . & . & 0 \\ 0 & . & 0 & (I-H_n)G_{n,n-1} & (I-H_n)G_{n,n} \end{bmatrix}
$$

Table 2: The multi-site matrix for the YLHG model. There are six age classes (one through six, hence a pre-birth census format) with ages four, five and six divided into breeders (B) and non-breeders (NB). S_i is a 2x2 matrix of age-specific survival-dispersal probability, and R_i is a 2x2 age specific fecundity matrix. α_i is the probability of becoming a breeder at age i = 4, 5, or 6. Each entry in the vectors is a 2x1 vector corresponding to the number of individuals for a given age/site category.

$$
\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_{4B} \\ n_{4NB} \\ n_{5B} \\ n_{5NB} \\ n_{6+B} \\ n_{6+NB} \end{bmatrix}_{t+1}
=
\begin{bmatrix}
0 & 0 & 0 & S_0 R_{4B} & 0 & S_0 R_{5B} & 0 & S_0 R_{6+B} & 0 \\
S_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \alpha_4 S_3 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & (1-\alpha_4)S_3 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \alpha_5 S_4 & \alpha_5 S_4 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & (1-\alpha_5)S_4 & (1-\alpha_5)S_4 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \alpha_6 S_5 & \alpha_6 S_5 & S_6 & S_6 \\
0 & 0 & 0 & 0 & 0 & (1-\alpha_6)S_5 & (1-\alpha_6)S_5 & 0 & 0
\end{bmatrix}
\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_{4B} \\ n_{4NB} \\ n_{5B} \\ n_{5NB} \\ n_{6+B} \\ n_{6+NB} \end{bmatrix}_{t}
$$

Table 3. Comparison of 1-site unconstrained and constrained optimization solution and relative harvest cost (T_{EFFORT}) between all 3 methods: linear programming (LP), 1-step sensitivity approximation (1step), and a Newton-Raphson iterative estimation (NR). In the absence of harvesting, $\lambda = 1.1035$; λ_H is the population growth rate after harvesting.

(a) Unconstrained: All models identify the age class to harvest as breeders in the 6+ category (6$^+$breeder).

(b) Constrained: Harvest was constrained assuming that adults cannot be aged in the field, and thus h is applied equally to 4,5 and 6$^+$ breeders.

(a)

Method	$\hat{h}_{6+breeder}$	λ_H	$\hat{T}_{EFFORT}$
LP	0.2267	1.0000	0.0690
1step	0.2040	1.0093	0.0627
NR	0.2267	1.000	0.0690

(b)

Method	$\hat{h}_{breeder}$	λ_H	$\hat{T}_{EFFORT}$
1step	0.1653	1.0055	0.0656
NR	0.1749	1.000	0.0693

Table 4. Comparison of multisite unconstrained optimization solution and relative harvest cost (T_{EFFORT}) between 1-step sensitivity approximation (1step), and a Newton-Raphson iterative estimation (NR). In the absence of harvesting and dispersal, $\lambda_G = 1.1035$, $\lambda_P = 1.0687$. Dispersal probabilities of 0.5 for both sites are assumed for the first age class. λ_H is the population growth rate after harvesting. (a) Dispersal probabilities of 0.5 for both sites for the second age class are assumed, and for the entire metapopulation $\lambda^* = 1.0869$. (b) In the second age class, emigration from the POOR site is 0.7 while emigration from the GOOD site is 0.35, and for the entire metapopulation $\lambda^* = 1.0929$. (c) In the second age class, emigration from the POOR site is 0.35 while emigration from the GOOD site is 0.7, and for the entire metapopulation $\lambda^* = 1.0808$.

(a)

Method	$\hat{h}_{breeder,site}$	λ_H	$\hat{T}_{EFFORT}$
1step	$4G=5G=6^+G = 1.0$ $6^+P = 0.0086$	1.000	0.0513
NR	$4G=5G=6^+G = 1.0$ $6^+P = 0.0086$	1.000	0.0513

(b)

Method	$\hat{h}_{breeder,site}$	λ_H	$\hat{T}_{EFFORT}$
1step	$6^+G = 0.2437$	1.0305	0.0382
NR	$6^+G = 0.6136$	1.0000	0.0558

(c)

Method	$\hat{h}_{breeder,site}$	λ_H	$\hat{T}_{EFFORT}$
1step	$4G=5G=6^+G = 1.0$ $6^+P = 0.0525$	1.0006	0.0505
NR	$4G=5G=6^+G = 1.0$ $6^+P = 0.0538$	1.000	0.0510

Table 5. Comparison of multisite constrained optimization solutions (assuming age determination was impossible in the field) and relative harvest cost (T_{EFFORT}) between 1-step sensitivity approximation (1step), and a Newton-Raphson iterative estimation (NR). In the absence of harvesting and dispersal, $\lambda_G = 1.1035$, $\lambda_P = 1.0687$. λ_H is the population growth rate of the metapopulation after harvesting. Harvesting was constrained to [1]breeding adults only on both sites; [2]all breeders on the good site and then the additional amount of harvest needed for breeders on the poor site was estimated. (a) Migration rates of 0.5 for both sites and both first and second age classes are assumed. (For the entire metapopulation $\lambda^* = 1.0869$).
(b) Dispersal probabilities of 0.5 for both sites are assumed for the first age class. In the second age class, emigration from the POOR site is 0.7 while emigration from the GOOD site is 0.35. (For the entire metapopulation $\lambda^* = 1.0929$).
 (c) Dispersal probabilities of 0.5 for both sites are assumed for the first age class. In the second age class, emigration from the POOR site is 0.35 while emigration from the GOOD site is 0.7. (For the entire metapopulation $\lambda^* = 1.0808$).

(a)

Method	Constraint	$\hat{h}_{breeder}$	λ_H	$\hat{T}_{EFFORT}$
1step[1]	Equal proportion in both sites	0.1403	1.0025	0.0593
1step[2]	Harvest GOOD site first, POOR if needed	0.0077	1.000	0.0513
NR[1]	Equal proportion in both sites	0.1445	1.000	0.0610
NR[2]	Harvest GOOD site first, POOR if needed	0.0077	1.000	0.0513

(b)

Method	Constraint	$\hat{h}_{breeder}$	λ_H	$\hat{T}_{EFFORT}$
1step[1]	Equal proportion in both sites	0.1507	1.0027	0.0622
1step[2]	Harvest GOOD site first, POOR if needed	0.2039	1.0256	0.0413
NR[1]	Equal proportion in both sites	0.1554	1.000	0.0641
NR[2]	Harvest GOOD site first, POOR if needed	0.3775	1.000	0.0562

(c)

Method	Constraint	$\hat{h}_{breeder}$	λ_H	$\hat{T}_{EFFORT}$
1step[1]	Equal proportion in both sites	0.1297	1.0022	0.0561
1step[2]	Harvest GOOD site first, POOR if needed	0.0463	1.0003	0.0508
NR[1]	Equal proportion in both sites	0.1333	1.000	0.0576
NR[2]	Harvest GOOD site first, POOR if needed	0.0468	1.000	0.0511

Table 6a: Comparison of unconstrained egging solutions for 1-site and multi-site models. Solutions come from the NR methods. λ^* is the population growth rate in the absence of harvesting. (a) Dispersal probabilities of 0.5 for both sites and both first and second age classes are assumed.
(b) Dispersal probabilities of 0.5 for both sites are assumed for the first age class. In the second age class, emigration from the POOR site is 0.7 while emigration from the GOOD site is 0.35.
(c) Dispersal probabilities of 0.5 for both sites are assumed for the first age class. In the second age class, emigration from the POOR site is 0.35 while emigration from the GOOD site is 0.7.

Model	$\hat{h}_{clutches}$	λ^*	$\hat{T}_{EFFORT}$
1-site	0.6576	1.1035	0.4025
Multi-site			
(a)	$\hat{h}_{clutches,good} = 1.0$ $\hat{h}_{clutches,poor} = 0.0661$	1.0869	0.3261
(b)	$\hat{h}_{clutches,good} = 0.8458$	1.0929	0.3493
(c)	$\hat{h}_{clutches,good} = 1.0$ $\hat{h}_{clutches,poor} = 0.3082$	1.0808	0.3212

Table 6b: Comparison of constrained egging solutions for 1-site and multi-site models. Estimates refer to the same amount of egging being performed on both sites. Solutions come from the NR methods. λ^* is the population growth rate in the absence of harvesting. (a) Dispersal probabilities of 0.5 for both sites and both first and second age classes are assumed.
(b) Dispersal probabilities of 0.5 for both sites are assumed for the first age class. In the second age class, emigration from the POOR site is 0.7 while emigration from the GOOD site is 0.35.
(c) Dispersal probabilities of 0.5 for both sites are assumed for the first age class. In the second age class, emigration from the POOR site is 0.35 while emigration from the GOOD site is 0.7.

Model	$\hat{h}_{clutches}$	λ^*	$\hat{T}_{EFFORT}$
1-site	0.6576	1.1035	0.4025
Multi-site			
(a)	$\hat{h}_{clutches} = 0.6049$	1.0869	0.3701
(b)	$\hat{h}_{clutches} = 0.6251$	1.0929	0.3825
(c)	$\hat{h}_{clutches} = 0.5824$	1.0808	0.3564

Figure 1a: The 1-step method estimates $h_{i,j}$ by projecting a tangent line with slope $\left(\dfrac{\partial \lambda^*}{\partial h_{i,j}}\right)$ from λ^* (population growth rate in absence of harvesting) and finding the intersection with the line $\lambda_H = 1.0$ (population growth rate with harvesting).
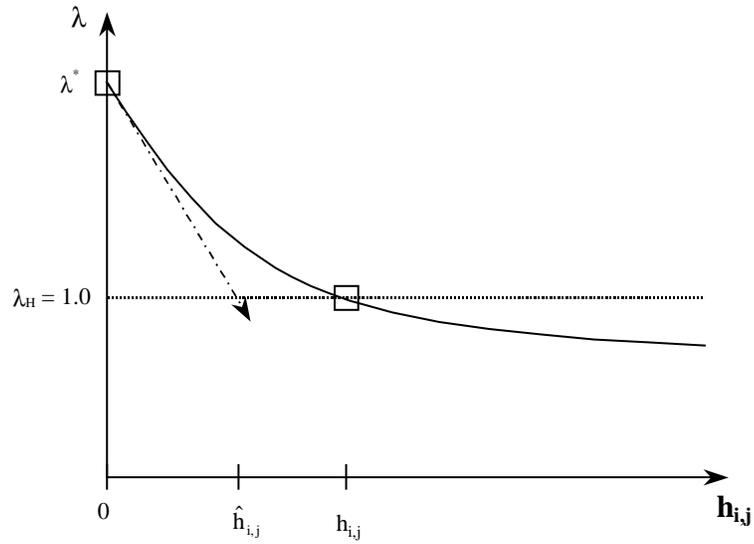
Figure 1b: The NR method estimates $h_{i,j}$ iteratively by projecting tangent lines with slopes $(\dfrac{\partial \lambda^{(k)}}{\partial \hat{h}_{i,j}^{(k)}})$ from points $\lambda^{(k)}$ until $\lambda^{(n)} = \lambda_H = 1.0$ is achieved.
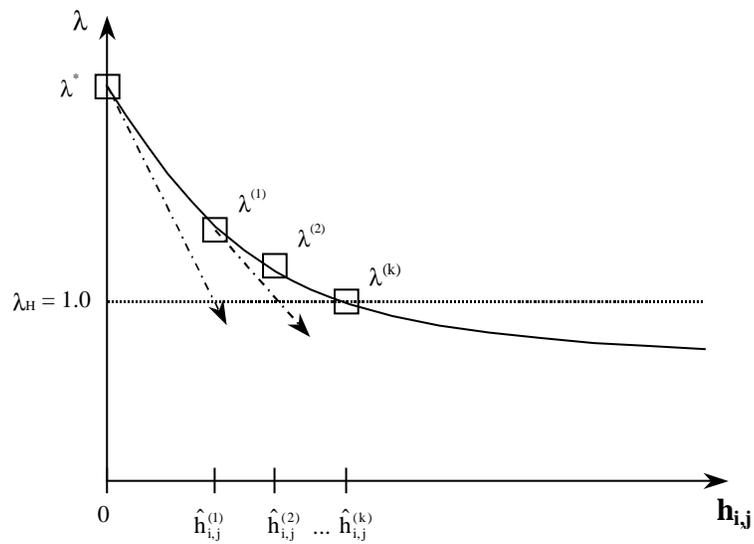
Chapter 3: Optimal harvesting in multi-site, age-structured populations:

The use of reproductive values to optimally remove surplus production

Abstract: Multi-site Leslie matrices were used to model population dynamics and yields from harvesting a fish population after a portion of fishable area was closed. I developed a methodology for determining the optimal age class to harvest from a density-dependent population. The unconstrained maximum sustainable yield (MSY) comes from removing individuals from the age class with the smallest ratio of reproductive value to harvest value. This vector can also be used to compare MSY *a priori* for different combinations of harvested age classes. The method is illustrated for a model of Arcto-Norwegian cod. Density-dependence operated on first year survival with a Ricker-type recruitment function. I explored MSY for a one-site model and compared results to a model that included a Marine Reserve where only a portion of the population was exploitable. Comparing the MSY between these two scenarios, I found that a 25% reserve produced yields that were 63-123% that in a 1-site system (assuming fishing was held to the optimal level), depending on the transfer rate, reproduction in the reserve, and the age classes harvested. When fishing in a 1-site system exceeded the optimum level by 1.5 or 2.0 times, then yields from the reserve model were always higher than the no-reserve model. Beginning from an unharvested population in equilibrium, the approach to MSY was gradual, whereas beginning from a harvested population and increasing the youngest age harvested showed a faster convergence to MSY.

Keywords: Optimal harvesting; density-dependent matrix model; sensitivity analysis; Arcto-Norwegian cod; *Gadus morhua*, marine reserve

1.0 Introduction

The first analytical treatments of optimal harvesting were presented in the 1970s by Beddington and Taylor (1973), Doubleday (1975), and Rorres and Fair (1975), although the subject of maximizing harvesting had been present in the literature since at least Baranov (1918) (translated in Vilim 1977). Working with a density-independent age-structured matrix model (i.e. the "Leslie" matrix, Leslie 1945), Beddington and Taylor (1973) and Rorres and Fair (1975) demonstrated analytically that the form of the optimal solution involved harvesting at most two age classes: the complete harvest of one age class and a partial harvest of a second (younger) age class. Doubleday (1975) was the first to recognize that optimal harvesting from a Leslie matrix could be easily solved by linear programming, and the 2-age class solution was shown to result directly from Linear Programming Theory (Getz and Haight 1989). Dynamic programming, invented by Bellman (1961), was first introduced into the fishery literature by Walters (1975) and Hillborn (1976). Other optimization techniques have been used, including graphical approaches and numeric searches where various potential strategies are explored and the resulting MSY is compared (Ricker 1958; Hilborn 1979; Hilborn 1985a; Hightower and Lenarz 1989; Jensen 1996). Hilborn and Walters (1992) review some of these techniques.

The methods described above are somewhat of a "black box," meaning that they rely on numeric computations and/or simulations to identify the optimal strategy without necessarily revealing the underlying biological reasons that make them optimal. In addition, this work pertained to single-site populations. For multi-site, stage-structured matrix models, Brooks and Lebreton (2001) introduced a new method for determining optimal harvest, which

provided a biological criterion for selecting the harvested stage and determining the amount of harvest required to maintain a stable population. They showed that the optimal stage (to minimize harvest cost of a pest) had the largest ratio of reproductive value: harvest cost, and their method for estimating harvest was based on sensitivity analysis (see, e.g. Caswell 1989). Alternatively, for a commercially valuable species, MSY would be maximized by harvesting the stage with the smallest ratio of reproductive value: harvest value.

For some harvested populations, it may be reasonable to assume that population size is maintained below the level where self-regulation occurs. However, the accumulated evidence from sustained high levels of fishing (and in some cases, overly high levels leading to recruitment overfishing) suggests the existence of density dependence (Shepherd and Cushing 1980; Hilborn and Walters 1992; Cushing 1995). This is significant for commercial industries where the size of recruited cohorts determines annual catches. This could be accounted for in a population model by including, for example, a Ricker or Beverton-Holt type of stock-recruitment relationship (Hilborn and Walters 1992; Cushing 1995).

Reed (1980) first dealt with optimal harvesting in a density-dependent context. He introduced a Ricker relationship for first year survival into the Leslie matrix for an Arcto-Norwegian cod population, and demonstrated how this non-linear harvesting problem could be solved by repeated application of a linear optimization. He found that the optimal strategy involved the harvest of at most 2 age classes, as in the density-independent models.

In this paper, the density-independent optimization methodology of Brooks and Lebreton (2001) is developed in a density-dependent context. I present the derivation of a biological criterion for selecting the optimal age- and site-class to harvest and then describe a means for determining the proportion of that class to be harvested. This method is illustrated with a

model of Arcto-Norwegian cod where first year survival is density dependent. Using the data presented in Reed (1980), I develop a one-site age-structured matrix model and estimate the optimal harvesting strategy. I then develop a 2-site model to predict optimal harvesting strategies when only a part of the population is available to the fishery as a result of a marine reserve being established. For both models, the optimal strategies can be interpreted as a "theoretical" MSY, since implementation problems guarantee a lower observed yield. I therefore address constrained harvesting scenarios and demonstrate how various alternative strategies can be ranked *a priori*. I discuss how the strategy differs between a one-site model (no-reserve system) and a two-site model (reserve system), and compare expected yields (short-term and equilibrium) and recruitment.

1.1 Marine reserve modelling

Increased fishing intensity coupled with increasingly sophisticated fishing gear, has intensified the problem of overfishing. Marine reserves, areas where fishing is prohibited year-round, are being evaluated as a means of maintaining the industry by conserving a portion of reproductive biomass that can re-stock the areas outside of the reserves and by acting as a hedge against recruitment failure altogether (Alcala 1988; Davis 1989; Carr and Reed 1992; Buxton 1993; Attwood and Bennett 1994; Ferreira and Russ 1995; Guenette, Lauck, and Clark 1998; Murawski et al 2000; see also Vol. 66(3) of Bull. Mar. Sci. 2000). Reserves could also maintain and/or increase species richness and abundance, protect the genetic diversity of wild stocks, and provide undisturbed breeding sites (Alcala 1988; Davis 1989; Carr and Reed 1992). Reserves are being considered as a viable management option because previous management strategies (e.g. quotas, bag limits, closed season, and size limits) have failed (Roberts et al. 1995). It is thought that reserves, once established, would

be "self-maintaining" (Plan Development Team 1990). Additionally, reserves could provide an insurance policy against collapse in non- reserves, should management fail again in those areas (Plan Development Team 1990).

The last decade has seen great interest in the development of models that variously attempt to predict necessary reserve size and effect on catch and/or spawning stock biomass (SSB). Cohort models were considered by Polacheck (1990) for Atlantic cod (*Gadus morhua*) and DeMartini (1993) for a suite of tropical fish with varying life-histories. They found that the main benefit of reserves was the increase in SSB, however this was at the expense of yield. Also, high transfer rates (movement of fish between reserve and non-reserve) tended to mitigate the benefits without necessarily producing a complementary gain in yield. However, by modeling the fate of only 1 cohort, one of the potentially greatest reserve benefits--enhanced recruitment--cannot be quantified.

Man et al. (1995) modified the original metapopulation model of Levin (1969) to include two state variables: the proportion of reserve or of non-reserve patches occupied by recruited individuals. Although this model incorporated recruitment, it lacked age-structure, so yield could not be quantified in terms of biomass. Also, solutions were examined at equilibrium conditions, so short-term consequences could not be evaluated, nor could one evaluate the length of time needed to reach equilibrium.

More recently, several models have incorporated age or size structure, and stock-recruitment relationships, and have addressed the immediate consequences of closures on catch as well as equilibrium dynamics. Holland and Brazee (1996) developed an age-structured population model for red snapper in the Gulf of Mexico, and focused on maximizing present value of harvests rather than maximizing sustainable yields. Sladek

Nowliss and Roberts (1997) and Sladek Nowliss and Roberts (1999) created size-structured "matrix" models for 4 tropical species (queen trigger fish, red hind, white grunt, and spiny lobster). They estimated optimal reserve size (via a numeric search) by attempting to maximize long-term sustainable yield. Guenette and Pitcher (1998) returned to the Atlantic cod (originally modeled by Polacheck 1990) and created an age-structured model to compare the benefits of several reserve sizes to a system managed without a reserve.

St. Mary et al. (2000, pp.675-676) summarized the usefulness of mathematical models of marine reserves as follows: "[they] can provide initial insight into the implications of alternative strategies and can reveal how the implications depend on specific characteristics of the managed system." This accurately summarizes the objectives of my reserve modeling. That is, I aim to compare MSY patterns (as predicted by my method) between adding a reserve versus alternative strategies of simply increasing the minimum age harvested or decreasing the level of harvest. I explore these yields for a given reserve size (25% of total area) under 3 different transfer rates. I also compare short-term consequences for yield for each action. My marine reserve model is a multi-site Leslie matrix (Le Bras 1971; Rogers 1974; Lebreton 1996) with density-dependent first-year survival.

1.2 Arcto-Norwegian cod

The Arcto-Norwegian cod is the largest species among the gadiforms, and is one of the most prolific egg producers—spawning up to 7 million eggs in a year (Paxton and Eschmeyer 1995). Maturation occurs between ages 7-13, although there is evidence that high fishing has led to earlier maturation in some stocks (Jorgensen 1990). Spawning occurs in the spring off the coast of Norway (Garrod 1967). The eggs drift Northeast towards the Barents Sea and the Spitsberger shelf, where the immature cod remain and spend the

majority of their time with only limited migration Southwest back towards the Norway coast (Garrod 1967). There is fairly strong evidence that density-dependent survival acts in the first year of life, and Cushing (1995, p. 265) noted that cod, among other gadoids, "do not distinguish their food from their children." In addition to cannibalism, there is much evidence that temperature plays a role in development time, summer migration and survival of young fish (Dickson, Pope, and Holden 1974; Kendall, Ahlstrom, and Moser 1984; Garrod 1985).

Fisheries from several countries have actively fished the Arcto-Norwegian cod, with increasing intensity since the end of World War II (Garrod 1967; Garrod 1977; Garrod 1985). There are three main regions fished, one which focuses on spawners off the coast of Norway in the spring, and two others which harvest a mix of immature and mature fish on the feeding grounds later in the year (Garrod 1985). For the first decade or two following the war, exploitation increased steadily while catches remained the same (Garrod 1967). In 1963, the minimum mesh size was increased from 110 to 120 mm (Garrod 1967). Despite this, catches continued to decline, and recruitment declined for much of the 1970s (Garrod 1985). Thus, catch per unit effort was in decline for much of the fishery's operation. Total landings in the early 1980s were one third that in the early 1960s (Garrod 1985) and by the late 1980s, the stock size had been reduced by about 75% compared to the 1940s (Jorgensen 1990). This picture of stock decline over a 40 year period suggests that traditional management techniques have been ineffective. As many stocks world-wide have shown similar or worse declines, interest in including closed areas as part of the management repertoire has increased. In this study, the potential benefits of creating a marine reserve are explored for Arcto-Norwegian cod.

2.0 Model Development and Methods

    2.1 One-site density-independent Leslie matrix

For populations that exhibit an annual birth pulse, and where annual survival and reproduction are similar among individuals of a given age, the Leslie matrix is a convenient model. Reproduction is assumed to occur as a "pulse," or at least in a short enough period of time that no mortality occurs contemporaneously. Mathematically, reproduction is represented by the $(n+1)$ x n matrix R. The first row of R contains age-specific fecundities, f_i (the fecundity of an age i individual). Rows 2 through $n+1$ contain the n x n identity matrix. Survival is represented by the n x $(n+1)$ matrix S. The first n rows and n columns of S form a diagonal matrix with entries corresponding to age specific survival (s_i). In the last row, the last entry is zero if n is the maximum age attainable. However, if age n is an "absorbing class" for individuals of age $\geq n$, then that last entry, s_{n+1}, is non-zero and represents annual survival beyond age n. When an "absorbing class" is included, an implicit assumption is that annual fecundity and survival are constant for the remainder of the lifespan, and hence, that senescence is negligible.

The Leslie matrix, L, can be represented in two ways, depending on when individuals are "counted" in relation to reproduction. In the "pre-birth" format, censusing occurs just prior to reproduction and so individuals range in age from 1 to n. A "post-birth" format counts newborns and so the age classes are 0 to n. I represent the pre-birth case by L = SR, thus L has dimension n x n. In the post-birth case, L = RS and so L has dimension $(n+1)$ x $(n+1)$.

The number of individuals within each age class at time t is given by the population vector, N_t. The size of the population one time-step later is $N_{t+1} = LN_t$, and the dimension of

N corresponds with L depending on whether or not newborns are counted. When all entries in L are constant, then the model is density-independent and population growth is exponential. If any of the entries in L involve a functional relationship with any entries in N_t, then the model is density-dependent and population growth is self-regulated.

Well known asymptotic results have been derived elsewhere (Caswell 1989) so I present only a few essential details. Population growth rate, λ, is the dominant eigenvalue of L. In the density-independent case, the population increases/decreases exponentially for $\lambda>1$ or $\lambda<1$, respectively. $\lambda=1$ indicates a stable population (in the density-dependent case, I always have $\lambda=1$ at equilibrium). Associated with λ are a right eigenvector, **w**, and left eigenvector, **v**. **w** gives the stable age structure and **v** gives age-specific reproductive value. The sensitivity of λ to perturbation of entry l_{ij} in L is given by: $\dfrac{\partial \lambda}{\partial l_{ij}} = \dfrac{v_i w_j}{<\mathbf{vw}>}$, where $<\mathbf{vw}>$ is the scalar product.

1.2 Density-dependent matrix models

Construction of a density-dependent matrix is the same as for density-independent matrices—there is a matrix for reproduction (R) and for survival (S). The only difference is that one or more parameters in R or S is a function of one or more age classes in the population vector, N_t. Because of this density-dependent relationship, the population increases up to an equilibrium value, which may or may not be stable. This has several implications for analysis of these models. First, the stability of the equilibrium can be determined by calculating the Jacobian of the matrix (evaluated at the equilibrium value) and then by finding its eigenvalues (Getz and Haight 1989). If all eigenvalues are less than 1 in magnitude, then the equilibrium is stable; any eigenvalues greater than 1 in magnitude means the equilibrium is unstable; an eigenvalue equal to 1 in magnitude indicates a bifurcation

(transition from stability to instability) (Getz and Haight 1989; Caswell 1989; and Caswell 1997).

A second implication relates to sensitivity analysis. As described above for density-independent models, one generally measures sensitivity to λ (population growth rate). However, in a density-dependent model, the population is self-regulating, and so $\lambda=1$ at equilibrium. Perturbing matrix elements will shift the equilibrium value but λ will return to 1. Takada and Nakajima (1992) developed a method for calculating sensitivity in a density-dependent Leslie model for quantities other than the population growth rate. For example, if κ is a density-dependent factor in my matrix model, M (with entries m_{ij}), then the sensitivity of κ to a change in m_{ij} is given by

$$\frac{\Delta\kappa}{\Delta m_{ij}} \approx \frac{\partial\kappa}{\partial m_{ij}} = \frac{v_i w_j}{-\displaystyle\sum_{i,j} v_i w_j \left[\dfrac{dm_{ij}(\kappa)}{d\kappa}\right]_{\kappa=\bar{\kappa}}} \qquad (1)$$

In (1), the sensitivity of κ to m_{ij} is proportional to the sensitivity of λ to m_{ij}, with the denominator containing the derivative of all m_{ij} containing κ and weighted by the corresponding elements of the left and right eigenvectors. This derivative is evaluated at $\bar{\kappa}$, the equilibrium value associated with the unperturbed matrix.

In the matrix models that follow, I introduce density-dependence into first year survival, following a Ricker form, so that the number of one-year olds alive at the end of one time step is given by: $x_1 = Ee^{\alpha-\beta E}$, where $E = \sum_i f_i x_i$, f_i is age-specific fecundity and x_i is the number of age i individuals (Ricker 1954; Reed 1980). In the Ricker equation, α is the coefficient of density-independent survival and β is a density-dependent factor (Cushing 1995). Alternatively, writing $\alpha' = e^{\alpha}$, then I can interpret α' as "the recruits per spawner at low

stock sizes" and β "describes how quickly the recruits-per-spawner drop as [stock size] increases" (Hillborn and Walters 1992, p.260). The stability of the equilibrium for various forms of density dependent first year survival is discussed in Getz and Haight (1989 pp.76-79). For the Ricker equation used in this model, Reed (1980) proved its stability. Further analysis specific to the Ricker model is given in Levin and Goodyear (1980). DeAngelis et al. (1980) proved that the equilibrium is both unique and stable.

1.3 Generalization to multiple sites

I briefly sketch the extension of Leslie-matrices to multiple sites, and refer readers to Lebreton (1996) and Brooks and Lebreton (2001) for a more thorough presentation. In the previous section, all entries in L were considered to be scalar. The multi-site Leslie matrix, M, can be visualized from L as follows. For a model of p sites, each entry in L (hence each entry in R and S) becomes a p x p sub-matrix. In each sub-matrix, the sites are nested within age classes. For example, the first p rows of R contain age specific sub-matrices R_a with entries f_{ij}^a. The age, a, is given on the superscript. The subscript j refers to the site of the mother and i is the site where the mother reproduced. In general, each p x p matrix of age-specific fecundities is considered to be diagonal, thus containing entries r_{ii}^a (Lebreton 1996).

The matrix of survivals also will contain p x p sub-matrices with entries representing the product of annual probability of survival and migration. For example, S contains age specific p x p survival matrices S_a. Entries in S_a are s_{ij}^a for survival of an age a individual that began the year in site j and survived and was present in site i at the start of the next time interval. In representing the process of survival and dispersal in an annual matrix, an assumption has to be made about the timing of migration, traditionally forcing the migration event to occur at the beginning or at the end of the time interval. For this model, I assume migration takes

place at the start of the survival process, which immediately follows reproduction (my matrix, M = SR). This is a simplification of the migration process that can have important implications for the model (see Appendix 1 of Chapter 4 for the implications of migration for the sensitivity of survival).

As in the one-site case, the order in which R and S are multiplied determines the dimension of M: when M = RS, M is $(n+1)p$ x $(n+1)p$; when M = SR, M is np x np. The corresponding population vector, N_t, again has dimensional agreement with M. The dominant eigenvalue of M gives the overall growth rate of the system, and the associated eigenvectors **w** and **v** give age-by-site stable structure and age-by-site reproductive value, respectively. The parameters in R and S can be density-independent or density-dependent.

1.4 Optimal harvesting

The total yield, Y, achieved in a given year is given by

$$Y = \sum_{i,j} \text{weight}_{i,j} x_{i,j} h_{i,j} \qquad (2)$$

where $\text{weight}_{i,j}$ is age- and site-specific weight, $x_{i,j}$ is the number of age i individuals in site j, and $h_{i,j}$ is the proportion harvested from age i in site j. The optimum strategy will maximize Y for all possible h, i.e. it will give the maximum sustainable yield (MSY). Since the only density-dependent term is survival in the first age class, then the number of individuals in age classes >1 at a given site can be calculated as the product of the number of age 1 year olds at the harvested equilibrium value for that site ($\overline{x}_{1(h),j}$) and the cumulative survival from harvesting to age i in that site ($L_{i(h),j}$) for the remaining age classes ($L_{1(h),j}$ is defined to be 1). Consider harvesting age i in site 1 only:

$$Y_{i,1} = \overline{x}_{1(h),1} \text{weight}_{i,1} L_{i,1} h_{a,1} \qquad (3),$$

where $L_{i,1}$ is the cumulative survival to age i in site 1 in the absence of harvesting.

The one-site stock-recruitment Ricker model:

$$x_1 = Ee^{\alpha - \beta E} = \varphi(E) \qquad (4)$$

with $E = \sum_i f_i x_i$, the number of eggs laid. Thus, $\varphi(E)$ provides the number of recruits that survive for a given number of eggs, E, produced in a year. In a multi-site context, (4) becomes:

$$x_{1,j} = E_j e^{\alpha_j - \beta_j E} = \varphi_j(E_j) \qquad (5)$$

where $E_j = \sum_i f_{i,j} x_{i,j}$ is the number of eggs produced by at site j; α_j and β_j are site-specific, Ricker parameters.

Returning to (3), the yield obtained from harvesting only age i at site 1, the sensitivity of the model to $h_{i,1}$ can be found by following (1). In my model, E_j is the density-dependent quantity that ultimately determines first year survivorship in site j. Suppose we have a two site system (j=1 or 2). $h_{i,1}$ will be found in matrix entries $m_{2i-1,2i-3}$ and $m_{2i-1,2i-2}$, which are $(1-h_{i,1})s_{1,1}^{i-1}$ and $(1-h_{i,1})s_{1,2}^{i-1}$. Using the chain rule in conjunction with the density-dependent formula for sensitivity from (1), the derivative of E_1 with respect to $h_{i,1}$ is:

$$\frac{\Delta E_1}{\Delta h_{i,1}} \approx \frac{\partial E_1}{\partial h_{i,1}} = \frac{- v_{i,1} w_{i-1,1} s_{1,1}^{i-1} - v_{i,1} w_{i-1,2} s_{1,2}^{i-1}}{-\sum_{i,j} v_{i,1} w_{i,1} \left[\dfrac{dm_{ij}(E_1)}{dE_1} \right]_{E_1 = \bar{E}_1}} \qquad (5).$$

Recalling that E_1 appears in only the first row of matrix M ($m_{1,j} = f_{1,1}^i \varphi_1(E_1)$), and that $w_{i,1} = w_{i-1,1} s_{1,1}^{i-1} + w_{i-1,2} s_{1,2}^{i-1}$ when $\lambda=1$, (5) simplifies to:

$$\frac{\Delta E_1}{\Delta h_{i,1}} \approx \frac{- v_{i,1} w_{i,1}}{-v_{1,1} \sum_j w_j f_{j,1} \varphi_1'(\bar{E}_1)} \qquad (6).$$

Given that $\Delta h_{i,1} = 0 - h_{i,1} = -h_{i,1}$, an estimate of $h_{i,1}$ is then:

$$\hat{h}_{i,1} = \frac{-\Delta E_1 \left(v_{1,1} \sum_j w_{j,1} f_{j,1} \varphi_1'(\overline{E}) \right)}{v_{i,1} w_{i,1}} \qquad (7).$$

Finally, recognizing that for $\lambda = 1$, $v_{1,1} = R_{0(1)} = \sum_j w_{j,1} f_{j,1}$ ($R_{0(1)}$ is the net reproductive rate at site 1),

$$\hat{h}_{i,1} = \frac{-\Delta E_1 \varphi_1'(\overline{E}_1) R_{0(1)}^2}{v_{i,1} w_{i,1}} \qquad (8).$$

Recall that the expression for yield when only one age is harvested was:

$$Y_{i,1} = \text{weight}_{i,1} \overline{x}_{1(h),1} L_{i,1} h_{i,1} \qquad (9).$$

Substituting $\hat{h}_{i,1}$ and $\overline{x}_{1(h),1} = \phi_1(E_{h_i,1})$, where $E_{h_i,1}$ is egg production in site 1 when age i is harvested by proportion h, the yield becomes:

$$Y_{i,1} = \frac{\text{weight}_{i,1} \phi_1(E_{h_i,1}) L_{i,1} (-\Delta E_1) \varphi_1'(\overline{E}_1) R_{0(1)}^2}{v_{i,1} w_{i,1}} \qquad (10).$$

Lastly, recognizing $L_{i,1} = w_{i,1}$ we have:

$$\hat{Y}_{i,1} = \frac{\phi_1(E_{h_i,1})(-\Delta E_1) \varphi_1'(\overline{E}_1) R_{0(1)}^2}{v_{i,1} \Big/ \text{weight}_{i,1}} \qquad (11).$$

For the harvest of a given age at a given site, there is one level of total egg production which yields the greatest surplus production (see Ricker 1975, p.284). Thus, regardless of the age harvested, $\varphi_1(E_{h_i,1})$ and ΔE_1 will be constant. In other words, there will be many removal strategies that will reduce the stock to a level where surplus production is maximized. However, we want to know which one of those strategies gives the maximum yield. Examining (11), the only age dependent terms are reproductive value in site 1 ($v_{i,1}$) and age-

specific weight in site 1 (weight$_{i,1}$). Thus, yield will increase as this ratio decreases, and the optimal harvesting strategy will be to harvest the age- and site-class with the smallest ratio of reproductive value to weight. (The development above is presented in a multi-site context, but will clearly hold for a one-site model.)

This is precisely the result obtained in the density-independent case by Brooks and Lebreton (2001). The interpretation is analogous also: if all age classes were of the same economic value, the greatest number of individuals could be removed from the least reproductively valuable age class. When economic value (weight in this example) varies with age and site, then an individual's reproductive capacity is "weighted" by his weight.

A general theme from this derivation and that in Brooks and Lebreton (2001) is that of harvesting surplus production. In the density-independent model (Brooks and Lebreton 2001), the aim was to hold population size constant (λ=1) for a species that realized exponential growth (λ^*>1) in the absence of harvesting. The optimal strategy therefore reduced the annual growth potential of the population ($\Delta \lambda = \lambda^* - 1$), i.e. the annual surplus. In the present density-dependent model, the goal was to harvest a population in equilibrium (where λ=1) so that it is reduced to a level ($E_h = \overline{E} - \Delta E$) where surplus production is maximized. Thus, both models dealt with the issue of a population surplus and finding the optimal way to harvest it.

1.5 Beverton-Holt formulation

The development in the previous section assumed a Ricker recruitment function. In the resulting yield equation (11), the only age- and site-specific dependent terms were in the denominator. In the numerator were two terms related to the point of maximum surplus production: $\varphi_1(E_{h_i,1})$ and ΔE_1. ΔE_1 was the change in egg production from the unharvested

equilibrium $\overline{E}_1$ and the level where surplus production was maximized, $E_{h_i,1}$. From Ricker (1975, p.292), the Beverton-Holt recruitment function also possesses one point at which surplus production is maximized. Therefore, whether a Ricker or Beverton-Holt relationship is assumed does not affect the result, because the terms in the final yield equation associated with the function ($\phi(E_{h_i})$ and $\phi'(\overline{E})$) will be constant. Thus, for a Beverton-Holt relation, the same ratio of reproductive value to weight can be used to identify the optimal age (and site) class to harvest.

1.6 Estimation of Proportion to harvest ($h_{i,1}$)

Having identified the optimum age class to harvest, one might look to (8) above, to estimate $h_{i,1}$. All quantities are known except ΔE_1, which is the difference in equilibrium recruitment between unharvested and harvested populations (i.e. $\Delta E_1 = \overline{E}_1 - E_{h_i,1}$). $E_{h_i,1}$ depends on $h_{i,1}$, so $h_{i,1}$ cannot be estimated analytically. Instead, $h_{i,1}$ can be varied between 0 and 1 and the resulting yields compared to identify the level of harvest producing the MSY. (But see Ricker 1975, Appendix III and Hilborn 1985b for a solution when both E and $\phi(E)$ have the same units).

I stated previously that the optimal solution from one-site models involved harvesting at most two age classes. This would be detected from my method as follows: first, the optimal age class, i, is identified from the vector **v**/**weight**; next, one varies $h_{i,1}$ from 0 to 1 and examines the resulting yield. If the yield increases monotonically, then the predicted MSY will occur for $h_{i,1} = 1$. There are two possibilities at this point: either the MSY involves complete harvest of age i at site 1 and no additional harvest, or a second (younger) age class will be harvested partially. To determine which possibility is correct, one returns to the original **v**/**w** vector and selects the age class with the second smallest value, e.g. age j at site k

(j<i necessarily). By fixing $h_{i,1}$ at 1.0, and varying $h_{j,k}$ from 0 to 1, MSY will either increase from the value when only age i was harvested completely or it will not. If it increases, the optimal harvesting strategy involves 2 age classes; if it does not, then only the first age should be harvested.

The reason for the two age strategy in a one-site model is simple: complete harvest of one age class effectively reduces the maximum age. Therefore, at any given time, only one age class can be harvested completely and a second age class partially. However, as Brooks and Lebreton (2001) pointed out, this result is particular to 1-site models. In a multi-site model, migration from unharvested sites can "replenish" age classes beyond the one completely exploited in the harvested site. Therefore, it is possible to obtain optimal solutions involving the harvest of more than 2 age classes in multi-site models. The method for identifying successive ages to harvest remains the same, though.

1.7 Finite versus instantaneous rates

The model parameters s and h have been implicitly assumed to be finite rates (h is akin to u, the finite annual exploitation in the fisheries literature). In the absence of fishing, instantaneous age-specific natural mortality, M_i, is:

$$M_i = -\ln(s_i).$$

The model development assumes age-specific (and site-specific, in a multi-site case) survivals and fecundities are known. Hence, the M_i should be known, regardless of the timing of the fishery. However, the timing of the fishery will affect the estimate of h_i, and hence of F_i (instantaneous fishing mortality). If a pulse fishery is assumed, then h_i can be estimated as outlined in section 2.6, and then F_i is:

$$F_i = -\ln(1 - h_i) \qquad \text{(pulse at start of the year)}$$

<div align="center">or</div>

$$F_i = -\ln(1 - h_i e^{M_i}) \qquad \text{(pulse at end of year)}.$$

If fishing occurs continuously throughout the year or for only a fraction, Δt, of the year, then there is no direct relationship between h and s (see Pollock et al. 1991 and Brooks et al. 1998 for instantaneous rates formulations for these cases). The method in section 2.5 will not work for these cases. Instead, F_i is varied from 0 to 5-M_i. Whereas h_i=1 implies no survival beyond age i, in an instantaneous formulation survival only approaches 0 asymptotically. However, for $Z_i = F_i + M_i \geq 5$, e^{-Z_i} is effectively 0. Thus, 5-M_i can be used as an upper bound for the estimate of F_i. To test whether the optimal strategy involves harvesting more than one age, the process is similar to that outlined in section 2.6—if MSY increases monotonically for F_i in [0,5-M_i], then fix F_i at 5-M_i and vary F_j from 0 to 5-M_j, where j corresponds to the age class with the second smallest ratio of reproductive value to weight.

3.0 The Arcto-Norwegian cod Model: An Illustration

3.1 The one-site case (No Reserve)

A 12 age-class, density-dependent matrix model was constructed using data presented in Reed (1980) (the data trace to Walters (1969) and ultimately to Garrod (1967)). Table 1 summarizes the age-specific values for annual survival, weight, and fecundity. Following the data provided in Reed (1980), I assume survival probability beyond age 12 is zero. Fecundity is given as the proportion mature multiplied by average weight at age (Walters 1969). For the Ricker relationship, $\overline{x}_1 = Ee^{\alpha - \beta E}$, $\alpha = 2.895$ and $\beta = 0.0174$ (Reed 1980).

For this model, I began with an arbitrary initial population structure and projected the model until it reached equilibrium with total population size, $\overline{N}$ (Table 2). At equilibrium, I

estimated the left eigenvector, **v**, which gives age-specific reproductive value. I then found

the ratio of age-specific reproductive value:age-specific weight (Table 3). From this new

vector (**v/w**), it was possible to identify the age class (i) that had the smallest ratio value—

making it the optimal age class to harvest. I then allowed h_i to vary between 0 and 1 and

compared the resulting yields to identify the harvest level giving maximum yield.

Since implementing a single age-class harvest would be impossible in practice, I

considered alternative (constrained) harvesting strategies by looking at the pattern of **v/w**

values. This vector allows one to evaluate *a priori* how different combinations of minimum

and maximum size restrictions will impact expected MSY. Perhaps the most realistic

harvesting strategy to implement involves specifying only a minimum age. This could be

most readily achieved with a minimum mesh size. However, Walters (1969) pointed out that

it was not appropriate to assume knife-edge mesh selection. Therefore, I used age specific

catchability coefficients for ages 3-6 (assuming age 7 was the age of full recruitment) of

0.05, 0.38, 0.62, and 0.85 (Walters 1969), respectively, and calculated yield for all possible

minimum sizes between age 3 and 12.

1.2 The two-site case (Reserve and Non-Reserve area)

A two-site density-dependent matrix model was constructed, using the same age-specific

survival, fecundity, and weight values as for the one-site case (see Table 1).   Site-specific

Ricker functions were created by adjusting α and β until the unfished equilibrium population

size in the reserve (R) was 25% of $\overline{N}$ and in the non-reserve (NR) was 75% of $\overline{N}$. These

adjusted values were: $\alpha_R = 2.39$, $\beta_R = 0.0357$, $\alpha_{NR} = 2.82$, and $\beta_{NR} = 0.0215$. All site-

specific equilibrium quantities are given in Table 4 (no harvesting, zero migration assumed).

To allow interaction between the reserve and non-reserve, parameter values for migration are needed. This parameter will be difficult to measure in practice, but could be estimated from tagging-studies (Arnason 1973; Hilborn 1990; Hestbeck et al. 1991; Schwarz et al. 1993; Brownie et al. 1993; Hanski et al. 2000). Migration is expected to vary with the size of the closed area, and could vary for different age-groups. Several papers on marine reserve systems have suggested a relationship for transfer rate as a function of reserve size (Polacheck 1990; Guenette and Pitcher 1998). However, for a given reserve size, the same total amount of area could be encompassed with one large reserve or several smaller reserves. The motivation for creating one or several reserves (cf. "SLOSS" debate in Diamond 1975; Simberloff and Abele 1976; Gilpin and Diamond 1980) would depend on the species in question, and its migration patterns and/or tendency to remain in distinct sub-units. Therefore, rather than infer a functional relationship, I begin with a fixed reserve size (R = 25% of total area) and explore several levels of transfer rate between reserve and non-reserve. My objective here is not to estimate the optimal reserve size, but rather to illustrate how the introduction of a closed area could affect yield and optimal harvesting strategies. In addition, I explore how constrained harvesting strategies could vary between a no-reserve versus a reserve system.

I consider three simple transfer rate scenarios assuming the population is well-mixed for all age classes (i.e. all age classes migrate with the same probability): *i*) transfer rates correspond directly to reserve proportion (25% of the fish population moves into the reserve and 75% of the fish population move into the non-reserve area annually); *ii*) equal migration of 50% between sites annually; and *iii*) limited, unequal migration of 10% moving from reserve to non-reserve and 15% moving from non-reserve to reserve annually. These wide

range of transfer rates is expected to cover the spectrum of movement possibilities for a reserve encompassing 25% of the total area previously fished.

The equipment employed for harvesting fish can be very destructive to the habitat. Closing an area to fishing could lead to a higher quality habitat in the reserve, which could positively influence survival and/or fecundity. I explored a situation where fish in the reserve are 10% more productive by increasing the Ricker parameters: $\alpha_{R(HF)} = 2.6$, $\beta_{R(HF)} = 0.035$ (HF = High Fecundity). Figure 1 shows a plot comparing the various Ricker curves used in the models. In the absence of harvesting, this additional fecundity brought the equilibrium population size to $\overline{N} = 1396.5$ (with no migration). I compare optimum yields from constrained harvesting for one-site, and two-site models with normal or high fecundity.

Lastly, I consider how creating a reserve would compare to a no-reserve case where the level of fishing exceeds the optimum. The yields calculated at the optimum harvest level in the no-reserve case are almost surely unattainable because it requires that all fisheries harvest at the exact mandated level. As many stocks are overexploited, it is unrealistic to compare yields with a reserve to yields that assume strict compliance. I therefore compare yields with a reserve to yields obtained without a reserve but where fishing level is 1.5 or 2.0 times the optimal harvest level.

4.0 Results

4.1 One site case (No Reserve)

Age 6 is the optimal age-class to harvest, as it has the smallest ratio of reproductive value:harvest value (= 3.3224, Table 3). Varying h_6 from 0 to 1 (by increments of 0.01), I found the maximum yield to occur when $h_6 = 0.45$ (MSY = 39.975). This agrees with Reed (1980). Examining the vector $\mathbf{v}/\mathbf{w}$, I can predict *a priori* that the best maximum yield for

constrained harvesting strategies (where both minimum and maximum age exploited can be controlled) will involve harvesting ages 5 and 6 and will decrease for other strategies in the the order listed in Table 4. MSY (and associated equilibrium values) corresponding to each of these strategies, assuming the level of harvest is equal for all age classes harvest (i.e. knife edge selectivity) is given in Table 5. This table is consistent with Figure 2 in Reed (1980), where he plotted MSY for several potential harvesting strategies.

As more age classes were exploited, the level of sustainable harvest decreased from a high of 0.45 when only age 6 was targeted to 0.07 when ages 3-12 were harvested (Table 5). This harvest rate can be interpreted as an annual exploitation rate (u in fisheries literature). For simplicity, it was assumed that this was a pulse fishery. Conversion to an instantaneous fishing mortality (F) is given in 2.7. Yield per recruit (YPR) decreased monotonically from 0.1354 to 0.0895, while equilibrium population size and number of recruits varied slightly (though unsystematically).

MSY for minimum age at entry to the fishery beginning with age 3 (with harvest scaled by age-specific selectivity) is given in Table 6. The maximum occurs for a low level of harvest for ages 5-12 (MSY = 29.003, h = 0.11). This value is about 73% of the theoretical MSY (when only age 6 is harvested). Increasing the minimum age causes MSY to decrease, with the sharpest decline when changing from a minimum age of 7 to 8. Harvesting ages 7-12 would achieve 62% of theoretical MSY. As the minimum age harvested increases, the amount of harvest that can be applied to the population increases, from a minimum of 0.1 for ages 3-12 to a maximum of nearly 1.0 for ages 11-12.

Figures 2 and 3 show the trajectory of MSY for several harvesting strategies. In Figure 2, I show the short term yields associated with initiating harvest on age 6 only, ages 5-12, or

ages 7-12, from an unharvested population. For about the first 20 years, harvest declines steadily, though more sharply for the "age 6 only" strategy. The oscillation of the curve as it approaches equilibrium MSY results in part from the effects of harvest "working its way through" the population age structure (see chapter 4 for a discussion of transient analysis in age-structured populations). The persistence of fluctuations and degree of change in initial MSY to equilibrium MSY is greater in Figure 2 than in Figure 3. MSY is attained more quickly (and smoothly) when the minimum age harvested is increased from 3 to 5 rather than from 3 to 7.

Tables 7 and 8 show the effect on the population and yields when the optimal fishing level, h, is exceeded by 1.5 or 2.0 times, respectively. At 1.5 times the optimal h, yields were 46 – 56% less than the optimal MSY, and the harvested population size ($\overline{N}_h$) is 25 – 30% the unharvested size for many of the harvest strategies. When ages 11-12 or only age 12 were harvested, the optimal h was already very high and could not be raised beyond 1.0. Thus, results for these 2 age classes are not representative of overfishing by 1.5 times optimal h as the other strategies are. This is also true in Table 8, where all but the last 2 strategies correspond to 2.0 times optimal h. At double the optimal h, yields are negligible, and so is the harvested population size, for that matter.

4.2 Two-site case (Reserve and Non-Reserve)

The ratios for age-specific reproductive value:harvest value were exactly the same as for the 1-site case (Table 3). Thus, regardless of migration pattern, age class 6 is still the optimal class to exploit when a reserve equal to 25% total fished area is created. The theoretical unconstrained MSY for migration pattern (*i*) is actually greater in the 2-site case than in the

one-site case, while it is only 86% and 70% the one-site value for migration patterns (*ii*) and (*iii*), respectively.

MSY for constrained harvesting follows the same age-category rankings as in the one-site case. Within each row of Table 9, MSY decreases (as do harvest level and YPR) as migration levels decrease. In general, MSY values from the two-site constrained scenarios in Table 9 were less than the one-site values – by 85-92%, 74-78%, and 65-69% for migration patterns (*i*), (*ii*) and (*iii*), respectively. The harvested equilibrium population size and number of recruits (total in both sites) was in approximately the same range as that found in the 1-site case (Tables 5 and 6). The level of harvest is approximately double the level of harvest in the 1-site model for migration pattern (*i*), and is similar to the 1-site levels for (*ii*) and (*iii*).

MSY in the non-reserve when only the minimum age harvested can be controlled is given in Table 10. As in the one-site case, the maximum yield occurs for harvesting ages 5-12. MSY decreases across rows as migration rates decrease. The sharpest decline within each column occurs between harvesting ages 7-12 versus ages 8-12. As in Table 9, the amount of harvest for (*i*) is nearly double that of harvest levels for the one-site model, while (*ii*) and (*iii*) are similar to one-site levels. Compared to constrained harvests from the one-site model, yields in Table 10 were 63-94%, 70-77%, or 60-66% those in Table 6 for (*i*), (*ii*) and (*iii*), respectively. However, all two-site constrained yields were greater than one-site yields for "over-fished" scenarios. (This comparison excludes the last two entries in Tables 7 and 8 because h could not be increased sufficiently.)

MSY trajectories beginning from an unharvested population at equilibrium are given in Figures 4, 5, and 6. There is very little difference that results from different migration patterns. For a population at equilibrium with harvesting of ages 3-12, the MSY trajectories

associated with increasing the minimum size harvested to 5 or 7 is given in Figures 7, 8 and 9. Again, the trajectory does not vary with migration pattern. Trajectories between the one- and two-site models were very similar.

Constrained yields from a scenario where fish realize a higher fecundity in the reserve are given in Table 11. For migration pattern (*i*) yields are greater when a reserve is in place for nearly all combinations of harvested age classes, measuring 101- 123% of yields in one-site models at optimal harvest levels. For migration patterns (*ii*) and (*iii*), yields are 74-89% and 65-72% that of one-site models, although they are greater than yields when reserve fish do not obtain higher fecundity. When the level of fishing in the one-site model exceeded the optimal level, yields from the reserve were higher.

All constrained MSY are compared in Figure 10. The best yields are obtained in a reserve system with high transfer rates out of the reserve (migration pattern (*i*)) and higher fecundity. The next best yields were obtained without a reserve when fishing is held to the optimum level, although yield from two other reserve scenarios were fairly close for most of this range (reserve for migration pattern *(ii)* + high fecundity, and reserve for migration patern (*i*)). When fishing exceeds the optimum level, yields in a reserve are greater for all harvesting strategies (except for strategies involving harvest of only the three oldest age classes).

5.0 Discussion

A very simple, biologically intuitive method for determining optimal harvesting strategies has been developed for density-dependent matrix models. Because matrix models have been in the literature for more than 50 years (Leslie 1945, density-independent case; Leslie 1948, density-dependent case), their construction and the calculation of their

asymptotic properties (eigenvalues and eigenvectors) is assumed to be routine. (The availability of mathematical software with linear algebra packages, such as MATLAB ® or MAPLE ®, makes this trivial). I suggest that anyone capable of creating a matrix model is equally capable of applying the criterion developed here to find optimal solutions to their harvesting problems. The optimal age class to harvest can be determined by simply examining age-specific life-time reproductive value (the left eigenvector at unharvested equilibrium) divided by age-specific weight. Yield will be maximized by harvesting the age class with the smallest ratio. If a second age class is to be harvested to attain MSY, it will be the age-class with the second smallest ratio. This criterion for selecting the optimal age class encapsulates the inherent harvesting trade-off between the value of a given age class to a fishery (in terms of weight) versus its value for the population (given by its expected life-time reproductive value). This conclusion is general and holds for multi-site models as well (both density-independent and density-dependent), and may involve harvesting more than two age classes.

While other methods exist for determining MSY, they are essentially numeric and lack a clear, biological motivation in their approach. My approach was based on sensitivity of equilibrium egg production ($\overline{E}$) to harvest. First year survival is a density dependent function of stock size (and the quantity of eggs they produce). Therefore, the sensitivity of $\overline{E}$ to harvest is expected to play a role in determining the optimal strategy, because survival (and, hence, recruitment to the fishery) depends on egg production.

Garrod (1985) stated that the life-history of cod is such that the pattern of YPR shows a maximum at low F values when the minimum age harvested is low, with the maximum shifting to higher F values when the minimum age harvested is increased. This was found to

be true in both one- and two-site models. Furthermore, by inspection of the vector **v**/**weight** various age-specific harvesting strategies can be ranked.

In summarizing some general characteristics of maximum yield policies, Walters (1969, pp.511-512) stated that they would be "most strongly determined by growth rates and reproductive parameters (relative fecundities, reproduction curve constants)…" and that "the best policy is to harvest each cohort close to the age when biomass loss through numbers decline balances biomass gain through growth…" Reed showed analytically that for increasing recruitment functions (i.e. no overcompensation), the optimal strategy will not occur before the age where natural biomass (defined as age specific weight multiplied by cumulative survival-to-age) reaches a maximum. Getz (1980) proved the same result for a more general class of recruitment functions (Getz and Haight 1989). These authors verbalized or analytically proved an MSY "guideline", i.e. they identified an age class that served as a lower bound for optimal harvesting strategies. However, a simple and explicit method for determining which age (or ages) should be harvested had been lacking. Furthermore, I propose that the issue of using natural biomass as a criterion is a "red herring," for I have shown that MSY is governed by the ratio of reproductive value to weight rather than the product of weight and survival. In Appendix 1, I provide a counter-example to demonstrate that the natural biomass criterion is not a general result. I propose that the ratio of life-time reproductive values to weight is the most informative measurement to consider. Prager (1987) suggested that life-time reproductive values be used as a guideline for evaluating alternative management strategies aimed at rebuilding fish stocks. This would be similar to my criterion, when the vector of weights (or economic value) is equal for all age-classes. However, the values he used for life-time reproduction actually correspond to

net-maternity values (see Caswell 1989, p.152), which will only be equivalent to elements of the left-eigenvector if $\lambda=1.0$.

Minimum age control is the most realistic of the harvest options I explored. The transient dynamics of MSY can be fairly smooth when the minimum age is shifted slightly (from age 3 to age 5 in my example) but can be expected to show larger oscillations when the minimum age is increased over a larger interval (age 3 to age 7, e.g.). These calculations and trajectories ignore the inherent variation in stock recruit dynamics, but I expect that for moderate levels of variability, the trajectories will remain the same. Other sources of variation, related to environment, predation, or prey abundance, could cloud the underlying pattern as oscillations associated with each source of "noise" run their course through the age structure. The trajectory pattern that I observed did not vary between one-site and two-site models, which indicates that the creation of a reserve will not create larger fluctuations when control actions are changed outside of the reserve.

When confronted with the need to introduce new management controls to reduce exploitation, there are two main options. The first is to try to decrease harvesting levels (either through increasing the minimum age harvested or decreasing total fishing pressure). This was the primary method used for most of the last century. The current status of many fish stocks indicates that this approach has not been successful. One reason is that implementation is not perfect. Also, by-catch mortality is difficult to control and may not have been accurately accounted for when new fishing recommendations were created. An alternative control is to close certain areas to fishing. Implementation is limited by enforcement (Murawski et al. 2000 report the use of ship and aircraft patrol as well as requiring all vessels to carry a satellite receiver/transmitter which tracks vessel location

hourly). The effect on yields depends on the size of the reserve, the transfer rates in and out of the reserve, and the quality of the reserve habitat and its effects on survival and reproduction of fish located inside the reserve. Intuitively, if fish live longer in a reserve, they will attain a greater size and should have higher fecundity.

It remains to be determined what an appropriate reserve size is, and what transfer rates could be expected. Also, deciding on reserve placement will probably have some social or political component factored into the decision. My simple model indicates that reasonable yields are still obtainable when a reserve is created. And when a stock is being overfished, creating a reserve led to higher sustainable yields. In addition to higher yields, another benefit of a reserve is that it provides insurance against collapse or severe recruitment overfishing .

Acknowledgements

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Table 1: Age-specific annual survival probability, annual fecundity rates, and weight-at-age for Arcto-Norwegian cod (*Gadus morhua*). Fecundity is average age-specific weight multiplied by proportion mature.

Age	Survival	weight	fecundity
1	(density-dependent)	--	--
2	0.72	--	--
3	0.72	0.2	--
4	0.72	0.53	--
5	0.72	1.01	--
6	0.7	1.6	--
7	0.6	2.35	0.1
8	0.5	2.91	0.38
9	0.5	3.58	0.94
10	0.61	4.22	1.76
11	0.68	4.82	3.05
12	0.61	5.37	4.36

Table 2: Equilibrium values for unharvested population in one site model.

Parameter	Description	Value
$\overline{N}$	Total Population Size	1261.5
$\overline{n}_1$	Recruitment	382.04
$\overline{E}$	Egg Production	59.743
$\varphi(\overline{E})$	Ricker Function	6.3947

Table 3: Vector of age-specific reproductive value (v_i) divided by age-specific weight (weight$_i$). Age class six has the lowest v_i/weight$_i$ value and is therefore the optimum age class to harvest.

Age	v_i/weight$_i$
1	--
2	--
3	9.6451
4	5.0551
5	3.6842
6	**3.3224**
7	3.7701
8	5.6497
9	7.8271
10	8.5503
11	7.5749
12	5.192

Table 4: 2-site model equilibrium values for unharvested population with no migration (R = Reserve, NR=Non-Reserve).

Parameter	Description	Value
$\overline{N}$	Total Population Size	1263.5
$\overline{N}_R$	Population Size in Reserve	316.16
$\overline{N}_{NR}$	Population Size in Non-Reserve	947.3
$\overline{n}_1$	Total Recruitment	382.63
$\overline{n}_{1R}$	Recruits in Reserve	95.747
$\overline{n}_{1NR}$	Recruits in Non-Reserve	286.88
$\overline{E}$	Total Egg Production	59.835
$\overline{E}_R$	Egg Production in Reserve	14.973
$\overline{E}_{NR}$	Egg Production in Non-Reserve	44.862
$\varphi(\overline{E}_R)$	Ricker Function in Reserve	6.3947
$\varphi(\overline{E}_{NR})$	Ricker Function in Non-Reserve	6.3947

Table 5: One-site constrained MSY for different combinations of harvested age classes. When more than one age class is harvested, it is assumed harvest is applied equally to all harvested age classes (i.e. full selectivity assumed). The row for age class 6 is in bold face type, indicating the theoretical MSY.

Age classes harvested	MSY	harvest level	Equilibrium Population	Number at Age 1	YPR
6	**39.975**	**0.45**	**918.58**	**295.14**	**0.13544**
5-6	37.709	0.26	892.66	293.5	0.12848
5-7	37.122	0.18	914.04	296.07	0.11935
4-7	33.752	0.14	880.91	293.09	0.11516
4-8	32.345	0.11	927.95	303.82	0.10646
4-9	30.787	0.10	903.22	294.14	0.10467
4-10	29.665	0.09	916.74	296.71	0.10000
4-11	28.984	0.09	872.56	282.5	0.10260
4-12	28.926	0.08	946.31	304.29	0.09506
3-12	26.386	0.07	923.64	304.53	0.08664

Table 6: One-site constrained MSY assuming control of only the minimum age class recruited is possible. Ages 7-12 were assumed to be fully recruited to the fishery, while for ages 3-6, age specific harvest was scaled by age specific selectivity (0.05, 0.38, 0.62, and 0.85, respectively). The row with ages 5-12 is in bold, indicating overall MSY.

Age classes harvested	MSY	harvest level	Equilibrium Population	Number of Recruits	YPR
3-12	28.509	0.1	924.48	293.96	0.0970
4-12	28.681	0.1	932.49	295.84	0.0969
5-12	**29.003**	**0.11**	**917.77**	**288.79**	**0.1004**
6-12	27.985	0.12	951.98	296.31	0.0944
7-12	24.715	0.15	938.22	289.63	0.0853
8-12	19.765	0.2	958.67	294.02	0.0672
9-12	17.028	0.29	986.66	301.5	0.0565
10-12	16.586	0.49	996.4	303.89	0.0546
11-12	17.515	0.94	1042.1	317.33	0.0552
12	14.383	1.0	1236.1	375.14	0.0383

Table 7: One-site constrained MSY when the level of fishing is 1.5 times optimal h. I assume control of only the minimum age class recruited is possible. Ages 7-12 were assumed to be fully recruited to the fishery, while for ages 3-6, age specific harvest was scaled by age specific selectivity (0.05, 0.38, and 0.85, respectively). The row with ages 11-12 is in bold, indicating overall MSY. For the last two rows, harvest level is not 1.5 times optimal h because h cannot be increased beyond 1.0.

Age classes harvested	MSY	harvest level	Equilibrium Population	Number of Recruits	YPR
3-12	15.279	0.15	358.0	116.3	0.1314
4-12	16.085	0.15	377.5	122.2	0.1356
5-12	13.469	0.165	307.9	98.5	0.1367
6-12	15.845	0.18	388.4	122.3	0.1295
7-12	11.799	0.225	325.3	101.2	0.1166
8-12	11.221	0.30	405.8	125.1	0.0897
9-12	11.960	0.435	537.1	164.65	0.0726
10-12	13.062	0.735	644.0	196.8	0.0664
11-12	**17.454**	**1.0**	**1015.7**	**309.4**	**0.0564**
12	14.383	1.0	1236.1	375.14	0.0383

Table 8: One-site constrained MSY when the level of fishing is 2.0 times optimal h. I assume control of only the minimum age class recruited is possible. Ages 7-12 were assumed to be fully recruited to the fishery, while for ages 3-6, age specific harvest was scaled by age specific selectivity (0.05, 0.38, and 0.85, respectively). The row with ages 11-12 is in bold, indicating overall MSY. For the last two rows, harvest level is not 2.0 times optimal h because h cannot be increased beyond 1.0.

Age classes harvested	MSY	harvest level	Equilibrium Population	Number of Recruits	YPR
3-12	0.0008	0.2	16.4	5.3	0.1588
4-12	0.0014	0.2	0.027	0.008	0.1593
5-12	0.0002	0.22	0.003	0.001	0.1661
6-12	0.0011	0.24	0.022	0.007	0.1586
7-12	0.0001	0.30	0.003	0.001	0.1424
8-12	0.0016	0.40	0.051	0.015	0.1073
9-12	0.2461	0.58	9.672	2.941	0.0837
10-12	5.5475	0.98	250.63	76.72	0.0723
11-12	**17.4535**	**1.0**	**1015.7**	**309.4**	**0.0564**
12	14.3831	1.0	1236.1	375.14	0.0383

Table 9: MSY for different combinations of harvested age classes in the Non-Reserve area. Transfer rate from Reserve to Non-Reserve was [1]0.75, [2]0.5, or [3]0.10. Transfer rate from Non-Reserve to Reserve was [1]0.25, [2]0.5, or [3]0.15. When more than one age class is harvested, it is assumed harvest is applied equally to all harvested age classes (i.e. full selectivity assumed). The row for age class 6 is in bold face type, indicating theoretical MSY.

Age classes harvested	MSY[1]	harvest level[1]	YPR[1]	MSY[2]	harvest level[2]	YPR[2]	MSY[3]	harvest level[3]	YPR[3]
6	**47.34**	**1.0**	**0.3010**	**34.372**	**0.67**	**0.2017**	**27.974**	**0.52**	**0.1565**
5-6	34.652	0.53	0.2188	29.106	0.35	0.1635	26.133	0.30	0.1446
5-7	32.934	0.36	0.2062	28.081	0.24	0.1568	25.292	0.21	0.1417
4-7	28.589	0.27	0.1781	25.041	0.18	0.1384	22.866	0.16	0.1273
4-8	27.745	0.22	0.1715	24.075	0.15	0.1342	21.706	0.13	0.1210
4-9	26.719	0.20	0.1688	22.978	0.13	0.1275	20.44	0.11	0.1127
4-10	25.994	0.18	0.1625	22.205	0.12	0.1243	19.51	0.10	0.1085
4-11	25.645	0.17	0.1596	21.815	0.11	0.1194	18.955	0.09	0.1026
4-12	25.618	0.17	0.1611	21.791	0.11	0.1210	18.83	0.09	0.1042
3-12	22.538	0.14	0.1374	19.569	0.09	0.1042	17.148	0.08	0.0958

Table 10: MSY for different combinations of minimum age harvested in the Non-Reserve area. Transfer rate from Reserve to Non-Reserve was [1]0.75, [2]0.5, or [3]0.10. Transfer rate from Non-Reserve to Reserve was [1]0.25, [2]0.5, or [3]0.15. Ages 7-12 were assumed to be fully recruited to the fishery, while for ages 3-6, age specific harvest was scaled by age specific catchability (0.05, 0.38, 0.62, and 0.85, respectively). The row for ages 5-12 is in bold, indicating overall MSY.

Age classes harvested	MSY[1]	harvest level[1]	YPR[1]	MSY[2]	harvest level[2]	YPR[2]	MSY[3]	harvest level[3]	YPR[3]
3-12	25.619	0.20	0.1588	21.548	0.13	0.1185	18.365	0.11	0.1045
4-12	25.85	0.20	0.1593	21.698	0.13	0.1186	18.486	0.11	0.1045
5-12	**26.569**	**0.22**	**0.1661**	**22.082**	**0.14**	**0.1212**	**18.652**	**0.12**	**0.1076**
6-12	26.103	0.25	0.1630	21.475	0.16	0.1186	17.924	0.13	0.1008
7-12	23.294	0.31	0.1455	19.075	0.20	0.1068	15.65	0.16	0.0899
8-12	17.968	0.39	0.1057	15.109	0.26	0.0814	12.325	0.20	0.0672
9-12	14.537	0.54	0.0811	12.762	0.37	0.0661	10.456	0.29	0.0565
10-12	13.235	0.79	0.0681	12.173	0.57	0.0593	10.027	0.47	0.0533
11-12	12.559	1.0	0.0564	12.645	0.99	0.0562	10.515	0.86	0.0531
12	9.026	1.0	0.0383	10.112	1.0	0.0383	9.526	1.0	0.0383

Table 11: MSY for different combinations of minimum age harvested in the Non-Reserve area when fecundity improves in the Reserve. Transfer rate from Reserve to Non-Reserve was [1]0.75, [2]0.5, or [3]0.10. Transfer rate from Non-Reserve to Reserve was [1]0.25, [2]0.5, or [3]0.15. Ages 7-12 were assumed to be fully recruited to the fishery, while for ages 3-6, age specific harvest was scaled by age specific catchability (0.05, 0.38, 0.62, and 0.85, respectively). The row for ages 5-12 is in bold, indicating overall MSY.

Age classes harvested	MSY[1]	harvest level[1]	YPR[1]	MSY[2]	harvest level[2]	YPR[2]	MSY[3]	harvest level[3]	YPR[3]
3-12	33.416	0.24	0.1767	24.773	0.15	0.1314	20.531	0.12	0.117
4-12	33.756	0.24	0.1774	24.973	0.15	0.1316	20.662	0.12	0.1117
5-12	**34.891**	**0.26**	**0.1840**	**25.462**	**0.16**	**0.1337**	**20.87**	**0.13**	**0.1145**
6-12	34.521	0.30	0.1828	24.793	0.18	0.1295	20.015	0.14	0.1069
7-12	30.988	0.37	0.1627	22.024	0.22	0.1147	17.467	0.17	0.0943
8-12	23.673	0.48	0.1186	17.341	0.29	0.0877	13.68	0.23	0.0746
9-12	18.788	0.64	0.0872	14.52	0.40	0.0693	11.532	0.32	0.0603
10-12	16.731	0.92	0.0712	13.702	0.63	0.0622	10.985	0.51	0.0558
11-12	14.903	1.0	0.564	13.921	1.0	0.0564	11.38	0.92	0.0547
12	10.174	1.0	0.0383	10.616	1.0	0.0383	9.868	1.0	0.0383

APPENDIX 1

The purpose of this Appendix is to demonstrate the generality of the criterion developed in this paper for identifying the optimal harvesting strategy, and to contrast it with previously published criterion that do not appear to have general applicability. The table below is adapted from Table 3. Columns two and three contain a vector of age-specific reproductive value (v_i) divided by age-specific weight (weight$_i$) [1]using values in Table 1 and [2]changing fecundity for age 12 from 4.36 to 3.36. Bold entries in these columns correspond to the optimum age classes to harvest. For the first example, age class 6 is optimal; for the second example, age class 12 should be harvested completely and age class 7 should be harvested at $h_7 = 0.76$. Bold italic entries (columns 4, 5, and 6) correspond to "predicted" optimum age classes to harvest based on criteria proposed in Reed (1980). In column 4, natural biomass, defined as age-specific weight (weight$_i$) times age-specific cumulative survival (L_i) is given. Reed claimed that the optimal age class to harvest will not occur before the age with maximum natural biomass. This is true for both examples (column 2 and 3), but it is shown to be only a lower bound as it cannot predict the exact age (or ages) to harvest. The last two columns give "the ratio of loss in natural biomass to average egg production between age j and the end of life" (Reed (1980). In his appendix, Reed proposed that the optimum age class to harvest will maximize this ratio. However, for both examples, the maximum value occurs for age class 4, which is not at all involved in the optimal strategy (for this paper it is age class 6 – and Reed also found this to be the optimal age through linear programming).

Age	$_1 v_i / weight_i$	$_2 v_i / weight_i$	$weight_i L_i$	$_1 weight_i L_i / v_i$	$_2 weight_i L_i / v_i$
1	--	--	--	--	--
2	--	--	--	--	--
3	9.6451	9.6451	0.10368	0.053748	0.053748
4	5.0551	5.0551	0.19782	*0.073836*	*0.073836*
5	3.6842	3.6842	0.27143	0.072943	0.072943
6	**3.3224**	2.9353	*0.30099*	0.056621	0.064087
7	3.7701	**2.7159**	0.26524	0.029938	0.041558
8	5.6497	3.6417	0.16423	0.0099891	0.015497
9	7.8271	4.9999	0.10102	0.0036051	0.0056436
10	8.5503	5.3705	0.07264	0.0020131	0.0032051
11	7.5749	4.5867	0.05642	0.0015452	0.0025519
12	5.192	**2.7125**	0.03834	0.0013752	0.0026321

Fig. 1: Ricker curves used in models (R=Reserve, NR = Non Reserve, HF = High Fecundity).
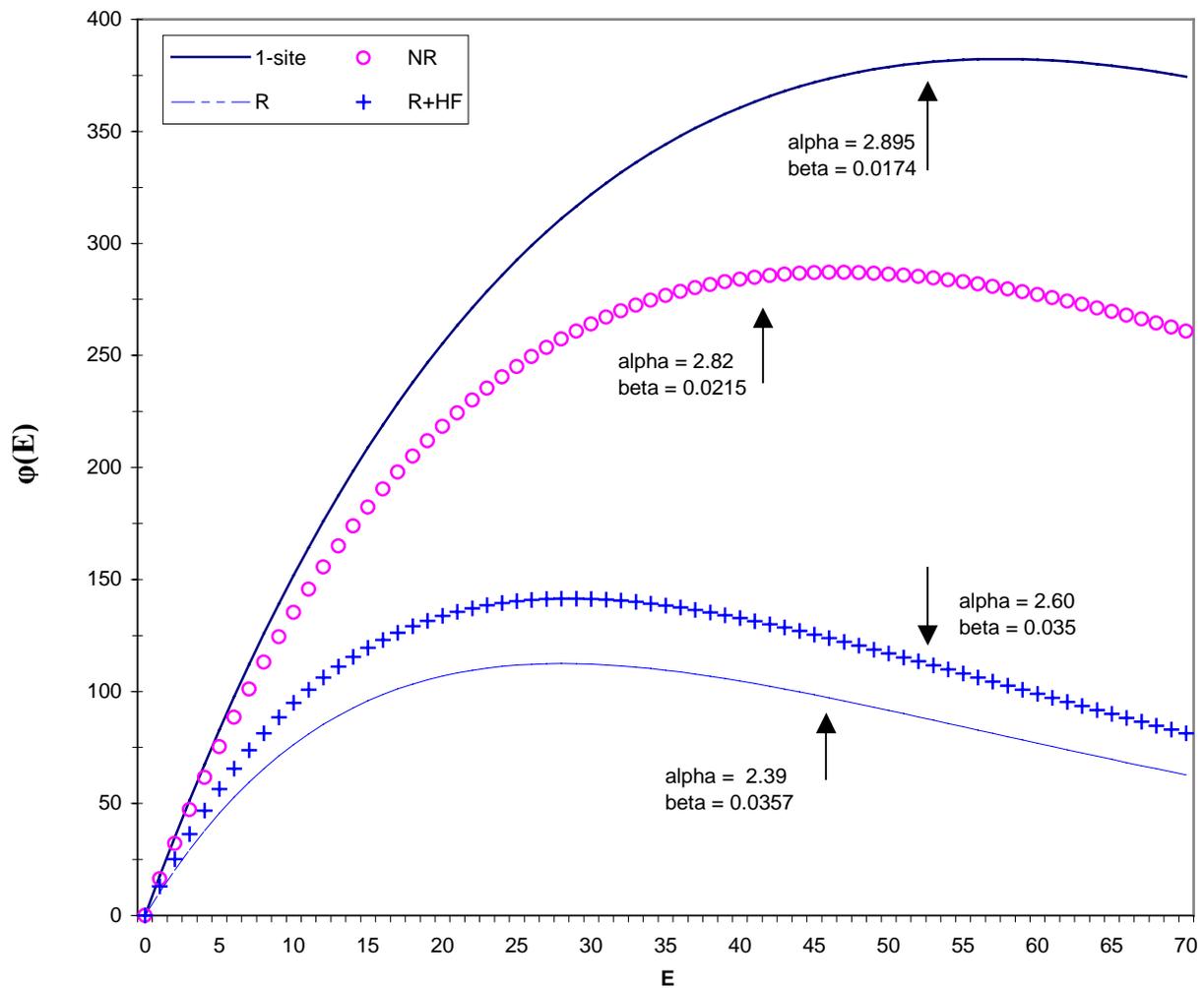
Fig. 2: One-site MSY over time starting from unharvested equilibrium population when age 6, ages 5-12, or ages 7-12 are harvested.
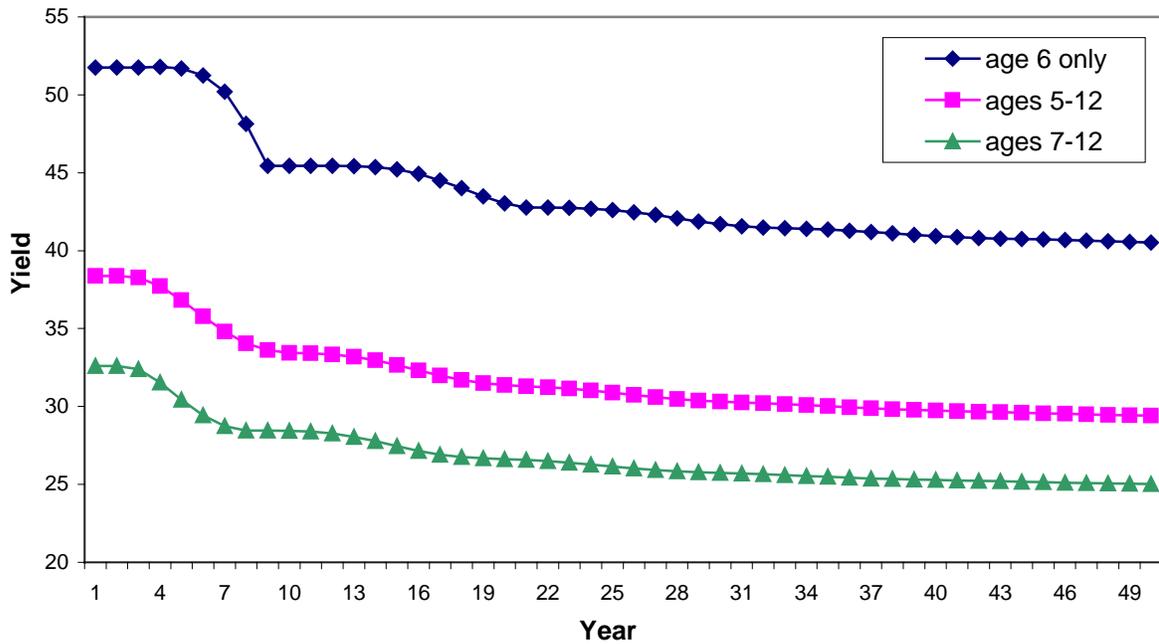
Fig. 3: One-site MSY trajectory when minimum size is increased from ages 3-12 to ages 5-12 or 7-12.
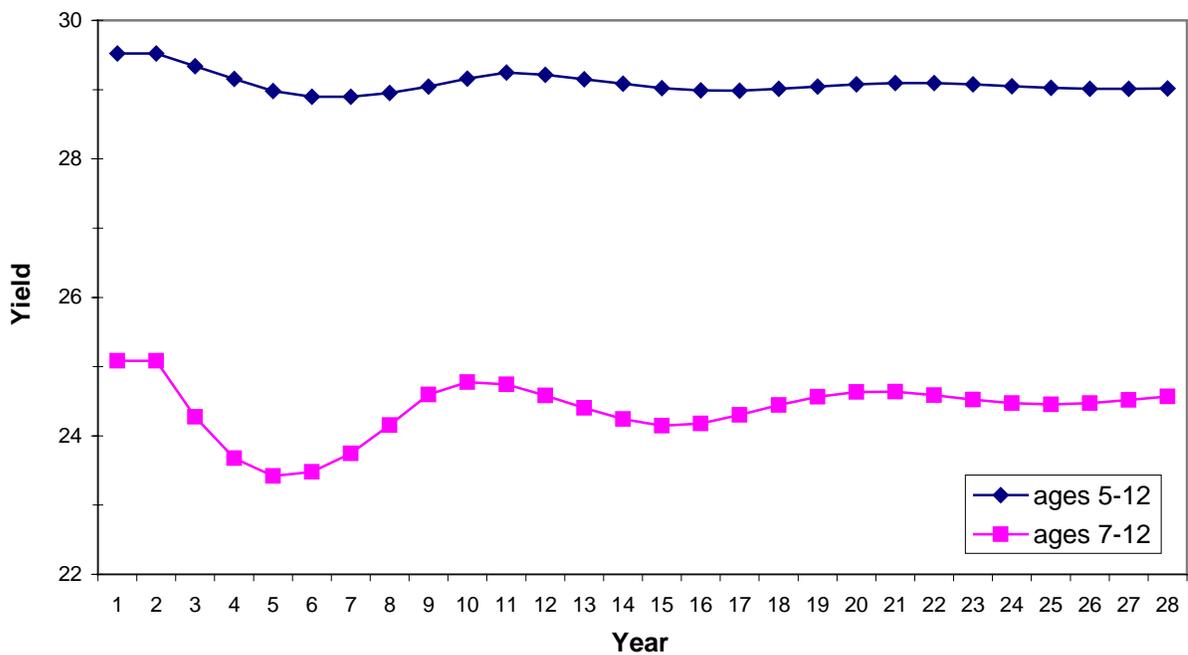
Fig 4: MSY over time in two-site model from unharvested equilibrium (migration=0.75 into vs 0.25 out of Reserve).
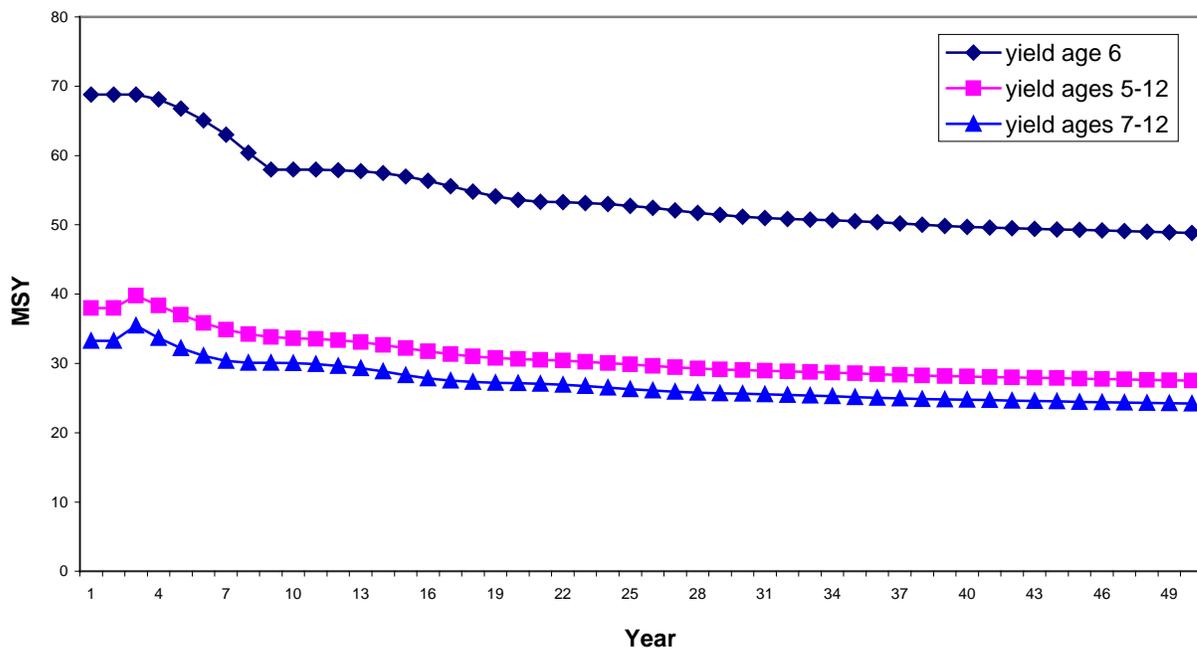
Fig. 5: MSY over time in two-site model from unharvested equilibrium (migration=0.5 into and out of Reserve).
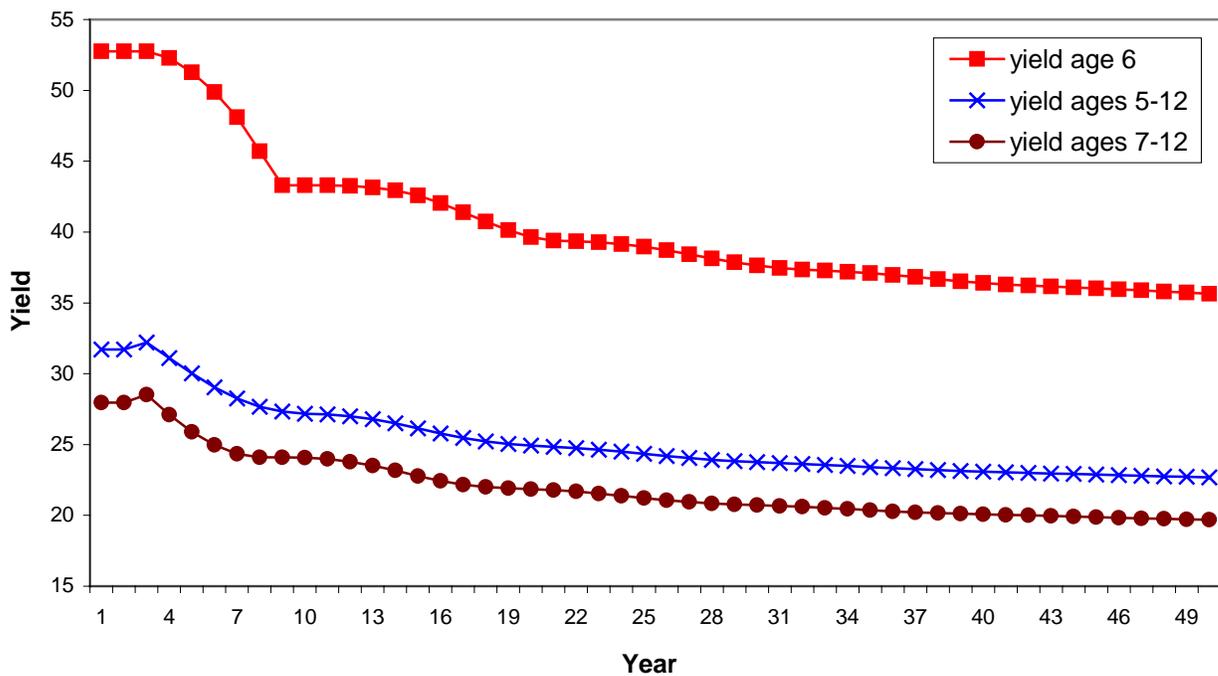
Fig. 6: Two-site MSY over time in 2-site model from unharvested equilibrium (migration=0.15 into vs 0.1 out of Reserve).
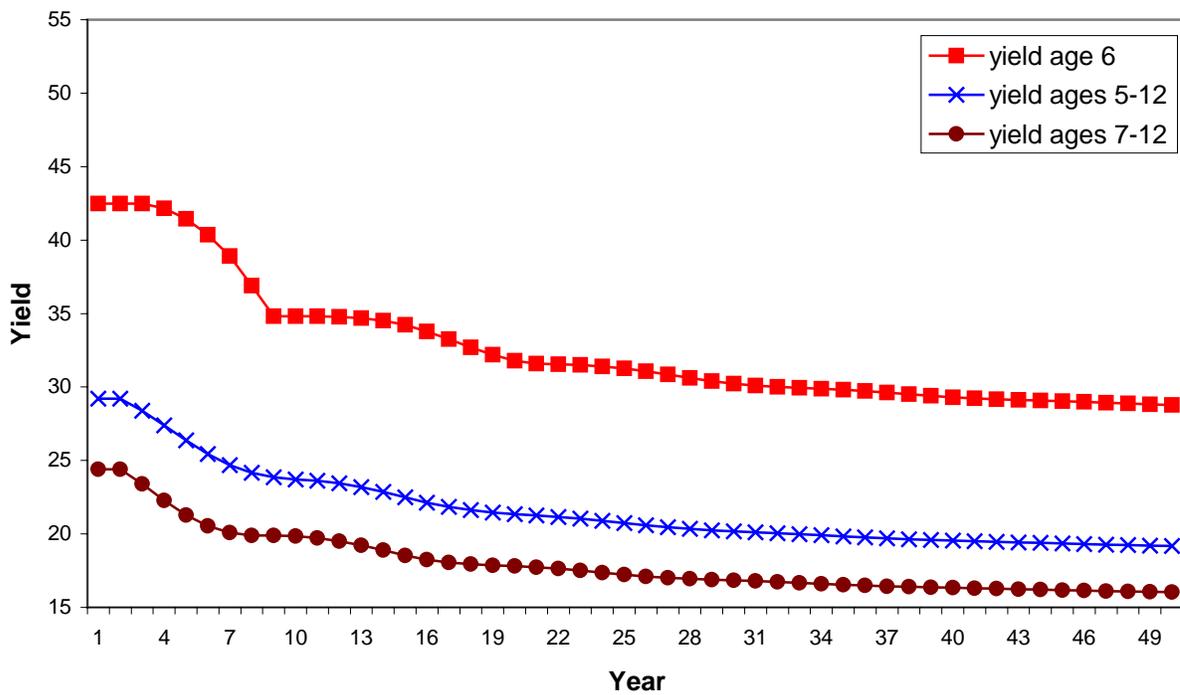
Fig 7: Two-site MSY trajectory when minimum size is increased from ages 3-12 (migration=0.75 into vs 0.25 out of Reserve).
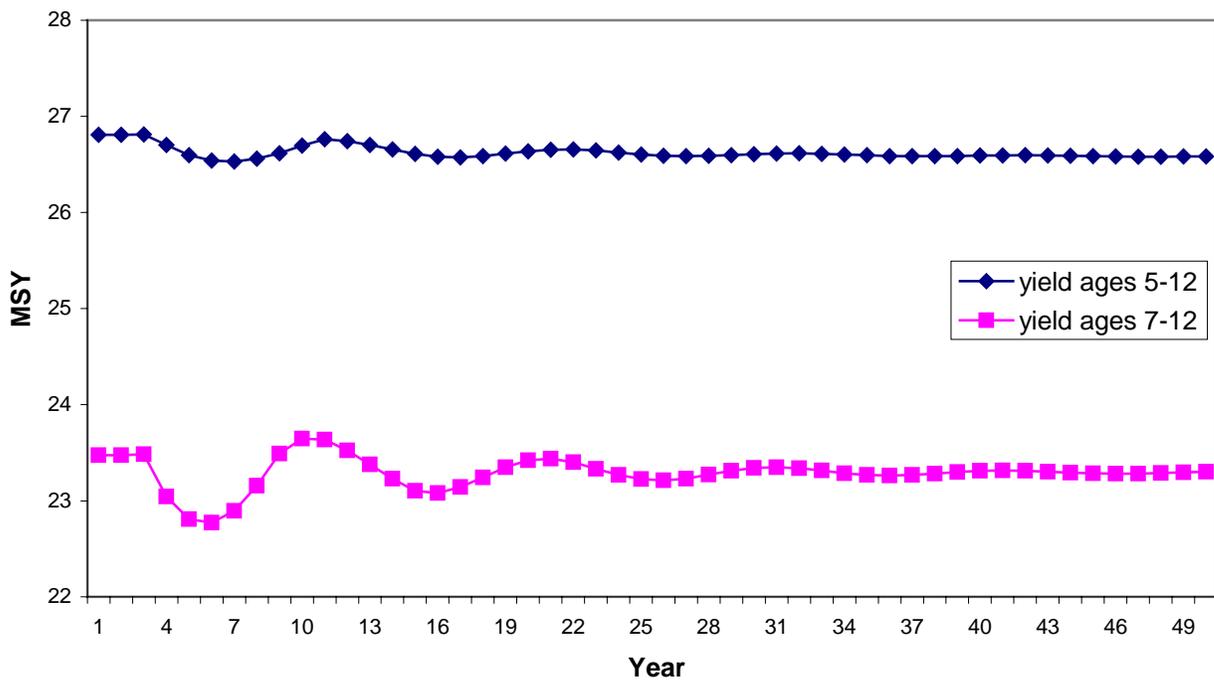
Fig. 8: MSY trajectory when minimum size is increased from ages 3-12 (migration is 0.5 into and out of Reserve).
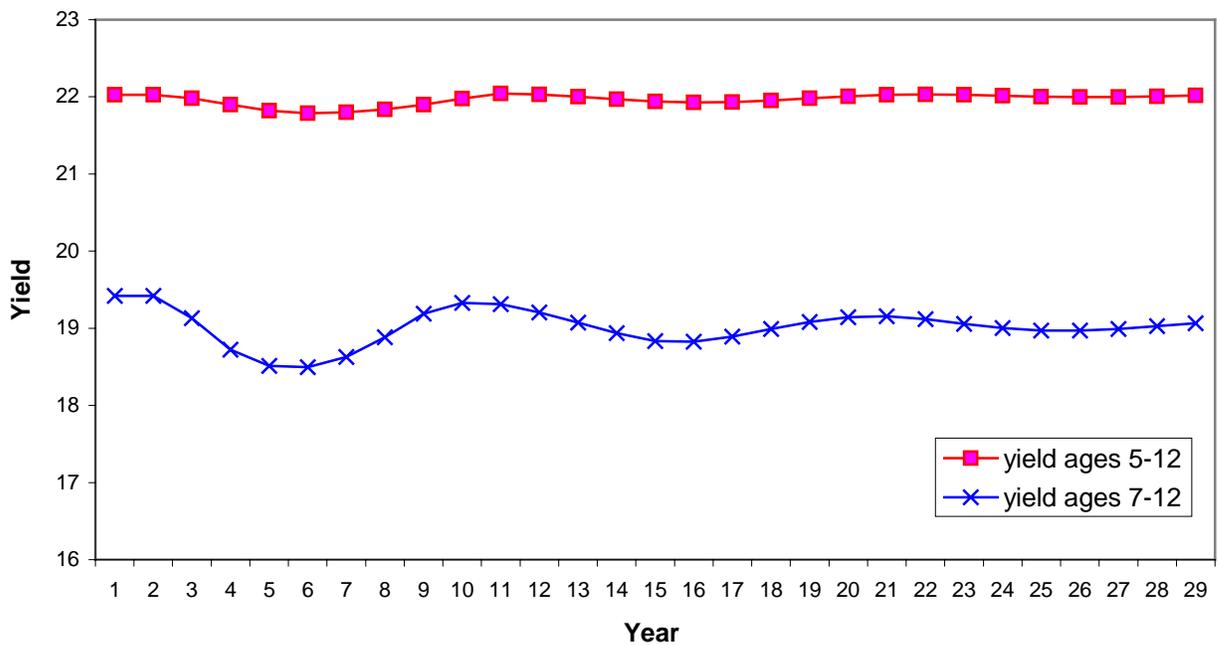
Fig. 9: MSY trajectory when minimum size is increased from ages 3-12 (migration is 0.15 into vs 0.1 out of Reserve).
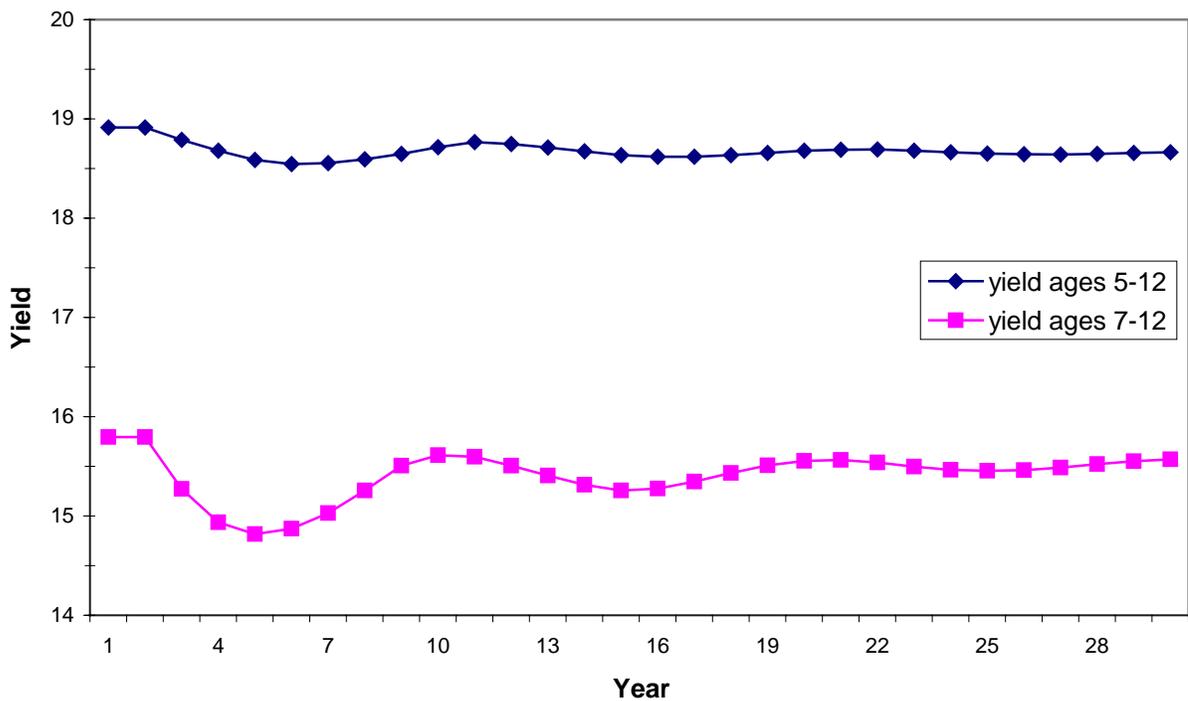
Fig. 10: MSY for alternative management scenarios. The transfer rates are abbreviated T1, T2, and T3; Reserve+HF are the cases where fish reproducing in the reserve obtain higher fecundity; the overfished scenarios are given by 1.5xH and 2.0xH.
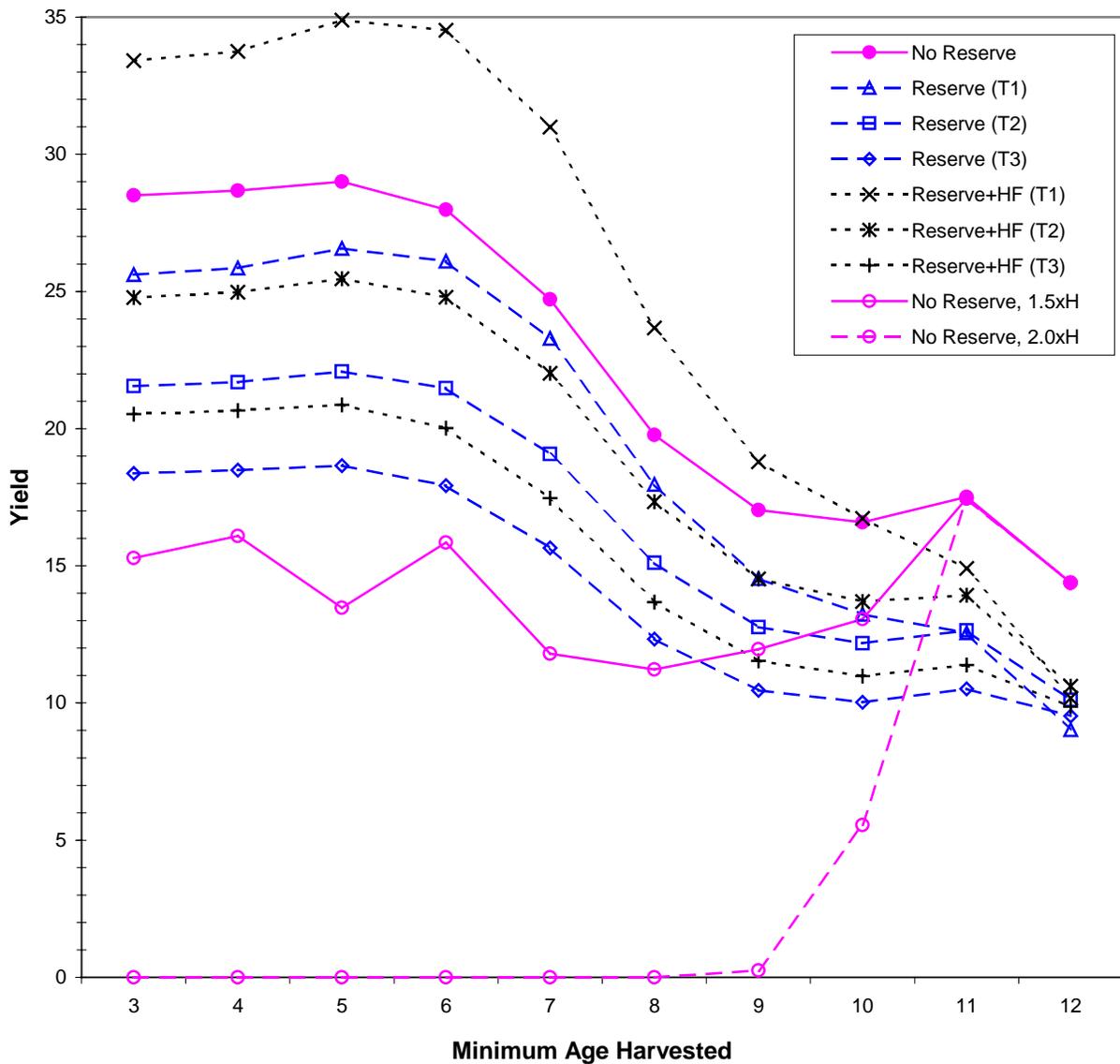
Chapter 4:   An analysis of transient dynamics and convergence times
in sub-divided populations

Abstract: In sub-divided populations, migration links local dynamics that combine to influence the overall dynamics of the system. Thus, in a system of sub-populations connected by migration, management actions performed at one site in the system influence the dynamics of all connected populations. I analyzed transient dynamics and convergence time of population growth rate (λ) after a permanent change that lowered either survival or fecundity by 50% at one site. Convergence was defined as the time when a measured population growth rate (and the growth rate in all subsequent years) was within 1% of the λ for the altered population. I compared results between representative r-selected and K-selected species modeled by 1- , 2- , or 3-site, density-independent, deterministic Leslie matrices. Migration occurred either in all age classes or in only the first age class.   Several levels of migration in and out of the altered site were explored.   In general, multi-site models required more time to converge than single-site models, especially at the altered site. Low levels of migration, especially when only the first age class migrated, led to longer convergence times.   Between r- and K-selected species, conclusions depended on migration patterns. For most cases when survival or fecundity was lowered, the models of the K-selected species converged more slowly than models of the r-selected species. When migration patterns favored emigration out of the altered site, convergence was rapid and both types of species showed similar convergence times.

Keywords: Sub-divided populations; life-history; convergence rates; transient dynamics; generation times

1.0 Introduction

In analyzing Leslie matrices (Leslie 1945), emphasis is generally placed on calculating the dominant eigenvalue, λ, which represents the population growth rate (Caswell 1989). The value of λ determines whether a given population is increasing ($\lambda > 1$), decreasing ($\lambda < 1$), or stable ($\lambda = 1$). One may also calculate how λ would change following an alteration of vital rates (whether induced directly or indirectly by man, or resulting from environmental change) by calculating sensitivities and elasticities (Caswell 1989). Various proposed management actions, addressing problems ranging from conservation to harvesting, can be compared in terms of their effect on λ (Lefkovitch 1967; Crouse et al. 1987; McEvoy and Coombs 1999). It is important to recognize that such comparisons are made between asymptotic values of λ, once the stable age structure has been attained. However, the new stable age structure resulting from a change in a vital rate is not attained immediately. In many management contexts, it also may be important to know the transient pattern and length of time before asymptotic values are attained. For instance, in a harvesting context, a proposed action might not be economically viable if the time required to attain projected yields is too long or the short-term yields vary too much.

Other studies of perturbations in Leslie matrices have focused on life-history and evolution. Since the seminal work of Cole (1954) and Lack (1954) describing the implications of life-history traits for reproduction and population growth, there have been many studies identifying consistent patterns for sensitivities and elasticities of λ to vital

rates for a given life-history (e.g. Fig. 1). In general, one observes greater sensitivity to fecundity in shorter-lived, highly fecund species (typical "r-selected" attributes) while longer-lived, slow-reproducing species (typical "K-selected" attributes) show greater sensitivity to adult survival (Caswell 1989; Lebreton and Clobert 1991; Heppell et al. 2000; Sæther and Bakke 2000). The relationship between elasticities, life-history, and generation length is relevant not only for the ultimate population growth rate, but also for the path to convergence. Depending on the vital rate changed and the number of age classes affected, a given change could require many years or only a few years to work its way through the population age-structure.

Several issues related to managing species with differing life-histories have been addressed in the literature. In a fisheries context, Francis (1986) discussed the fact that "K-selected" species produce much less annual surplus (individuals beyond that required for replacement) and therefore have a greater propensity to be overfished. This presents great difficulty for managers of a multi-species fishery looking to manage as a single unit species with different life-spans (Francis 1986). Similarly, the time required to rehabilitate overexploited stocks varies with life-history, with longer-lived species requiring more time to recover than shorter-lived species (Francis 1986; Hightower and Grossman 1987).

The measurement of convergence to asymptotic values has been addressed in the literature largely from a theoretical context. For density-independent, deterministic Leslie-matrices, various metrics of distance to asymptotic values (e.g., λ or stable-age structure) have been introduced (Golubitsky et al. 1975, Demetrius 1975, Horst 1977, Cohen 1979, Tuljapurkar 1982). Grant and Benton (1996) analyzed convergence of

stochastic matrices and concluded that measures derived from the mean matrix provided an adequate prediction of convergence. In a density-dependent context, DeAngelis et al. (1980) looked at return times to equilibrium population size following perturbation (a temporary change) of matrix elements. They compared return times for 5 different fish species with maximum ages ranging from 8-15 years and looked at the number of years until the population size returned to 95% of its pre-perturbation level. They noted that the rate of return increased with higher levels of compensation (incorporated into first year survival) and that a lower limit on return times seemed to be related to the number of age classes. For the models in this paper, I permanently reduce a vital rate and define convergence to be within 1% of asymptotic λ (corresponding to the altered matrix).

Convergence and transient dynamics of age-structured populations have been analyzed only for single-site populations despite recognition of the importance of the spatial structure of populations and the exponential growth of metapopulation literature (Hanski and Simberloff, 1997, report a doubling time of 2 years). Although there is a large body of work on metapopulations (see Hanski 1999, Hanski and Gilpin 1997, and references therein), the work described here does not fit the classical metapopulation framework. Whereas the term metapopulation suggests systems where patches experience extinction and re-colonization events, I considered a more general system with no pre-requisite for extinction events. Also, metapopulation models usually incorporate low levels of migration, but I explored a wide range of migration, from very low to very high levels. For these reasons, I adopted the term "sub-divided populations" in this study to separate it from the traditional metapopulation definition.

Objectives- In this paper, I examined three main issues related to transient dynamics and convergence rates in sub-divided populations. First, I considered how connections between populations affect population growth rates and convergence times by comparing projections of one-, two-, and three-site Leslie-matrices following an event that lowers permanently either survival or fecundity at one site by 50%. The rationale for the comparison is this: suppose you were unaware of connections between populations (or, alternatively, you were aware of migration but considered it to be at a low enough level to ignore) and you calculated the effects of a planned action on the local population only—how far off would your predictions be from models that incorporate additional sites? This would be especially important if predicted growth rates differ markedly (from $\lambda<1$ to $\lambda>1$) or if estimated time to convergence is a lot shorter or much longer between single- and multi-site models.

Second, within multi-site models, I examined how the level of migration in and out of the altered site affects the amount of time and the path to convergence. When survival and/or fecundity differ between linked populations, the level of migration will determine the overall system dynamics. Similarly, when a management action is imposed on one site in a system, the presence of migration can "spread" the impact to connected sites. I compared the pattern and persistence of transient dynamics in two- and three-site models for several possible levels of migration. I also compared the effect of different age classes migrating by assuming migration occurs in all age classes with equal probability or in the first age class only.

Third, I anticipated that convergence times would vary between life-histories, with longer-lived species requiring more time to converge than shorter-lived species.

Following on the observation of DeAngelis et al. (1980) that there appeared to be a connection between the lower limit of convergence rates and the number of age classes in the population, I suspected convergence might be associated with generation times. The rationale for this is that after one generation, a change in a vital rate of one age-class will have affected all age classes. Therefore, I explored the implications of life-history on convergence by comparing results for a hypothetical r-selected and K-selected species.

2.0 Methods and Models

2.1 Mathematical Models

For all populations, I assumed survival and fecundity parameters were constant within an age-class, and that the sex-ratio was 1:1. I used a Leslie matrix to model female population dynamics and to determine convergence. For the one-site models, I refer the reader to Caswell (1989) for more results and history of the model. Lebreton (1996) derives the generalization and analogous results for multi-site matrix models.

The general matrix projection model consists of a population vector, $\mathbf{N}(t)$, which is partitioned into number of individuals in a given age class, i, at time t ($n_i(t)$). The state of the population one time step later, $\mathbf{N}(t+1)$, is obtained by pre-multiplying $\mathbf{N}(t)$ by the Leslie matrix $\mathbf{L}$. $\mathbf{L}$ contains elements of age-specific fecundity in the first row and age-specific survival on the first sub-diagonal. As a general rule, $\mathbf{L}$ is primitive, irreducible and non-negative, and so one can take advantage of the Perron-Frobenius theorem which guarantees the existence of a real dominant eigenvalue (greater than all others in magnitude) and associated right and left eigenvectors which contain all positive elements (Caswell 1989). The dominant eigenvalue, λ, describes asymptotic population growth, which indicates an increasing ($\lambda > 1$), stable ($\lambda = 1$), or decreasing ($\lambda < 1$) population. The

right eigenvector, **w**, describes the stable age structure, and **v**, the left eigenvector, describes age specific reproductive value.

The sensitivity of λ to an element, $l_{i,j}$, of matrix **L** is given by $\dfrac{\partial \lambda}{\partial l_{i,j}} = \dfrac{v_i w_j}{<\mathbf{vw}>}$, where $<\mathbf{vw}>$ is the scalar product (Caswell 1989). The sign and magnitude of sensitivities determine the direction and strength of change in λ following a change in $l_{i,j}$. Elasticities, also called relative sensitivities, account for the fact that matrix parameters may be measured on different scales (as fecundities and survivals usually are) by expressing the proportional change in λ resulting from a proportional change in a parameter. Therefore, direct comparisons can be made between the elasticity of different model parameters.

Elasticities are calculated as: $\dfrac{\partial \log(\lambda)}{\partial \log(l_{i,j})} = \dfrac{l_{i,j}}{\lambda} \bullet \dfrac{v_i w_j}{<\mathbf{vw}>}$ (Caswell 1989).

In a multi-site context, the matrix **M** is structured similarly to **L**. Whereas **L** contained scalar entries, **M** contains sub-matrices: the first p rows (corresponding to a model with p sites) contain p x p matrices of age- and site-specific fecundity. The first sub-diagonal contains p x p matrices of age- and site-specific (survival x dispersal) probabilities. In discretizing the events of survival and dispersal, one generally makes a simplifying assumption as to the timing of migration so that it occurs either at the beginning of the time interval or at the end. This assumption can have important implications for parameter sensitivity and for λ (Appendix 1). I assumed that migration occurs at the beginning of the time interval. For mild assumptions of connectivity between sites, the Perron-Frobenius theorem remains applicable (Lebreton 1996). In this instance, λ represents the asymptotic growth of the entire population system rather than the growth of one particular site. The stable age/site structure is given by **w**, and

reproductive value per age/site is given by **v**. The population vector, **N**(t), is partitioned into age-by-site classes. Sensitivities and elasticities are calculated in a similar fashion.

2.2 Representative r and K Models

I created models of hypothetical r- and K-selected species based on expected life-history characteristics. Female survival and fecundity parameters used in all models are given in Table 1. All models were of the "pre-birth" census format, meaning that fecundities in the first row are multiplied by first year survival (s_0), hence the first age class is 1-year olds.

For the r-selected species, I used a two-age class model for individuals of age 1 and age ≥ 2. The survival parameters were chosen so that the maximum age was 5 (i.e. $s_0 s_1 s_2^3 < 0.01$). Fecundities were chosen to produce a large annual growth rate ($\lambda = 1.1504$), and without too great of a difference between the two age classes. For the K-selected species, I used a ten-age class model, with age class 10 containing individuals ≥ 10 years. The maximum age was 50 ($s_0 s_1 s_2 \ldots s_{10}^{40} < 0.01$). Reproduction began at age 6, with fecundity increasing up to a maximum achieved at age 10. Population growth for the K-selected species ($\lambda = 1.0504$) is much lower than for the r-selected species. For these patterns of reproduction and survival, population doubling would occur approximately every 5 years for the r-selected species and every 14 years for the K-selected species.

The mean generation time, $\overline{T}$, is given by

$$\overline{T} = \frac{\sum_i i \lambda^{-i} F_i \left(\prod_{j=1}^{i-1} S_i \right)}{\sum_i \lambda^{-i} F_i \left(\prod_{j=1}^{i-1} S_i \right)}$$

(Caswell 1989). Given a cohort of newborns, $\overline{T}$ is the average age of the mothers that produced them (assuming the population is at the stable age structure). For the r-selected species, $\overline{T}_r$ =1.64 years and for the K-selected species, $\overline{T}_K$ =12.28 years.

For both representative species, I created 1- , 2- , and 3-site models (Fig 2). The 1-site model is the standard Leslie-matrix ($\mathbf{L}_r$ and $\mathbf{L}_K$, for the two species), while 2- and 3-site models are multi-site Leslie matrices ($\mathbf{M}_r$ and $\mathbf{M}_K$). The multi-site models contained migration between sites as indicated in Figure 2. Migration rates, $m_{i,j}$, are expressed as a probability of moving from site j to site i in a given year. I explored three levels of migration (0.05, 0.35, and 0.75) and defined three categories of migration, according to the probability of migrating into/out of site 1: EQUAL, MORE IN, MORE OUT. For all models, I explored 2 migration structures: either all age classes migrated with the same probability, or only the first age class migrated.

2.3 Modeling Approach

I first calculated elasticities for all model parameters to determine which age- specific survival and fecundity rate λ had greatest elasticity to (referred to as s^* and f^*). For the r-selected species, $s^*=s_0$ and $f^*=f_1$, while for the K-selected species $s^*=s_{10}$ and $f^*=f_{10}$ (Table 2). For all models, I decreased either s^* or f^* by 50% at site 1, and obtained "new" matrices $\mathbf{L}_r^*$, $\mathbf{L}_K^*$, $\mathbf{M}_r^*$, and $\mathbf{M}_K^*$, with corresponding "new" population growth rates, λ^* (Tables 3-7). Starting at the same initial population size, $\mathbf{N}(0)$, for each model, I projected the model and calculated annual population sizes $\mathbf{N}(t)$ and transient growth rates, $\tilde{\lambda}_t = \dfrac{\mathbf{N}(t)}{\mathbf{N}(t-1)}$. I continued projecting the model until time c, where all $\tilde{\lambda}_t (t \geq c)$ were within 1% of λ^*. c is thus my measure of convergence time. In multi-site models, I

calculated convergence of the system to λ^* and also the number of years until the population growth rate in each site had converged to this value. Site-specific growth rates were calculated as $\tilde{\lambda}_{t(i)} = \dfrac{\mathbf{N}_i(t)}{\mathbf{N}_i(t-1)}$, where $\mathbf{N}_i(t)$ is the number of individuals in site i at time t.

3.0 Results

3.1 Growth Rates and Convergence Times for Spatial versus Non-spatial Models

In 1-site (non-spatial) models, all r-models and half of the K-models led to $\lambda^*<1$, indicating decreasing populations (Table 3). In contrast to this, only about 25% of 2- and 3- site (spatial) r-models and about 5% of spatial K-models led to $\lambda^*<1$ (Tables 4-7; Fig. 3a-b). Between 2- and 3-site models, all but one 3-site model yielded a higher λ^*. In these spatial models, the largest λ^*s occurred when the probability of migrating out of site 1 was greater than the probability of migrating in (the MORE OUT pattern).

The time required to converge within 1% of λ^* for spatial models (at both the system and site-level) compared with 1-site convergence times are given in Tables 8-11. In models for the r-selected species, convergence of the system to λ^* in spatial models was almost always slower than in non-spatial models, with 3-site models requiring the longest time to converge (Fig. 4a). There were several exceptions where the 1-site model took as long or longer to converge. All of these cases were associated with high (0.35) or very high (0.75) migration levels, most notably at the highest level for the EQUAL pattern and for both levels of the MORE OUT pattern. Convergence of one or both sites to λ^* was always slower than non-spatial models. In all cases for spatial models, the altered site converged slower than the system.

In spatial models for the K-selected species, convergence of the system to λ^* was as slow or slower than 1-site models in about 40% of all cases. In general, convergence was longer for spatial models at the lowest level of migration for the EQUAL pattern or when the pattern was MORE IN, especially when only the first age class migrated (Fig. 4b). The decrease in λ was greatest for MORE IN, which is probably why convergence times were greatest in these cases. When the probability of migrating was 0.05 in the EQUAL pattern, the decrease in λ was intermediate for the cases explored, so it is most likely the reduced number of individuals migrating (particularly when only the first age class moves) that causes convergence times to increase. For the cases where convergence was faster in spatial models, I suggest that this is due to a much smaller decrease in λ combined with high migration levels, especially when migration occurred in all age classes. Also, λ decreased much less proportionally for K- than for r-selected species, because the elasticities to s^* and f^* were much less (Table 2). Convergence at the site-level in spatial models was slower than in non-spatial model in 77% of all cases. As in the r-selected species, the exceptions occurred for the MORE OUT pattern and in the higher migration levels in the EQUAL pattern (especially when migration occurred in all age classes). Also, convergence at the site-level was slower than for the system in all spatial models.

3.2 Convergence Times According to Migration Levels and Patterns in Spatial Models

In 2- and 3- site models, the longest convergence times at the system and site level occurred at the lowest level of migration (0.05) for the EQUAL pattern and for the MORE IN pattern (Fig. 5a-b). The fastest convergence times in both 2- and 3-site

models occurred at the two highest levels of migration (0.75 and 0.35) for the EQUAL pattern, and at both migration levels for the MORE OUT pattern. This was true regardless of whether migration occurred in all or only the first age class.

In general, site 1 (the altered site) converged the slowest (Tables 8-11). Only for the MORE IN patterns in 2-site models and the EQUAL pattern (at the highest migration level) in 3-site models did site 2 converge more slowly. For the MORE IN pattern in 2-site models, site 2 experienced a greater net loss from migration and received fewer immigrants from the altered site. In 3-site models, this did not occur for the MORE IN pattern because site 2 was also receiving immigrants from site 3. However, at the highest level of migration in the EQUAL pattern, there were a few exceptions. This is probably due to the fact that site 2 experienced a complete turn-over at each time step, because 100% of individuals at that site emigrate.

Patterns of transient dynamics at the site- and system-level were consistent according to migration patterns and life-history, and did not depend on the parameter that was decreased. For the K-selected species, oscillations were strong for the EQUAL and the MORE IN patterns, and were very weak for the MORE OUT pattern (Fig. 6a-b). The r-models showed no oscillations, except at the highest level of migration for the EQUAL pattern when all ages migrated.

In the K-models, the period of oscillations was almost always 10 years (also true for 1-site models). Oscillations are due to the presence of complex eigenvalues in the spectra of the matrix. The period of an oscillation due to a given complex eigenvalue, λ_C, is calculated by $\dfrac{2\pi}{\text{angle}(\lambda_C)}$ (Caswell 1989). For K-models, this angle was almost always in the interval [0.63-0.68], which gave a period of 9-10 years. The generation time for the

K-selected species ranged from 10-13 years, depending on migration and whether survival or fecundity was reduced. Thus, the period of oscillation tended to be slightly shorter than the generation time. Also, the generation time did not closely predict convergence times. To verify that the period length found in K-models was not an artifact of the number of age classes, I tried several cases for expanded (10 or 15 age classes) and full (50 age classes) models and found the same period of oscillation, and the same ranges for the angle and the generation times. In only 2 cases for r-models did the matrix spectra contain complex eigenvalues (at the highest level of migration in the EQUAL pattern when only the first age class migrated). However, no oscillations were perceptible in these cases. The generation time for r-selected species ranged from 1.64 to 2.09 years.

Exceptions to the above patterns of transients occurred at the highest level of migration in the EQUAL pattern for both 2- and 3- site models. When all age classes migrate in both the r- and K-models, site 1 and site 2 have completely opposite annual cycles (Fig. 7a-b). When only the first age class migrates, an exception occurred only in a 3-site model for the K-selected species. This case occurred at the highest level of migration in the EQUAL pattern, and I found that the period length and oscillations were slightly irregular (Fig. 8). These irregular oscillations are probably due to the amount of time before first year migrants reproduce. This could explain the apparent "superimposed" oscillation that appears in year 11 for site 2. In the other cases where all ages migrate and the sites displayed mirror-image cycles, this is probably due to the fact that all ages (including breeders) enter and exit the altered site annually, effectively shifting the site with the greater proportion of individuals each year.

At the system-level, no oscillations were found for the r-models while in K-models, the period of oscillation was again 10 years. For models of both species, the system λ was nearly mid-way between the site λ's for the EQUAL pattern. For the MORE OUT pattern, the system λ closely tracked site 2 whereas for the MORE IN pattern it tracked site 1 (Fig. 6a-b). Thus, the transient dynamics of the system were more closely tied to the site receiving the greater proportion of migration.

3.3 Differences in Convergence Between r- and K-selected Species

For 2- and 3- site models, convergence times at the system and site-level for the K-selected species were almost always greater than for the r-species, except when migration occurred in all age classes (Fig. 9a-b). Within the cases where all age classes migrate, the K-selected species converged more slowly than the r-selected species when the migration pattern was MORE IN. These were the cases where the changes in λ were greatest. When the migration pattern was MORE OUT, both species converged at about the same time at both the system- and site-level. These were the cases where the changes in λ were smallest.

4.0   Discussion

The majority of results were as expected, namely that most spatial models required more time to converge than non-spatial models, and that a longer-lived species generally converged more slowly than a shorter lived species. Exceptional cases to the above results consistently occurred for specific migration patterns. This highlights the importance of migration as a process that can strongly affect population dynamics, and emphasizes the need to estimate it in addition to survival and fecundity rates.

In the metapopulation/sub-divided population literature, there are studies describing the stabilizing role of migration for local dynamics (e.g. Lebreton and Gonzalez-Davila 1993; Ruxton et al. 1997). These studies differ from mine in two respects: the models were density-dependent, and were not age-structured. Age-structure is an essential component to my research because it permits the exploration of outcomes when only a certain portion of the population experiences a change in a vital rate, and when not all age classes migrate. The alteration of a vital rate in only one-age class is a realistic scenario, because managers will often try to identify an age or stage class on which to concentrate their efforts (e.g. Crouse et al. 1987). These crucial age classes are usually identified by a sensitivity or elasticity analysis, and the result can vary dramatically between life-histories.

DeAngelis et al. (1980) found that convergence times were associated with the number of age classes, but that result was not apparent in this study, nor were convergence times associated with generation length as hypothesized. Instead, convergence times seem to be influenced by a whole suite of factors, such as the age class experiencing a reduced vital rate, the elasticity of that rate, the level and pattern of migration, the age classes that migrate, and the life-history of the species. Although a linear arrangement was the only scheme explored for a 3-site model, I suspect that spatial arrangement will also influence convergence times. The remaining possible 3-site spatial arrangements (linear with the altered site in the middle, or a "ring" pattern with all three sites connected) would probably show faster convergence rates, as the altered site would then be receiving input from two sites rather than one.

Several of the proposed metrics for convergence dealt with measuring distance from the asymptotic stable age structure. I chose to measure convergence to the asymptotic population growth rate, by measuring $\tilde{\lambda}_i$ from two successive population counts. In practice, there would probably be less error associated with estimates of population size than estimates of the proportion of individuals in each age class because age may be difficult to determine, especially for long-lived species. Also, Lebreton and Clobert (1991) point out that stable age structures are less sensitive to changes in vital rates, especially when all are changed in the same proportion. In such a case, λ changes but the stable age structure does not (Lebreton and Clobert 1991), and I expect results would be similar to models without age structure.

All of the models in this study were deterministic, with constant migration rates. Thus, migration rates do not change following a change in vital rates. This will probably not be true for real populations, but it is expected that species may require several years to adjust their migration pattern in response. Thus, my models might reflect the initial result of a changed vital rate, but not the ultimate result if a secondary change in migration rates occurs. However, this sort of effect would be hard to predict and incorporate into a model. Alternatively, migration could be dependent on the density or quality of the site from which an individual leaves. Successful incorporation into the new site could also depend on the density and quality there, and this factor could be considered as well. Another implicit assumption in these models is that migration is instantaneous, and no mortality occurs during migration. Incorporating a mortality risk component into migration would effectively lower the overall migration level, and would therefore be expected to lengthen convergence times.

5.0   Management Implications

Several results with very clear management implications emerged from this study. First, all spatial models yielded higher growth rates than non-spatial models after a 50% decrease in a vital rate, and in many cases this changed the resulting λ from a value less than 1 to a value greater than 1. This was due to migration, for as more individuals left the altered site, fewer experienced the lowered vital rate. (This results from the assumption of migration occurring at the beginning of the year; an analytical treatment of this assumption is given in Appendix 1). The implications of this are that a "closed population" assumption (i.e. ignoring immigration and emigration) will lead to an overestimation of the effect of a decreased vital rate on λ. This will be especially important if potential actions are compared in terms of their ability to maintain a stable (or slightly increasing) rather than a decreasing population growth rate. Also, spatial models generally yielded longer convergence times (particularly for the altered site) than non-spatial models.   Ignoring migration would negatively bias projections for convergence times. This was especially true at the lowest levels of migration (0.05), which might be on a scale where one would be inclined to ignore it.

Among spatial models, the level and pattern of migration affected both λ and convergence times. Thus, in the management of sub-divided populations, one should have a basic understanding of existing migration patterns prior to implementing any control. In practice, migration rates can be difficult to measure, and studies can be expensive and time-consuming as they require enormous banding/tagging effort as well as resighting/recapture information. Model development in this area has been receiving a lot of attention in recent years (Hilborn 1990; Hestbeck et al. 1991; Schwarz et al. 1993;

Brownie et al. 1993; Hanski et al. 2000) although there is still a paucity of available data to use in these models. Even if exact measurements of migration cannot be obtained, general descriptions as to the level (high or low) and the direction of flow (more coming in or more going out) can be helpful in predicting site-specific and system level responses.

Comparisons between life-histories are slightly confounded by the fact that vital rates have different elasticities, and the parameters with greatest elasticity occur in different age classes and affect different proportions of age classes. This emphasizes the difficulty of managing species with different life-spans under one "umbrella policy." Where practical, management policies ought to be "life-history specific," meaning that species with similar life-histories could be managed as a unit, even if complete data are not available for all species included in the unit. A species-specific approach would not be practical, as data requirements would be enormous.

Short-term dynamics following a change in a vital rate did not create annual fluctuations for the short-lived species in this study except for very high levels of migration in the EQUAL pattern. Thus, the approach to predicted λ can be expected to be smooth for short-lived species. For longer-lived species, fluctuations were present in nearly all cases, though the strength of oscillations was influenced by migration. If high variation in annual growth rates (or annual yields from harvesting) is undesirable, particular attention should be given to studying migration patterns. Although not explored here, it is possible that a management strategy to implement an action at more than one site (at the same or different levels) could create a smoother path to convergence. Also, the observed oscillations occurred not just at the altered site, but for

the other sites as well. Again, it is the level and pattern of migration rates that determine how much a given action at one site "spreads" to other sites in the system, and thus a basic understanding of migration is essential for responsible management.

This study has focused on sub-divided populations, and it is most natural to envision geographically separated populations. However, in some cases, it is possible that the division of a population is imposed by managers. One example of this would be designating a portion of otherwise contiguous habitat as a "reserve" where hunting or fishing activities are prohibited. In this case, migration would refer to individuals that cross the management boundary. Rather than migration being a discrete event occurring once a year, individuals could change sites many times throughout the year. Home range sizes, foraging distances, and quality of each portion of the habitat are several factors that could influence migration in this setting, and would need to be studied before delineating the boundary for each site.

Acknowledgements

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Appendix 1

Two questions are explored in this appendix:

I. How does migration affect the sensitivity of λ to survival in a given site?

II. How does the timing of migration affect the sensitivity of λ to survival in a given site
    (or, when does timing not matter)?

Notation:

- S_a is a diagonal matrix of survival of individuals from age a to age a+1 during

  the time interval (t, t+1). For a 2-site model, I have: $S_a = \begin{bmatrix} s_{a,1} & 0 \\ 0 & s_{a,2} \end{bmatrix}$, where

  $s_{a,i}$ is the survival of an age a individual in site i.

- D_a is a matrix of migration probabilities for age a individuals during the

  interval (t, t+1): $D_a = \begin{bmatrix} 1-m_{2,1} & m_{1,2} \\ m_{2,1} & 1-m_{1,2} \end{bmatrix}$ where $m_{i,j}$ is the probability an

  individual migrates from site j to site i during the interval.

- **v** is the left eigenvector associated with the dominant eigenvalue, λ, and **w** is

  the associated right eigenvector. In multi-site models, **v** and **w** are partitioned

  according to age-by-site classes. For example, $v_{a,i}$ is the reproductive value of

  an age a individual in site j.

Cases considered:

1. Migration occurs at the beginning of the year ($S_a D_a$).

2. Migration occurs at the end of the year ($D_a S_a$).

3. Migration occurs at some time Δt during the time interval t to t+1

($S_a D_a (1 - \Delta t) + D_a S_a \Delta t$).

Results (I) – I compare sensitivity of λ to survival at age a with and without migration.

Case 1: In the absence of migration, $\left. \dfrac{\partial \lambda}{\partial s_{a,1}} \right|_{No\_mig.} = v_{a,1} w_{a-1,1}$.

In the presence of migration, $\left. \dfrac{\partial \lambda}{\partial s_{a,1}} \right|_{mig.} = v_{a,1} w_{a-1,1}(1 - m_{2,1}) + v_{a,1} w_{a-1,2} m_{1,2}$.

The question is whether migration will increase or decrease the sensitivity of λ to survival

at a given site in a multi-site context. I will have $\left. \dfrac{\partial \lambda}{\partial s_{a,1}} \right|_{mig.} > \left. \dfrac{\partial \lambda}{\partial s_{a,1}} \right|_{No\_mig.}$ when

$$v_{a,1} w_{a-1,1}(1 - m_{2,1}) + v_{a,1} w_{a-1,2} m_{1,2} > v_{a,1} w_{a-1,1} ,$$

i.e. when

$$w_{a-1,2} m_{1,2} > w_{a-1,1} m_{2,1} .$$

Thus, migration increases the sensitivity of λ to survival when the proportion migrating

into site 1 is greater than the proportion migrating out of site 1. Likewise, sensitivity

would be decreased if migration favors emigration. This result is also true for the

sensitivity of λ to fecundity.

Case 2: Following a similar procedure, migration will increase the sensitivity of λ to

survival when

$$m_{2,1} \left(\frac{v_{a,2}}{v_{a,1}} - 1 \right) > 0 .$$

Thus, the sensitivity of λ to survival in site 1 is increased when individuals migrate to a

site with greater reproductive value. Again, the same result is true for fecundity.

Case 3: Migration will increase the sensitivity of λ to survival when

$$\frac{w_{a-1,2}}{w_{a-1,1}}(1-\Delta t)m_{1,2} > m_{2,1}\left(1 - \frac{v_{a,2}}{v_{a,1}}\Delta t\right).$$

The interpretation of this expression is not so straightforward, though it clearly falls

between the first two cases.

Results (II)

The timing of migration does not matter when

$$v_{a,1}w_{a-1,2}m_{1,2} = v_{a,2}w_{a-1,1}m_{2,1}.$$

Thus, when the proportion of individuals leaving site 2 and the proportion of individuals

leaving site 1 have the same reproductive value, the sensitivity of λ to survival at a

particular site is the same regardless of when the migration occurs.

Table 1: Age-specific fecundity (f_x) and survival (s_x) parameters for hypothetical r- or K-selected species. For the r-selected species, age class 2 contains individuals ≥ 2; for the K-selected species, age class 10 contains individuals ≥ 10. (s_x is survival from age x to x+1).

Age	r-selected		K-selected	
	f_x	s_x	f_x	s_x
0	-	0.32	-	0.70
1	2.1	0.44	0	0.80
2	2.55	0.40	0	0.85
3			0	0.87
4			0	0.87
5			0	0.87
6			0.25	0.87
7			0.45	0.87
8			0.60	0.87
9			0.90	0.87
10			1.00	0.87

Table 2: Elasticities of λ to all survival ($e(s_s)$) and fecundity ($e(f_x)$) parameters for both r- and K-selected models. Bold entries in the table indicate the parameters to which λ has greatest elasticity.

Age	r-selected		K-selected	
	$e(f_x)$	$e(s_x)$	$e(f_x)$	$e(s_x)$
0	-	**0.6107**	-	0.0815
1	**0.3567**	0.2540	0	0.0815
2	0.2540	0.1354	0	0.0815
3			0	0.0815
4			0	0.0815
5			0	0.0815
6			0.0048	0.0767
7			0.0071	0.0696
8			0.0078	0.0618
9			0.0097	0.0521
10			**0.0521**	**0.2511**

Table 3: Population growth rates for **1-site** models with no altered vital rates, or when either the survival or fecundity to which λ has greatest elasticity is decreased by 50%.

Vital rate altered	r-selected λ	K-selected λ
None	1.1504	1.0504
Survival	0.7929	0.9816
Fecundity	0.9681	1.016

Table 4: Population growth rates for **2-site** models of **r-selected** species when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1.   In a multi-site context, λ represents the overall growth of the system. Values from the 1-site model are given for comparison.

Pr(migr)		Decrease Survival		Decrease Fecundity	
out of, into altered site		Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
	(1-site)	0.7929	0.7929	0.9681	0.9681
EQUAL	0.75,0.75	0.9635	0.9532	1.0472	1.0486
	0.35,0.35	0.9867	0.9974	1.0578	1.0597
	0.05,0.05	1.0996	1.1171	1.1075	1.1198
MORE OUT	0.75,0.05	1.1299	1.1308	1.1385	1.1385
	0.35,0.05	1.1195	1.1249	1.1310	1.1324
MORE IN	0.05,0.75	0.8182	0.8219	0.9789	0.9790
	0.05,0.35	0.8774	0.9310	0.9965	1.0021

Table 5: Population growth rates for **2-site** models of **K-selected** species when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1. In a multi-site context, λ represents the overall growth of the system. Values from the 1-site model are given for comparison.

Pr(migr) out of, into altered site		Decrease Survival		Decrease Fecundity	
		Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
(1-site)		0.9816	0.9816	1.016	1.016
EQUAL	0.75,0.75	1.0021	1.0234	1.0353	1.0342
EQUAL	0.35,0.35	1.0072	1.0306	1.0353	1.0367
EQUAL	0.05,0.05	1.0242	1.0463	1.0364	1.0465
MORE OUT	0.75,0.05	1.0432	1.0482	1.0487	1.0488
MORE OUT	0.35,0.05	1.0397	1.0474	1.0469	1.0480
MORE IN	0.05,0.75	0.984	0.9936	1.0188	1.0191
MORE IN	0.05,0.35	0.9885	1.0201	1.0214	1.0265

Table 6: Population growth rates for **3-site** models of **r-selected** species when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1. In a multi-site context, λ represents the overall growth of the system. Values from the 1-site model are given for comparison.

Pr(migration) from		Decrease Survival		Decrease Fecundity	
site1→ site 2, site2→site 1/ site2→site 3, site 3→site 2		Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
	(1-site)	0.7929	0.7929	0.9681	0.9681
EQUAL	0.75,0.75 / 0.25,0.75	0.9972	0.9959	1.0639	1.0665
	0.35,0.35 / 0.35,0.35	1.0637	1.0792	1.0963	1.1003
	0.05, 0.05 / 0.05, 0.05	1.1302	1.1375	1.1323	1.1382
MORE OUT	0.75,0.05 / 0.05, 0.05	1.1409	1.1419	1.1446	1.1449
	0.35, 0.05 / 0.05, 0.05	1.1368	1.1398	1.1412	1.1423
MORE IN	0.05, 0.75 / 0.05, 0.05	1.0972	1.1177	1.0981	1.1179
	0.05, 0.35 / 0.05, 0.05	1.1020	1.1205	1.1036	1.1209

Table 7: Population growth rates for **3-site** models of **K-selected** species when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1. In a multi-site context, λ represents the overall growth of the system. Values from the 1-site model are given for comparison.

Pr(migration) from		Decrease Survival		Decrease Fecundity	
site1→ site 2, site2→site 1/ site2→site 3, site 3→site 2		Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
	(1-site)	0.9816	0.9816	1.016	1.016
EQUAL	0.75,0.75 / 0.25,0.75	1.0084	1.0305	1.0377	1.0374
EQUAL	0.35,0.35 / 0.35,0.35	1.0228	1.0418	1.0407	1.0435
EQUAL	0.05, 0.05 / 0.05, 0.05	1.0377	1.0488	1.0426	1.0489
MORE OUT	0.75,0.05 / 0.05, 0.05	1.0468	1.0494	1.0495	1.0497
MORE OUT	0.35, 0.05 / 0.05, 0.05	1.0461	1.0492	1.0486	1.0494
MORE IN	0.05, 0.75 / 0.05, 0.05	1.0070	1.0464	1.0229	1.0464
MORE IN	0.05, 0.35 / 0.05, 0.05	1.0138	1.0467	1.0277	1.0467

Table 8: Number of years to convergence within 1% of asymptotic λ for **2-site** models of **r-selected species** when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1.   Convergence times are given for site 1, site 2, system (on a separate line). Values from the 1-site model are given for comparison.

Pr(migr) out of, into altered site		Decrease Survival		Decrease Fecundity	
		Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
	(1-site)	1	1	2	2
EQUAL	0.75,0.75	6, 5,	3, 3,	4, 4,	2, 2,
		1	2	1	1
	0.35,0.35	4, 4,	8, 6,	2, 2,	4, 3,
		2	3	2	2
	0.05,0.05	15, 5,	18, 4,	19, 6,	25, 5,
		9	10	10	13
MORE OUT	0.75,0.05	3, 2,	7, 2,	2, 1,	3, 1,
		1	1	1	1
	0.35,0.05	6, 3,	10, 3,	5, 1,	8, 1,
		2	2	1	1
MORE IN	0.05,0.75	2, 4,	5, 9,	2, 2,	2, 3,
		1	2	2	2
	0.05,0.35	9, 10,	19, 12,	4, 6,	7, 12,
		6	15	2	2

Table 9: Number of years to convergence within 1% of asymptotic λ for **2-site** models of **K-selected** species when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1. Convergence times are given as: site 1, site 2, system (on a separate line). Values from the 1-site model are given for comparison.

Pr(migr) out of, into altered site	Decrease Survival		Decrease Fecundity	
	Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
(1-site)	5	5	3	3
EQUAL				
0.75,0.75	6, 5,	10, 7,	3, 2,	7, 5,
	5	4	2	2
0.35,0.35	3, 5,	14, 2,	3, 1,	4, 1,
	1	6	2	3
0.05,0.05	15, 8,	57, 1,	11, 2,	71, 1,
	5	23	3	13
MORE OUT				
0.75,0.05	3, 1,	7, 1,	2, 1,	2, 1,
	1	1	1	1
0.35,0.05	5, 2,	21, 1,	3, 1,	15, 1,
	1	1	1	1
MORE IN				
0.05,0.75	9, 14,	14, 19,	3, 3,	3, 8,
	9	14	3	3
0.05,0.35	9, 10,	49, 12,	3, 1,	11, 10,
	9	34	3	4

Table 10: Number of years to convergence within 1% of asymptotic λ for **3-site** models of **r-selected** species when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1. Convergence times are given for site 1, site 2, site 3, system (on a separate line). Values from the 1-site model are given for comparison.

Pr(migration) from		Decrease Survival		Decrease Fecundity	
site1→ site 2, site2→site 1/ site2→site 3, site 3→site 2		Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
	(1-site)	1	1	2	2
EQUAL	0.75,0.75 / 0.25,0.75	11, 12, 10, 1	7, 2, 7, 1	8, 8, 7, 1	3, 2, 3, 1
	0.35,0.35 / 0.35,0.35	9, 4, 6, 3	12, 7, 8, 6	6, 1, 4, 2	9, 2, 6, 2
	0.05, 0.05 / 0.05, 0.05	20, 15, 9, 8	22, 15, 6, 9	24, 1, 9, 10	30, 1, 4, 11
MORE OUT	0.75,0.05 / 0.05, 0.05	6, 1, 1, 1	8, 1, 1, 1	3, 1, 1, 1	4, 1, 1, 1
	0.35, 0.05 / 0.05, 0.05	10, 7, 5, 1	14, 1, 1, 2	7, 1, 1, 1	11, 1, 1, 1
MORE IN	0.05, 0.75 / 0.05, 0.05	27, 21, 9, 20	29, 22, 7, 20	47, 37, 12, 36	49, 36, 10, 36
	0.05, 0.35 / 0.05, 0.05	26, 21, 9, 18	31, 26, 9, 19	41, 31, 13, 30	45, 34, 11, 31

Table 11: Number of years to convergence within 1% of asymptotic λ for **3-site** models of **K-selected** species when either the survival or fecundity to which λ has greatest elasticity is decreased by 50% at site 1. Convergence times are given for site 1, site 2, site 3, system (on a separate line). Values from the 1-site model are given for comparison.

	Pr(migration) from site1→ site 2, site2→site 1/ site2→site 3, site 3→site 2	Decrease Survival		Decrease Fecundity	
		Migr. in ALL Classes	Migr. in FIRST Class	Migr. in ALL Classes	Migr. in FIRST Class
	(1-site)	5	5	3	3
EQUAL	0.75,0.75 /	6, 8, 6,	4, 8, 11,	3, 4, 3,	1, 5, 1,
	0.25,0.75	1	4	2	2
	0.35,0.35 /	5, 3, 4,	25, 5, 1,	3, 2, 1,	14, 2, 1,
	0.35,0.35	1	6	2	1
	0.05, 0.05 /	25, 2, 7,	60, 1, 1,	14, 1, 1,	79, 1, 1,
	0.05, 0.05	5	15	2	4
MORE OUT	0.75,0.05 /	3, 1, 1,	8, 1, 1,	2, 1, 1,	3, 1, 1,
	0.05, 0.05	1	1	1	1
	0.35, 0.05 /	6, 1, 1,	23, 1, 1,	4, 1, 1,	17, 1, 1,
	0.05, 0.05	1	1	1	1
MORE IN	0.05, 0.75 /	54, 35, 29,	115, 80, 1,	4, 3, 24,	175, 109,
	0.05, 0.05	34	72	3	1, 105
	0.05, 0.35 /	42, 25, 23,	116, 87, 1,	4, 1, 19,	150, 14, 1,
	0.05, 0.05	24	57	3	71

Figure 1: Elasticity of population growth rate (λ) to survival increases with generation length while elasticity to fecundity decreases (after Lebreton and Clobert 1991, p. 109 Fig. 5.2).
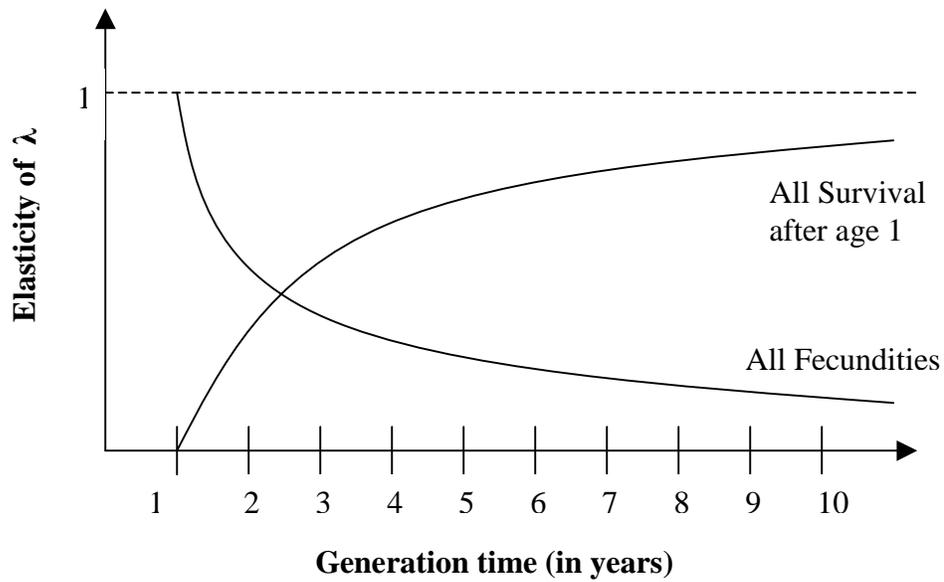
Figure 2: Schematic of 1-, 2- , and 3- site models (a, b, c, respectively). For all models, site 1 is where survival or fecundity is lowered by 50%. Arrows represent migration. For the 3-site case, we explore only a linear arrangement with the altered site at one end of the chain.
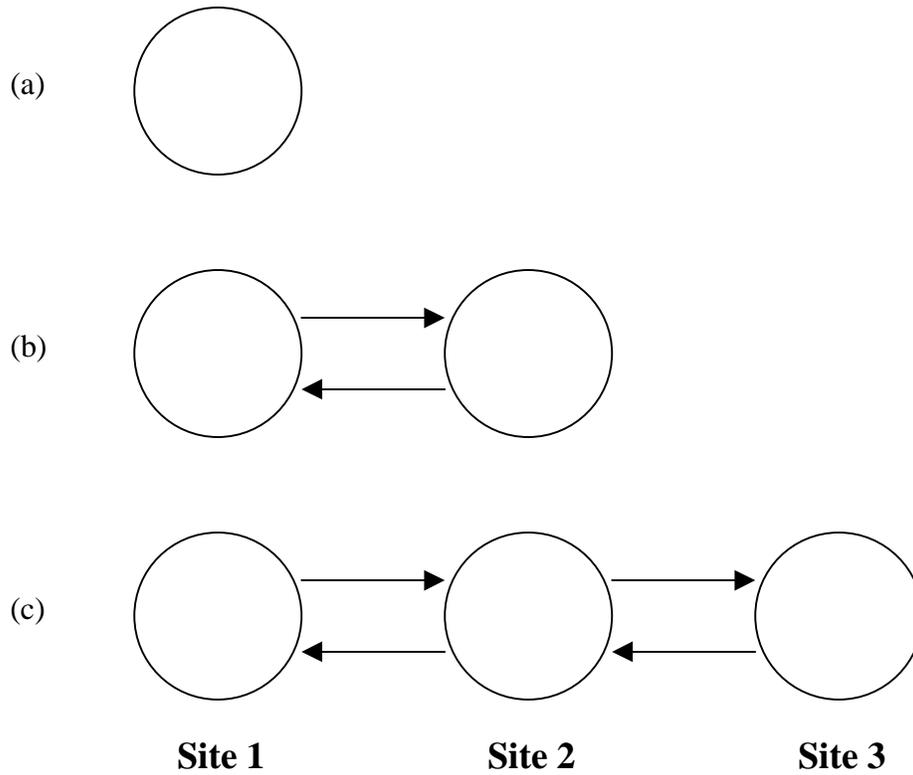
(a)

(b)

(c)

Site 1   **Site 2**   **Site 3**

Figure 3: Population growth rate of 1-site versus 2- and 3-site models after s^* was lowered by 50% in site 1 for (a) an r-selected species or (b) a K-selected species. For multi-site models, migration is given as the probability of moving out of, into the altered site. Migration was assumed to occur in all age classes. Values above (below) the line at 1 indicate increasing (decreasing) populations.

(a) r-selected species
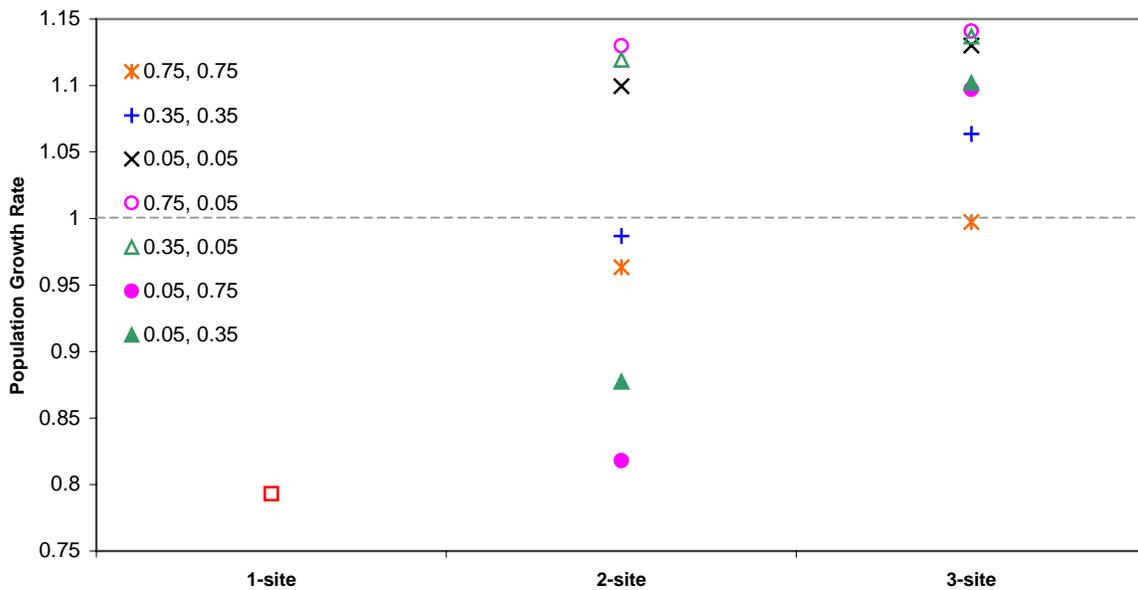
(b) K-selected species
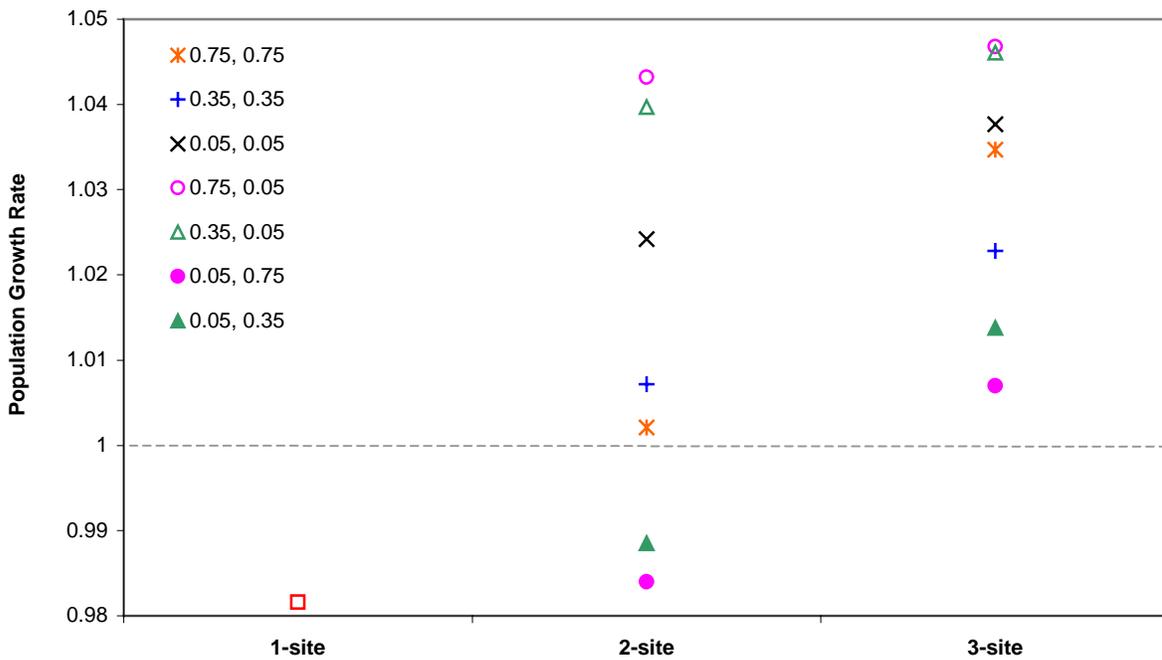
Figure 4: Years to convergence (at system-level in multi-site models) for 1- , 2- and 3-site models when s^* is decreased by 50% at site 1 for (a) an r-selected species or (b) a K-selected species. Migration was assumed to occur in only the first age class. For multi-site models, migration is given as the probability of moving out of, into the altered site.

(a) r-selected species
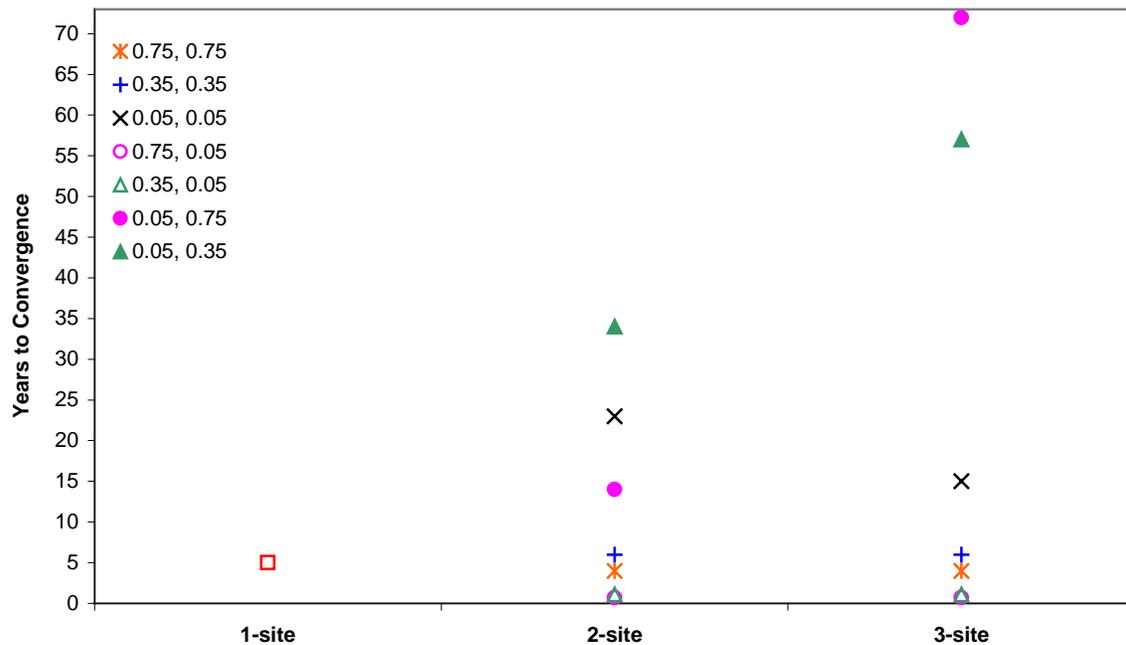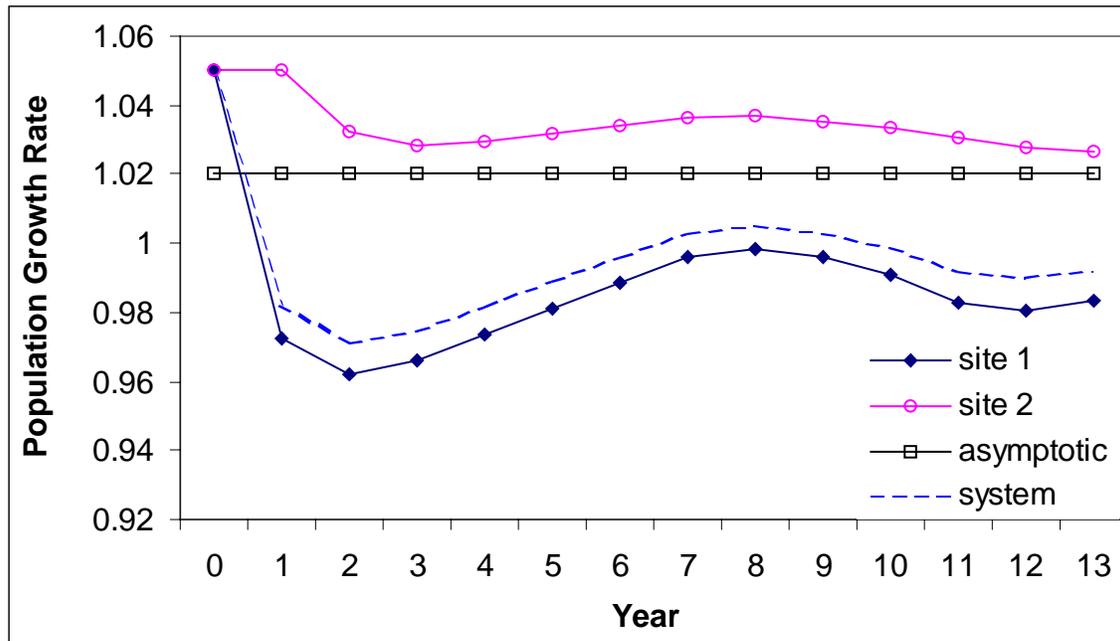

(b) K-selected species

Figure 5: Years to convergence at the system-level in 2- and 3- site models after s* is decreased by 50% at site 1 for (a) an r-selected species or (b) a K-selected species. Migration was assumed to occur in only the first age class, and is given as the probability of moving out of, into the altered site.

(a) r-selected species
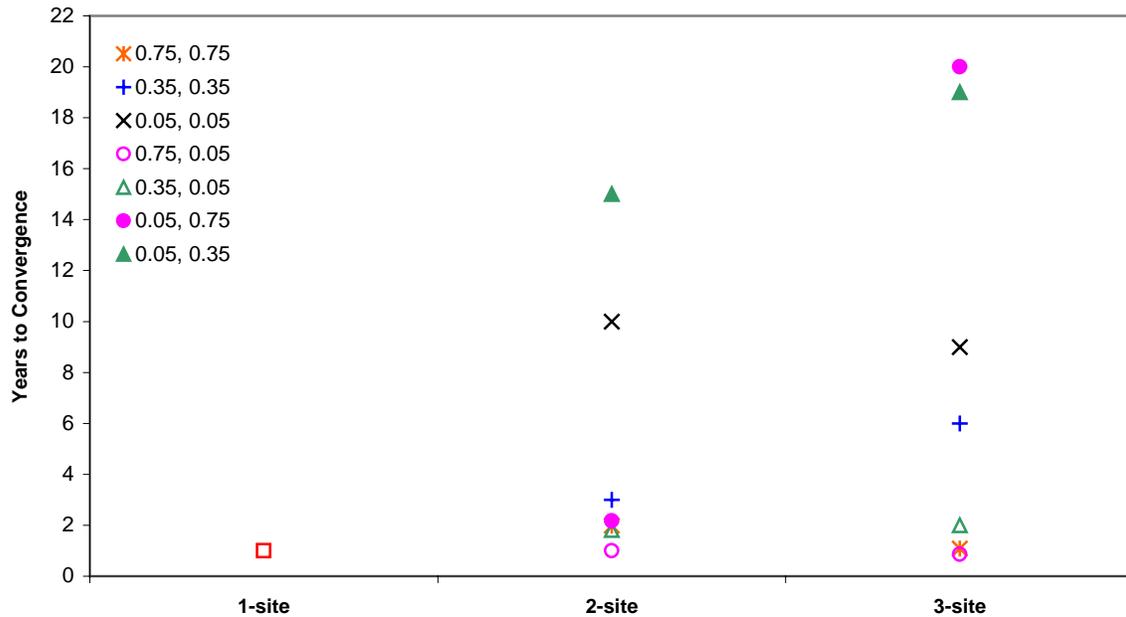
(b) K-selected species

Figure 6: Transient dynamics of population growth rate for a 2-site model of a K-selected species when s^* is decreased at site 1. Migration is assumed to occur in only the first age class, where the probability of migrating out of, into the altered site is (a) 0.05, 0.35 (MORE IN pattern) or (b) 0.35, 0.05 (MORE OUT pattern). Year "0" is the initial population growth rate prior to decreasing s^*.
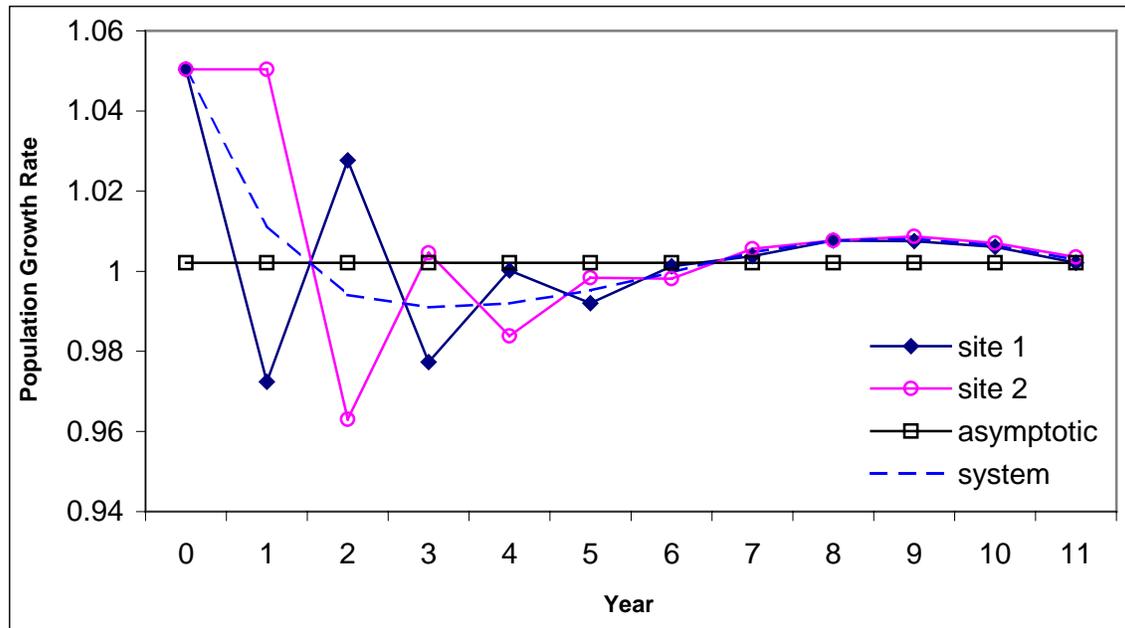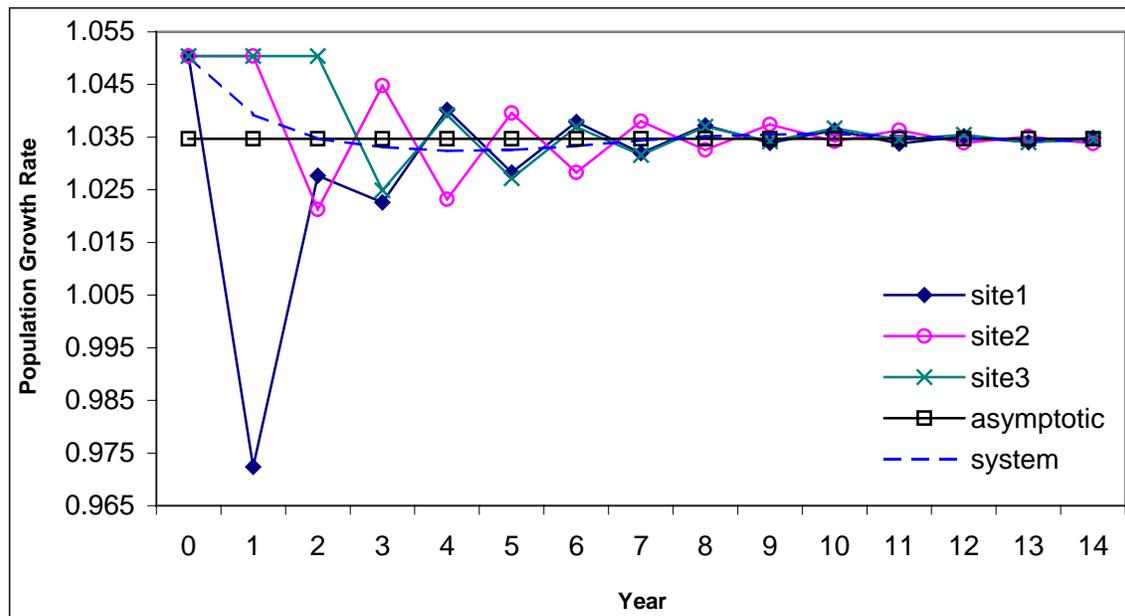
(a) MORE IN

(b) MORE OUT
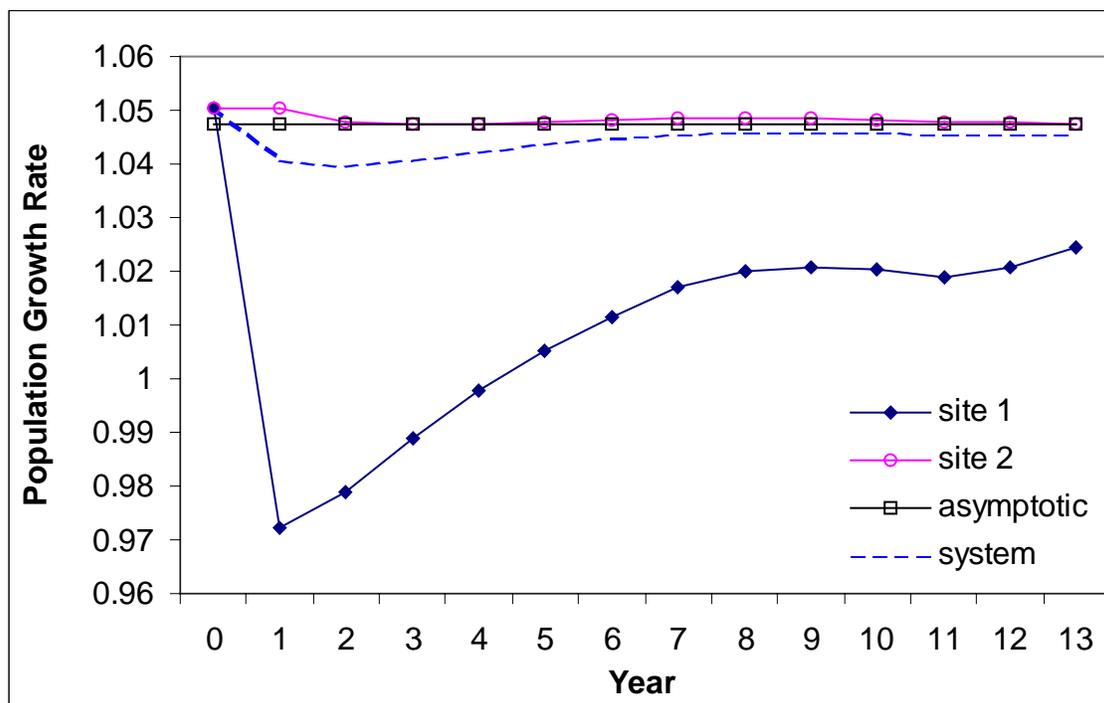
Figure 7: Transient dynamics of population growth rate for (a) a 2-site model or (b) a 3-site model of a K-selected species when s* is decreased at site 1. Migration is assumed to occur in all age classes, at the highest level (0.75) of the EQUAL pattern. Year "0" is the initial population growth rate prior to decreasing s*.

(a) 2-site

(b) 3-site

Figure 8: Transient dynamics of population growth rate for a 3-site model of a K-selected species when s^* is decreased at site 1. Migration is assumed to occur in only the first age class, at the highest level (0.75) of the EQUAL pattern. Year "0" is the initial population growth rate prior to decreasing s^*.
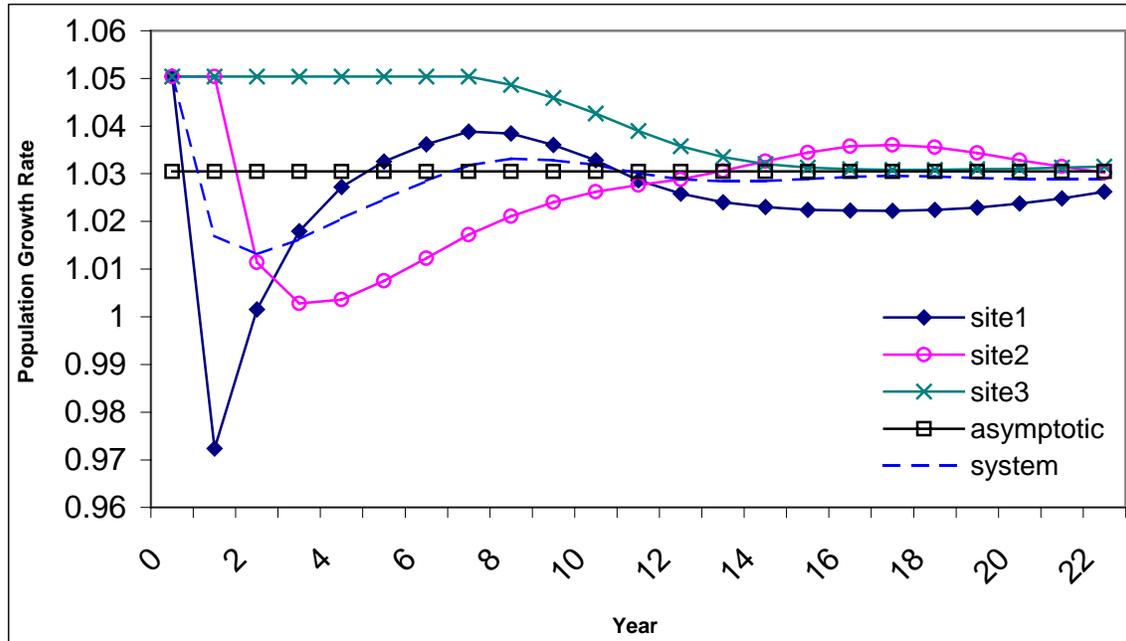
Figure 9: Difference in years to convergence at the system-level of K-selected species and r-selected species when (a) migration occurs in the first age class only or (b) migration occurs in all age classes. Migration probabilities refer to migration out of, into the altered site. Points above the line at zero indicate that the K-selected species required more years to converge, i.e. (Years for K-species) – (Years for r-species) > 0.

(a) Migration in first age class
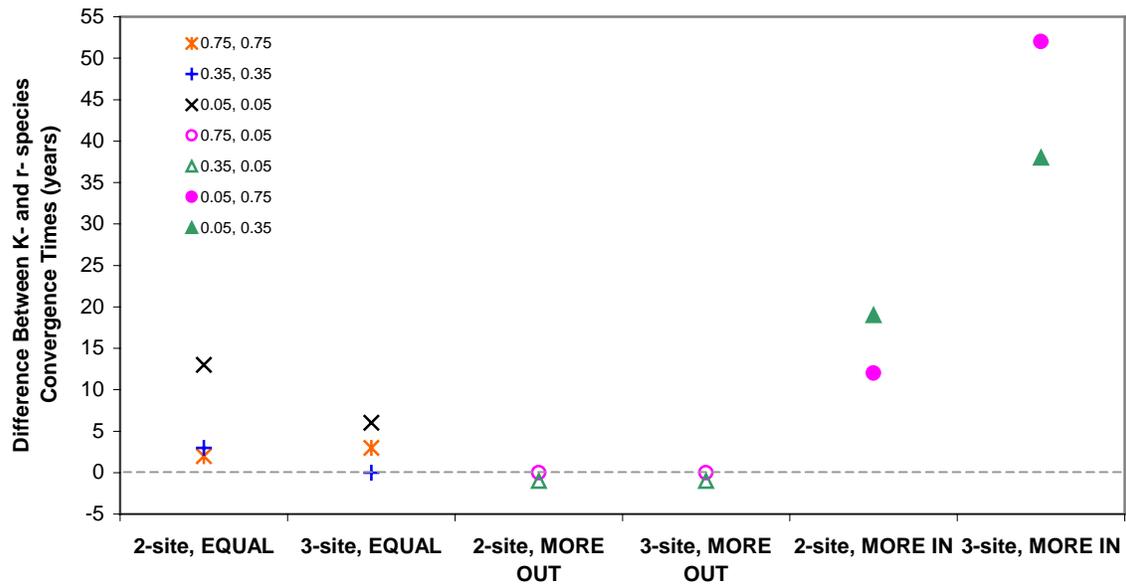
(b) Migration in all age classes
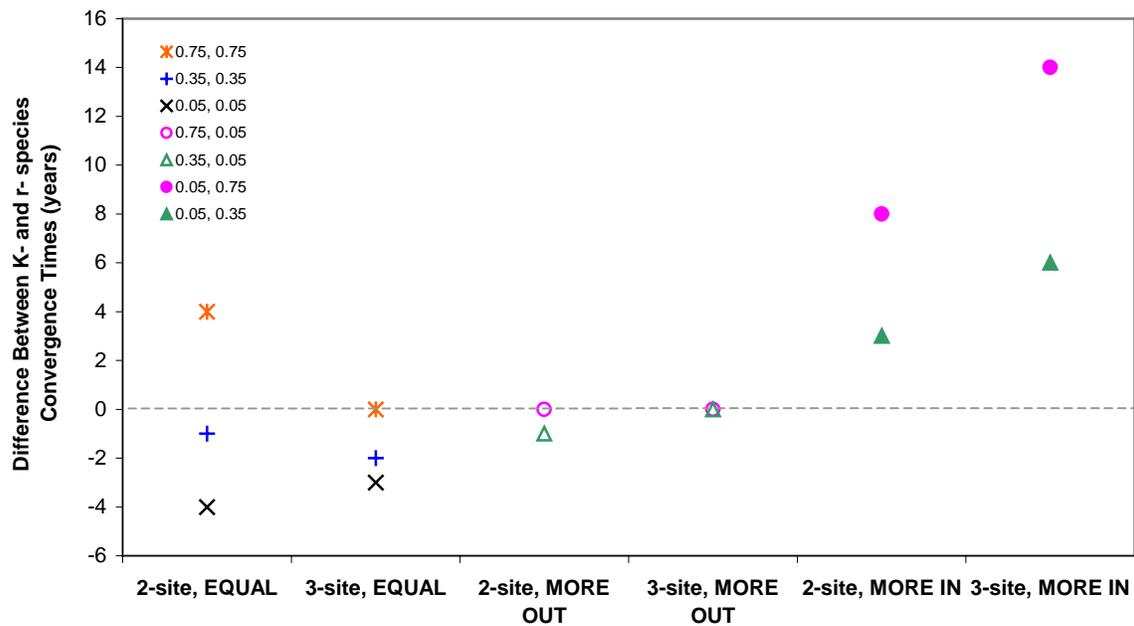
Chapter 5: Conclusions and Future Research

In both a density-independent and a density-dependent context, it was shown that the optimal strategy could be determined from inspection of elements of the left eigenvector (i.e. reproductive value) divided by a vector of age specific harvest value/cost. The maximum sustained yield is obtained when the age class with the smallest ratio is harvested. Depending on population parameters, this age-class should be harvested partially or completely. In one-site models, it is possible that a second (younger) age class could be harvested following complete removal of the first (older) age class. However, in multi-site models, the presence of migration permits the replenishment of age classes beyond the one fully exploited in a harvested site, and thus the optimal strategy can sometimes involve harvest of more than two age classes.

A unifying theme between the density-independent and density-dependent model was that of surplus production, and finding an optimal way to harvest it. In the density-independent model, the goal was to optimally harvest the surplus of an increasing population so that population size remained constant from year to year (hence, the population was reduced to equilibrium). In the density-dependent model, the goal was to optimally harvest a population that was at equilibrium to reduce it to a size where surplus production was maximized. The tool used to identify the optimal strategy was the same in both cases: the vector of reproductive values/weight (or cost). This ratio encapsulated the trade-off in harvesting—a balance needs to be attained between the value of an individual to the harvester and the value (reproductively speaking) of that individual to the population. Many individuals with low reproductive value could be removed with the

same effect on the population as removing only a few individuals with high reproductive value. However, when economic value varies between age-classes, each removal strategy will produce a different yield. The optimal strategy maximizes the yield from individuals removed.

The concept of a "closed population" is a simplifying assumption rather than a biological reality. The existence of migration between apparently isolated, "local" populations necessitates multi-site models. As was seen in Chapter 4, when a management action is performed at one site in a system of connected sub-populations, the effects can spread to additional sites. It is thus important to be able to identify migration levels and patterns.

While migration rates are an important component of the dynamics of sub-divided populations, estimating migration rates is a difficult task. While the modeler easily can think up more complex models of migration, migration rates must be measured to parameterize the models. Even assuming that migration rates are constant still requires a large amount of data. Nevertheless, I believe that the models used in this thesis could be made more realistic (with possibly greater predictive value) by making the migration rates more complex. I considered the simplest case for migration (constant rates), but many migration events are associated with seeking out a place to breed. Clearly, an individual cannot successfully migrate if there are no available territories. The easiest way to dismiss this is to assume that the population is below a level where density matters. This may be the case for harvested populations, and possibly will become the case for the Yellow Legged Herring Gull (Chapter 2) if culling efforts are very

successful. However, if a refuge is designated (as in Chapter 3 for Arcto-Norwegian cod), density effects could become important within the refuge.

Another topic for future research would be to incorporate stochasticity in migration rates. Grant and Benton (1996) explored a stochastic, one-site model, but they did not compare observed convergence (from model projections) with predicted convergence. Instead, they looked at a theoretical measure of convergence, the damping ratio (the ratio of the first to the second eigenvalue). Although not reported in Chapter 4, I found that the damping ratio had no predictive value in multi-site models. Adding a stochastic component to migration in multi-site models could be interesting for comparing the confidence interval for observed convergence times between various migration patterns. In my study, models with high migration rates converged most quickly. But if variability is proportional to (or increases with) the level of migration, then the confidence interval on convergence time may or may not differ significantly between high and low migration rates.

A final topic for consideration is the prediction and measurement of convergence rate. In Chapter 4, I defined convergence to be within 1% of asymptotic values. This is an empirical measure, but a theoretical value that could be obtained directly from the matrix would be useful. As mentioned above, I found that the damping ratio was uninformative about convergence times in multi-site models. The failure of the damping ratio suggests a closer examination of the relationship between migration parameters and the sub-dominant eigenvalue. Or, one might look at how migration rates "weight" site-specific growth rates as reflected in the dominant eigenvalue (in the absence of migration, the dominant eigenvalue is that of the "best" site—Lebreton 1996).