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# Workshop Proceedings on the Development of Spatially Structured Population Models for Northwestern Hawaiian Islands Lobster Resources 

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## INTRODUCTION

The Northwestern Hawaiian Islands (NWHI) lobster trap fishery, which commenced in the mid 1970s, is a multispecies fishery and the major commercial marine invertebrate fishery in the western Pacific. The Hawaiian spiny lobster (Panulirus marginatus) and slipper lobster (Scyllarides squammosus) constitute the majority of reported catches; green spiny lobster ( $P$. penicillatus), ridgeback slipper lobster ( $S$. haanii), and Chinese slipper lobster (Parribacus antarcticus) are also caught, but catches are low. While as many as 16 banks within the NWHI were fished annually, reported fishing effort and catch vary both spatially and temporally. Shifts in fishing effort between banks are attributed to declines in spiny lobster catch-per-unit-effort (CPUE); as spiny lobster were fished down and catch rates at a particular bank fell below some minimum economic threshold, fishing effort shifted to more productive banks. By the mid 1990s fishing was generally limited to Necker Island where relatively higher concentrations of spiny lobster were found. With the adoption of spatial management in 1998 fishing effort was redistributed throughout the NWHI, and the fishery's major target changed to slipper lobster.

The fishery developed quickly during the 1980s, was partially abandoned in the mid 1990s, and was closed in 2000 because of increasing uncertainty in the population models used to assess stock status. The uncertainties stem from processes that are related to spatial scale and the pooling of species-specific data. The present models express the number of exploitable lobsters (all species, all locations combined) in a given month as a function of the number of exploitable lobsters in the previous month, adjusted for natural mortality, fishing mortality, and recruitment. Pooling the commercial data across banks disregards spatial heterogeneity and assumes synchronous dynamics among local populations of lobsters, regardless of species and location, in the NWHI. Lobster populations in the NWHI have undergone significant changes in abundance and distribution over the past 2 decades, and many of the biological processes exhibit considerable spatiotemporal variability. In addition, the life histories of spiny and slipper lobsters differ, and it is likely that differences exist between population dynamics parameters (e.g., natural mortality, growth, etc.).

A further indicator of the unsatisfactory state of the present models has emerged in different estimates of key biological and fishery assessment parameters (DiNardo and Marshall, 2001). In addition, the models do not use all available information, in particular data from the National Marine Fisheries Service (NMFS) annual NWHI fishery-independent lobster resource survey which spans 20 years. Integrating all sources of information into the models would likely lead to a better understanding of the dynamics of NWHI lobster populations and sound management strategies.

Given the shortcoming of the present NWHI lobster population models, a workshop was convened at the NMFS Honolulu Laboratory from December 4 to 6, 2001 to develop a blueprint for improving models and methods for NWHI lobster stock assessments. Scientists with expertise in crustacean biology and population modeling and scientists from the State of Hawaii's Division of Aquatic Resources and Western Pacific Regional Fishery Management Council were invited. To facilitate development of the blueprint NWHI lobster biology, fisheries, oceanography, and current assessment methods were reviewed; weaknesses and inadequacies in current assessment methods and supporting data were identified; and alternative approaches to modeling and stock assessments were discussed. A course of action to improve stock assessment methods
and associated data collection was recommended by workshop participants and is consistent with the recent NWHI lobster research and monitoring plan developed by Honolulu Laboratory scientists (DiNardo and Marshall, 2001). The proceeding of the workshop, as well as the recommended course of action, are described in this report. The workshop's agenda is outlined in Appendix A, while a list of the participants is included in Appendix B.

## SOURCES OF DATA

In this section, we describe the availability of oceanographic data and resource monitoring and research conducted by the NMFS-HL to support NWHI lobster stock assessments. The availability and quality of the data collected by the various NWHI lobster monitoring programs from 1983 to the present are summarized and presented as information matrices (Tables 1 and 2). Earlier data are described separately. The availability of various biological and ecological data for NWHI lobsters is summarized in Table 3.

Four subjective categories describing the quality of data are defined for the information matrices. Blanks in the matrices indicate no data. Open circles indicate poor data with high uncertainty, no corroborative analyses, and low frequency (only 1-3 years of data available). Half filled circles indicate moderate data with moderate uncertainties, anecdotal corroborative evidence, and moderate frequency (4-6 years of data). Filled circles indicate good data with low uncertainties, corroborative analyses, and sufficient time series ( $\succ 6$ years of data).

The temporal extent of data for the NWHI (pooled across all banks) is depicted in Table 1, while the spatial extent of the data (at the bank level) is depicted in Table 2. Since 1995, monitoring of both the fishery and lobster populations has increased significantly to provide necessary data for advancing population model development and stock assessments.

The majority of fishery-dependent data is collected by logbooks. Fishery size composition data are collected through a voluntary observer program established in 1997 and recent fishery performance data are collected as part of the tagging experiments.

One obvious deficiency with the fishery-independent monitoring programs is the general lack of spatial resolution. Resource monitoring programs have generally been limited to Necker Island and Maro Reef, which has received the majority of fishing effort in recent years.

Summaries of the research and resource monitoring programs as well as the availability of oceanographic data follow.

## Resource Monitoring and Research Programs

## Pre-Exploitation Data: NWHI Marine Resource Surveys

In 1975, a multiagency agreement was established to conduct a 5 -year study on the marine resources of the Northwestern Hawaiian Islands (NWHI) with field work beginning in 1976. Participants in this study were the NMFS (offshore resources), U.S. Fish and Wildlife Service (sea bird resources), Hawaii Division of Fish and Game
(nearshore resources), and the University of Hawaii Sea Grant College Program. The objective of the study was to survey and assess the resources for the purpose of protecting wildlife and managing potential fisheries resources. Several types of fishing operations targeting se veral different fishery resources were conducted on exploratory surveys aboard the NOAA ship Townsend Cromwell. Lobster trapping was one of these activities and was conducted on most of the survey cruises. The California two-chambered wire mesh trap which was the standard gear of the small fledgling industry at that time, was used. Commercial lobster fishing during this period consisted of a few small multipurpose vessels landing iced bottomfish and live lobster, with most of the fishing effort conducted at Necker Island. Standardized strings of eight traps spaced at 35 m were set at various locations around most of the NWHI banks. Spatial coverage was broad (archipelago wide), but effort at any one location was limited. Each bank was divided into $0.1^{\circ}$ latitude by $0.1^{\circ}$ longitude quadrats with sampling stations stratified by depth (innershelf $18-36 \mathrm{~m}$; outer-shelf $36-45 \mathrm{~m}$; shelf edge $45-90 \mathrm{~m}$; slope zone $90-360 \mathrm{~m}$ ). Data collected included sampling location, date, time, depth of fishing, species count (and often weight) by trap for all species caught, and lobster sex and size measurements.

## Post-Explo itation Data: Fishery-Dependent Programs

Commercial catch and effort monitoring--To provide fishery information for stock assessment and management purposes vessel captains have been required under Amendment 1 of the Crustaceans Fishery Management Plan (FMP) to submit a trip logbook with data on daily catch (in numbers), lobsters retained (landings), reproductive condition (berried), fishing effort (number of traps hauled), and area fished (bank), providing an 18-year time series (1983-2000). Fishery statistics during the early developmental phase of the fishery (1976-82), prior to the establishment of the Crustaceans FMP, are scant. Also, despite significant changes in trap configuration during the 1980s, information identifying the type of trap fished is not available.

Catch size composition sampling--Size composition data from the commercial catch has been routinely collected by biological technicians aboard commercial fishing vessels only since 1997. Approximately 50 lobsters are randomly selected from the catch of each trap string; for each sampled lobster, tail width, reproductive condition, and sampling location (latitude and longitude) are recorded. The biological technicians also reported on daily fishing, sorting, and discard methods. Prior to 1997, size composition data are scant and not representative of the commercial catch.

## Post-Exploitation Data: Fishery-Independ ent Programs

Honolulu Laboratory NWHI lobster resource survey--A fishery-independent trap survey was conducted annually from 1984 to 1988 and 1990 to 2000 using the NOAA ship Townsend Cromwell to (1) evaluate the performance of commercial and research survey gear, (2) calibrate gear types, and (3) monitor local populations of lobster in the NWHI. The survey has also been used as a platform for short-term experiments (e.g., studies of handling mortality), tagging, and the collection of biological and oceanographic data.

The survey uses a fixed-site design stratified by depth, and at each site shallow ( $<20$ fathoms) and deep ( $\geq 20$ fathoms) stations are sampled. Ten strings of eight traps each are set at the shallow station, and two to four strings of 20 traps each are set at the deep station. Traps are fished overnight and baited with 1.5-2.0 pounds of cut-up, previously frozen mackerel. Data on species, tail width, sex, and reproductive condition (berried or unberried) are collected for each lobster caught, as well as the latitude and
longitude of the traps recorded at the string level. Species counts of all bycatch at the trap level are also collected. The geographical extent of the trap survey has generally been limited to Necker Island and Maro Reef, with infrequent trips to adjacent banks.

Between 1984 and 1991, a variety of gears and gear configurations were used in the research survey. California two-chambered wire lobster traps were used from 1985 to 1991. Fathom Plus ${ }^{\circledR}$ black polyethylene plastic traps, without escape vents, were first used in 1984 and since 1992 have been used exclusively in the survey. While trap comparison studies were conducted to provide a conversion formula for California trap and black plastic trap CPUE, the studies were incomplete. Thus, in computing CPUE from research survey data we are limited to years in which black plastic traps were fished in significant numbers at both shallow and deep stations ( $\geq 50 \%$ of the total traps fished). For Maro Reef this corresponds to years 1987-2000 and for Necker Island years 19882000.

Up until 1997 the spatial distribution of sampling at Necker Island was not random with respect to the distribution of lobsters at Necker Island. Sampling was generally limited to habitat for juvenile spiny lobster, and areas not sampled contained higher proportions of larger spiny lobster.

Lobster tagging studies--With wide support from industry a NWHI lobster tagging program to provide independent estimates of population size and updated estimates of population dynamics and fishing parameters was developed and implemented by the Honolulu Laboratory in 1998. The tagging program was intended to be multiyear, initially focusing on spiny lobster at Necker Island and then expanding to include other banks and species, in particular slipper lobster. The commercial fishery would provide the platform for recaptures with additional recaptures coming from the annual Honolulu Laboratory NWHI lobster resource survey. The program was prematurely terminated after only 1 year. However, efforts are underway to continue spiny lobster tagging at Necker Island in 2002 and beyond, using chartered vessels.

To date, tagging cruises have been conducted at Necker Island during September 1998 and March and June 1999; the 1999 NWHI commercial lobster fishery provided the platform for recaptures. Approximately 6,000 spiny lobster were tagged and released at Necker Island, and about 320 tagged spiny lobster were recaptured during the 1999 commercial lobster fishery. Biological technicians examined all decked lobsters for tags and recorded the necessary information. Available data consist of tag and release date, time, and location (latitude and longitude); morphometric information at time of release (sex, size, etc.); tag number; recapture date, time, and location (latitude and longitude); and morphometric information at time of recapture (sex, size, etc.).

Subsequent recaptures during the annual NWHI lobster research survey (aboard the NOAA ship Townsend Cromwell) number approximately 50 in 1999, 30 in 2000, and 7 in 2001.

## Availability of Oceanographic Data

Because of the protracted larval phase of spiny lobster ( $\approx 1$ year) and slipper lobster (3-4 months) in the NWHI and its impact on recruitment processes, understanding and quantifying dispersal characteristics are paramount to the development of spatially structured population models. Coupled physical-biological models will also play an
important role in understanding the efficacy of using marine reserves as a tool for managing NWHI lobster populations.

The data sets required to derive mesoscale ocean currents from satellite are highprecision satellite altimetry and ocean surface vector winds. Availability of each of these data sets is shown in Table 4. The measure of sea surface height derived from the TOPEX/POSEIDON and JASON altimeters is used to derive geostrophic currents using basic equations of motion. For purposes of this study, these currents are assumed to represent a mean flow effective over a vertical range reaching from the seasonal thermocline to the ocean surface. The minimum temporal resolution of these data is limited by the 10-day repeat time of the exact repeat orbits: the spacing of these tracks and the need to interpolate across a sparse data set restricts the spatial resolution. The utility of using altimetry data from the TOPEX/Poseidon satellite to simulate transport dynamics of spiny lobster in the NWHI was recently documented by Polovina et al. (1999).

The ocean surface wind vectors are used to calculate "Ekman" currents using the methods of Lagerloaf et al. (1999). These currents describe the mean wind-induced ocean circulation for the upper water column (typically 40 to 50 meters deep). For purposes of developing a NWHI hydrographic model, ocean surface currents will be partitioned into two layers: the upper surface layer ( 0 to 50 meters depth) in which the currents are taken to be the sum of the Ekman and the geostrophic currents, and the lower surface layer ( 50 to 200 meters depth) in which the current is that due to geostrophic effects only.

The Central Pacific Regional CoastWatch Node, based at the Honolulu Laboratory, routinely produces these quantities for the entire Pacific Basin and will make them available to researchers on request under the Oceans Atlas project (funded by the NOAA Pelagic Fisheries Research Program). This project is to provide environmental data from a variety of platforms in forms useful and accessible to both nonexpert and expert users.

## Derived Properties

Using information provided by the Oceans Atlas project a NWHI hydrographic model can be developed and run for a variety of conditions and times to describe the rate of larval transfer between the various islands. The utility of this method lies in its independence from assumptions concerning initial larval abundance at the source. The actual transfer rates between areas are then found simply by multiplying the seeding density by the transfer coefficients. Figure 1 shows an example of this approach in which the NWHI have been divided into three distinct groups based on regions with similar oceanographic characteristics. The actual transfer coefficients will be calculated at 0.5 degree intervals; thus, transfer coefficients between any user-defined regions can be constructed without rerunning the circulation model.

## POPULATION MODEL DEVELOPMENT

The underlying conceptual model adopted by the workshop participants for lobster populations in the NWHI entails consideration of dispersal processes affecting recruitment during the larval stages at each location and losses due to fishing mortality and natural mortality (Fig. 2). The relative importance of recruitment derived from local sources, recruitment subsidies derived from other locations, and dispersal of larvae from
the natal location to other areas is critical in understanding the metapopulation structure of spiny and slipper lobsters in this region.

The workshop considered the development of lobster population models to account explicitly for these features. Development of a NWHI hydrographic model will provide the methodology to assess lobster recruitment dynamics and will be necessary to advance population model development. The models differed from the previous assessment models used for lobster resources in the NWHI in treating spiny and slipper lobsters separately and in accounting for spatial structure. In the following, we describe model structures that could be employed in assessments for lobster resources in this region based on available information derived from fishery-dependent sources, fishery independent research vessel surveys, and studies of regional physical oceanography. In the following, we describe several classes of models including a simple age-structured delay difference model, a size-structured population model, and an alternative age- or size-structured model using MULTIFAN-CL. The workshop participants anticipate that the delay-difference model will be undertaken first. Accordingly, the structure of this model is described in greater detail to provide a blueprint for action.

A key issue in the development of a spatial model for NWHI lobster populations is the choice of spatial resolution to be employed. It is recommended that models be developed that represent each of the known populations (at Nihoa Island, Necker Island, French Frigate Shoals, Brooks Bank, St. Rogatien Bank, Gardner Pinnacles, Maro Reef, Laysan Island, North Hampton Bank, Pioneer Bank, Lisianski Island, Pearl and Hermes Reef, Midway Atoll and Kure Atoll). However, initially a coarser level of spatial resolution must be employed because of data limitations.

## Age-Structured Delay Difference Model

The number of individuals of a particular species at location $i$ at time $t+l$ can be expressed as:

$$
\begin{equation*}
N_{i, t+1}=s_{i, t}\left(N_{i, t}-C_{i, t}\right)+R_{i, t+1} \tag{1}
\end{equation*}
$$

where $s_{i, t}$ is the probability of survival from all sources of mortality other than harvesting, $N_{i, t}$ is the number of individuals, $C_{i, t}$ is the catch in numbers, and $R_{i, t+l}$ is the number recruiting to location $i$ at time $t+1$. This specification implicitly assumes that natural mortality and fishing mortality do not occur concurrently. An alternative specification that removes this constraint and utilizes information on fishing effort rather than catch is:

$$
\begin{equation*}
N_{i, t+1}=N_{i, t} e^{-\left(M_{i, t}+q_{i, t} f_{i, t}\right)}+R_{i, t+1}, \tag{2}
\end{equation*}
$$

where $M_{i, t}$ is the instantaneous rate of natural mortality, $q_{i, t}$ is the catchability coefficient for a standardized unit of fishing effort, $f_{i, t}$ is standardized fishing effort, and all other terms are defined as before.

We next consider a model incorporating a stock-recruitment function and dispersal among locations:

$$
\begin{equation*}
N_{i, t+1}=S_{i, t}\left(N_{i \neq t}-C_{i, t}\right)+d_{i j, t}\left[f\left(S_{i, t+1-k}\right)\right]+\sum_{j=1}^{n} d_{i, j, t}\left[f\left(S_{j, t+1-k}\right)\right] \tag{3}
\end{equation*}
$$

where $S_{i, t+l-k}$ is the adult biomass, $d_{i, i, t}$ is the probability of retention of a prerecruit individual within the natal region, $f\left(S_{i, t+1-k}\right)$ is the relationship between the adult population biomass at time $t+1-k$ and subsequent recruitment $k$ years later, and $d_{i, j, t}$ is the probability of a prerecruit individual dispersing from location $j$ to location $i$. The alternative form utilizing fishing effort data is:

$$
\begin{equation*}
N_{i, t+1}=N_{i, t} e^{-\left(M M_{i, k}+q_{i, k} f_{i, 2}\right)}+d_{i z, t}\left[f\left(S_{i, t+1-k}\right)\right]+\sum_{j=1}^{n} d_{i, j, t}\left[f\left(S_{j, t+1-k}\right)\right], \tag{4}
\end{equation*}
$$

where all terms are defined as before.
The null recruitment model is taken to be density-independent

$$
\begin{equation*}
f\left(S_{i, t+1-k}\right)=R_{i, t+1}=\alpha_{i} S_{i, t+1-k} \tag{5}
\end{equation*}
$$

and the full model is then:

$$
\begin{equation*}
N_{i, t+1}=S_{i, t}\left(N_{i, t}-C_{i, t}\right)+d_{i j, t} \alpha_{i} S_{i, t+1-k}+\sum_{j=1}^{n} d_{i, j, t} \alpha_{j} S_{j, t+1-k} \tag{6}
\end{equation*}
$$

for the case where harvest and natural mortality are not concurrent. The alternative form utilizing fishing effort data is:

$$
\begin{equation*}
N_{i, t+1}=N_{i, t} e^{-\left(M_{l, i}+q_{l, k} f_{l, k}\right)}+d_{i ;, t} \alpha_{i} S_{i \neq+1-k}+\sum_{j=1}^{n} d_{i, j, t} \alpha_{j} S_{j, t+1-k} \tag{7}
\end{equation*}
$$

The workshop participants recommend that the null model be fit initially and diagnostic checks performed to examine the adequacy of the model. If evidence for compensatory processes during the prerecruit stage is obtained, alternative stockrecruitment models must be considered. Further, it will be necessary to consider whether the compensatory process occurs prior to or following settlement and the model structure adjusted accordingly.

One possible form for the stock-recruitment relationship incorporating compensatory processes during the prerecruit stage is a generalized Ricker model:

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$$
\begin{equation*}
f\left(S_{i, t+1-k}\right)=R_{i, t+1}=\alpha_{i} S_{i, t+1-k}^{\gamma} e^{-\beta S_{i, t+1-k}}, \tag{8}
\end{equation*}
$$

where $\alpha_{i}$ is the rate of recruitment at very low spawning stock size, $\gamma$ is a parameter controlling the shape of the stock recruitment curve (for $\gamma=1$ we obtain the Ricker model), and $\beta_{i} S_{i, t+l-k}$ is the instantaneous rate of compensatory mortality.

## Regime Shifts

Workshop participants further recognized that direct consideration of potential regime shifts will be necessary. It has been hypothesized that changes in wind fields affecting mixed layer depth and overall levels of productivity in the NWHI have affected lobster population levels through trophic pathways and through possible effects on transport processes. If the regime shift concept is accepted for lobster populations, it will be necessary to consider recruitment models that allow for low-frequency variation in recruitment, and the simple recruitment models described above will have to be augmented.

Persistent changes in recruitment levels that might occur under regime shifts hold important implications for management. Levels of fishing mortality that are sustainable under a higher productivity regime may not be under less productive conditions (Fig. 3).

## Species Interactions

The potential for interspecific interactions between spiny and slipper lobsters was considered at the workshop. Increases in slipper lobster populations in some locations where spiny lobster have been depleted by harvesting have led to the hypothesis that these species may compete for critical resources. An alternative hypothesis for these apparent inverse abundance trends is that environmental changes have differentially affected these species groups.

The workshop participants recommend that hypotheses concerning potential interactions between spiny and slipper lobsters be examined. If evidence supports the concept of competitive interactions, the development of a multispecies model should be considered.

## Parameter Estimation

The general strategy envisioned for estimating the parameters of the models above is based on a nonlinear regression approach using time series information on relative abundance derived from research vessel surveys, catch and effort data from the commercial fishery, and auxiliary information from biological studies and physical oceanographic studies of transport processes in the NWHI. For this phase, the time step for analysis will be annual to match the research vessel survey schedule.

Although total population numbers are not directly observed, relative abundance estimates are available from standardized research vessel surveys. The relationship between the survey abundance index for recruited lobsters and total population size of fully recruited lobsters is:

$$
\begin{equation*}
n_{i, t}=q^{\prime} N_{i, t} \tag{9}
\end{equation*}
$$

where $n_{i, t}$ is the survey abundance index, and $q^{\prime}$ the coefficient of proportionality between the survey index and total population size. Similarly, the relationship between the survey recruitment index and the recruitment level in the population is:

$$
\begin{equation*}
r_{i, t}=q_{r}^{\prime} R_{i, t^{\prime}} \tag{10}
\end{equation*}
$$

where $r_{i, t}$ is the survey recruitment index, and $q_{r}{ }^{\prime}$ the coefficient of proportionality between the survey index of recruitment and the actual recruitment.

It is anticipated that in the estimation phase it will be necessary to consider process error and measurement error models. The former will account for fundamental uncertainties in factors such as the nature of the dispersal processes, the nature of the stock recruitment relationship, and those affecting recruitment variability not explicitly considered in the model. The latter will account for the fact that the survey indices are measured with error.

It is further recommended that Bayesian methods be used in parameter estimation. Where possible, informative prior distributions should be constructed for model parameters utilizing (1) independent information derived from tagging (for demographic parameters and for fishery-related parameters), (2) demographic parameter estimates from other lobster populations, and (3) from physical oceanographic studies to quantify potential exchange rates and dispersal among locations.

Time series of abundance estimates from research vessel surveys are available for only Necker Island and Maro Reef. It will be necessary to explore the use of commercial CPUE data as an index of abundance for the other locations to be included in the model. Calibration studies between survey indices and CPUE at Necker and Maro should be undertaken to examine the implications of using CPUE data for the other areas.

## Size-Structured Model

While it is more complicated, there are several reasons for formulating an estimation model in terms of size. First, all available data are usually size-based (e.g., carapace length or tail width); therefore, estimation using size-structured models would allow direct expression of the error structure and make any shortcomings of the data explicit. Above we propose that the initial step in improving the stock assessment for NWHI lobsters be an improved age-structured approximation, but such a model will involve critical assumptions regarding size-related issues. The foremost is the fraction of a cohort that recruits into the fishery (i.e., becomes greater than the fishery size limit) at each age. This involves knowing, or assuming you know, the growth pattern.

A second reason for using a size-structured model is that it allows us to take advantage of available size data collected in pre-fishery cruises to obtain an estimate of natural mortality rate. Experience with size-structured approaches in other fisheries indicates that using data from an unfished population is the best way to estimate natural mortality rate from a single or a low number of size distributions, provided auxiliary
information on growth is available. Because mortality rate is confounded with growth rate in size distributions, estimation of vital rates from size distributions requires auxiliary information on growth (Barry and Tegner, 1990; Botsford et al., 1994; Smith et al., 1998, 1999). Some methods obtain this information from modes in the size structure, which occur most frequently at low sizes, but other methods obtain it from other measurements such as size increments (e.g., Smith et al., 1999).

Because current growth information (including auxiliary data) on NWHI lobsters is scant, implementing a size-structured model at this time is problematic and demonstrates the need for growth studies. Growth of crustaceans is typically described in terms of molt increments and molt durations as functions of size (Botsford, 1985). As a point of departure, the utility of using existing information or information on growth of other similar species (i.e., some sort of meta-analysis) to quantify growth patterns in NWHI lobsters should be assessed.

A sketch of the size-structured model, with some notes on potential problems that will have to be pursued, is the more appropriate course of action now. As more data become available and growth patterns determined, the utility of size-structured models can be explored further. In the model, size distribution for bank $i$ at time $t+l$ is a function of the size distribution at the previous time and the fishing mortality rate or catch:

$$
\begin{equation*}
N_{i}(s, t+1)=f\left(N_{i}(s, t), F_{t}, S_{l}, R_{i, t}\right), \tag{11}
\end{equation*}
$$

where $F_{t}$ is the fishing mortality rate at time $t, S_{l}$ is the lower size limit, and $R_{i, t}$ is the recruitment for bank $i$ at time $t$. The time step could be annual, and data from the annual NWHI lobster resource survey could be incorporated into the analysis using the criterion function from Schnute and Fournier (1980). Fishing can be handled either by removing the catch by size class each year or estimating $F$ and fitting it to the catch data and size distributions. One could start with the pristine size distributions and estimate $F$ for each bank where there was adequate annual data. The estimates of $R$ could then be combined to evaluate potential metapopulation relationships, paying attention to the differences in size variable (i.e., carapace length vs. tail width).

## Integrated Statistical Model (MULTIFAN-CL)

After reviewing the available data and supporting biological information, the workshop concluded that the application of MULTIFAN-CL or a similar type of model to at least spiny lobster should be explored further. At this stage, it is not feasible to develop a two-species model or a stand-alone model for slipper lobster because of the lack of tagging data, few size composition samples, and a general absence of supporting biological information.

It was agreed that a relatively simple MULTIFAN-CL application to spiny lobster should be developed as a feasibility exercise. Recommendations for the structure of such a model and the data that would be required to support it are given below. Full technical specifications of the model structure are available in Hampton and Fournier (2001).

## Model Structure

Computational time step--The fishery is strongly seasonal by regulation, and the fishing period has narrowed in recent years as quotas have been decreased. As most of the data are available by month (or finer resolution), a monthly time step to replicate these aspects of the fishery would be possible. Also, there may be information to be gained from within-season depletion of the population by the fishery. A monthly time step would allow depletion effects to be represented.

Spatial structure--Spiny lobster occur at a number of discrete banks in the NWHI, and movement between banks does not occur. However, dispersal of larvae and subsequent settlement among banks are likely to occur. The model would therefore need to have a bank-specific (or perhaps quasi-bank-specific) spatial structure. To keep the model tractable, it might be necessary to aggregate some neighboring banks in order to minimize the number of subpopulations being modeled. The following groups of banks might initially be defined to represent the spatial (or subpopulation) structure of the model:

1. Necker Island + Nihoa Island
2. French Frigate Shoals + Brooks Bank + St. Rogatien
3. Gardner Pinnacles
4. Maro Reef + Raita
5. All banks from Laysan to Kure inclusive

Movement of post-recruited animals between these subpopulations would be assumed to be zero.

Age structure--The current lobster assessment model is a delay-difference model with no age structure. However, it would seem desirable from an assessment and management view to disaggregate the population into at least two annual age classes (or stages): one that would consist of the youngest age class significantly represented in the exploitable population (the recruitment), and a plus group consisting of all older animals. Extensions to three or four age classes could also be tried and improvement in model performance (fit) evaluated. In all cases, the final age group would represent a plus group.

Recruitment--Since reproduction in spiny lobster is strongly seasonal, it is likely that settlement of larvae and the subsequent recruitment to the exploitable subpopulations are also seasonal. As an initial hypothesis, recruitment could be assumed to occur to each subpopulation as a discrete annual event in a particular month. The month chosen could be the midpoint of the spawning season or the month in which the smallest individuals tend to appear in size composition samples.

Recruitment would be modeled for each subpopulation as an average recruitment with annual anomalies. The "average" recruitment could be ultimately related to prior adult biomass (with an appropriate lag) in each subpopulation according to a larval dispersal model based on mesoscale oceanic circulation. For this feasibility exercise, the recruitment parameters will be estimated free of the larval dispersal considerations to see if there is any evidence in the fishery and survey data of such a link.

Sex structure and growth--It is apparent in the size composition samples taken during research surveys that male and female spiny lobster display quite different growth patterns, with males dominating the larger size classes. For this reason, it would be desirable (if not essential) to have a sex-structured model with a separate growth
parameterization for each sex. The feasibility of deriving catch estimates by sex will be investigated and if feasible, sex structure will be included in the initial model.

Initial examination of the size composition data showed little growth information. If this is the case, growth parameters may need to be fixed or heavily constrained until alternative data (e.g., length-increment data from tagged lobsters) are available for incorporation into the model.

Natural mortality--A single value of $M$ (i.e., no age or subpopulation dependency) would be estimated. It may be possible (and necessary) to construct an informative prior for $M$ based on information for this or similar species elsewhere.

Fisheries, fishing effort, selectivity and catchability--Initially, at least five commercial fisheries (one in each spatial stratum) would be defined. Additionally, a research survey "fishery" at Necker Island and Maro Reef would be defined to incorporate the catch, effort, and size data from the lobster resource surveys into the model. Because the surveys have been carried out in the same way and according to the same design, it is reasonable to assume that the survey CPUE would provide a better index of lobster abundance than the commercial data. The way in which this assumption can be incorporated into a MULTIFAN-CL model is to assume that the variability of the effort deviations for the surveys is lower than for the commercial fisheries. Also, it might be reasonable to assume that catchability is constant over time for the surveys, but possibly variable (e.g., due to targeting changes) for the commercial fisheries.

Potentially, each fishery could have independent selectivity and catchability parameters: the survey fishery would certainly have independent parameters. However, it may be reasonable to assume that selectivity and possibly catchability are common among the commercial fisheries. This would simplify the parameterization considerably. There have been some gear changes (trap design) in both the resource surveys and the commercial fishery. The initial results of the analysis will provide an indication (by examining the fit of the size composition data over time) of whether such gear changes have significantly changed selectivity and catchability. If so, it may be necessary to define separate fisheries to correspond with the different trap designs.

## Data

The model outlined above would be fit simultaneously to several data sets - the total catch data, size composition data, and tagging data. Each component would therefore have a contribution to the overall likelihood function.

Total catch data--The total catch of spiny lobster would be stratified by fishery and month. If including sex structure proved to be feasible, then catches would also need to be disaggregated by sex. The form of the likelihood function would be the sum of the squared differences in the logs of observed and predicted catches. The variance term in the likelihood function for total catches would be set to a relatively small value, such that the standard deviation of the residuals was equal to about 0.05 . This reflects an assumption that the total catches are observed without bias and with high precision.

Size composition data--Size composition data are available in two forms for some times and banks. The pre-exploitation surveys collected carapace length measurements. After 1981, the surveys collected tail width as the measure of size. There are also tail width measurements for a limited period (1997-99) for the commercial fishery.

A MULTIFAN-CL type model can use size composition data wherever they are available. For convenience, it would be desirable to transform the early carapace length measurements to tail width estimates so that a common size measure is available for the whole time series. All size composition data (survey and commercial) can be stratified by sex.

The form of the likelihood function for the size composition data approximates a robustified, self-scaling minimum chi-squared statistic. The variance depends on sample size and observed frequencies in the data. Normally we reduce the sample size by an arbitrary factor (10) to acknowledge nonrandom sampling. Consideration might be given to reducing this factor (possibly to 1) for the lobster analysis. Given the high coverage of commercial vessel sampling when it took place and the systematic sampling practices used during the resource surveys, it is likely that the assumption of sample randomness would in fact be satisfied.

Tagging data--Approximately 6,000 spiny lobster were tagged and released in three separate tag release events in 1998 and 1999 at Necker Island. Some 320 tags were recovered by the 1999 commercial fishery and 50, 30, and 7 tags by the 1999, 2000, and 2001 resource surveys, respectively. Tags were recovered by biological technicians on commercial vessels and by scientific staff on resource surveys; therefore, it is expected that tag-reporting rates were high and can probably be assumed to be $100 \%$. Tagged lobsters were released throughout Necker Island; therefore, it may be reasonable to assume that they were well mixed with the untagged lobsters in this subpopulation. All tag releases were accompanied by information on sex; therefore, a male/female stratification of the data would be possible.

MULTIFAN-CL has several options for the likelihood function for tagging data, including the Poisson and negative binomial. The negative binomial offers the advantage of allowing overdispersion relative to the Poisson, where the variance of the per-stratum tag returns is completely determined by the expected value. The negative binomial allows the variance to be independently estimated so that apparent overdispersion can be accommodated. If overdispersion is not detected, the negative binomial approaches the Poisson at its limit.

## Feasibility Analysis

The conduct of a feasibility analysis would require the following:

1. Estimate effort and total catches of spiny lobster by month for each of the five subpopulations defined above. For Necker Island and Maro Reef, available resource survey data should be compiled in the same way. The data should be stratified by sex if possible.
2. Compile size composition data for each fishery by month and sex. Early carapace length measurements will need to be converted to tail-width measurements.
3. Compile catch effort and size composition data into MULTIFAN-CL file formats.
4. Set up MULTIFAN-CL to accommodate a sex-specific analysis if required.
5. Set up initial model runs and evaluate results.

## INDEPENDENT RESEARCH TO SUPPORT MODEL DEVELOPMENT

Several analyses that are needed would be best done outside the framework of the estimation model. These analyses are required to better understand the dynamics of several critical processes and will provide guidance as to how to structure further modifications of the estimation process.

## Biology and Ecology

Studies to better understand NWHI lobster growth are required. Apart from discerning growth pattern versus age, this information could also be used to estimate natural mortality rate from data on pristine size distributions. In addition, growth information will also be needed to develop recruitment time series and simple agestructured models we might propose. Initial attempts to develop lobster growth models should use existing data, but it is likely that model advancement will require the collection of additional tagging and other types of data.

Comprehensive habitat mapping at all banks in the NWHI (including commercial fishing depths) should be initiated. Possible platforms for the collection of these data are the existing Honolulu Laboratory Coral Reef Research initiative or as a new initiative within the Ecosystem and Habitat Task. Current habitat data lack the necessary spatial resolution to develop archipelago-wide maps to assess habitat requirements for NWHI lobster populations. Knowledge of habitat requirements will assist in interpreting CPUE time series, as well as facilitating the design of marine reserves and assessing their effectiveness.

Experiments to assess the extent of competitive interactions between spiny and slipper lobsters should be undertaken. Increases in slipper lobster populations in some locations where spiny lobster have been depleted by harvesting suggest that these species may compete for critical resources. However, it could just as easily result from environmental changes differentially affecting these species groups. If evidence supports the concept of competitive interactions, the development of a multispecies model should be considered.

## Population Dynamics

NWHI lobster tagging experiments need to continue not only as a vehicle for verifying (ground-truthing) model output but also as a way of providing initial estimates for key model input parameters. If NMFS is serious about advancing model development and understanding NWHI lobster populations, there is a need to view this research as long term ( $5+$ years) and provide sufficient resources (funding and manpower). Current tagging experiments were limited to spiny lobster at Necker Island, and while this may provide valuable information for this bank, information from other banks is nonexistent. The development of spatially explicit population models for NWHI lobster resources will require data from more of the banks, as well as other lobster species (e.g., slipper lobster).

A coupled physical-biological model that captures the metapopulation dynamics of NWHI lobster populations is needed. As a point of departure, this research should be conducted concurrently with the ongoing Oceans Atlas project, and limitations of the dispersal matrices should be explored. The coupled physical-biological model could be used to assess the range of dispersal matrices that would lead to the current metapopulation state; i.e., some banks at low abundance and not recovering in spite of the absence of fishing for at least 10 years.

## Economics

An economic study to determine how fishermen behavior influences the relative amount of each species caught should be initiated. The null hypothesis would be that there is no special behavior and that relative catch is proportional to relative abundance. The study should also examine other aspects of fishermen behavior, such as how anticipated abundance and price influence the bank that is fished. This kind of information will be needed to anticipate the responses of fishermen to proposed marine reserves.

## Management

Studies should be initiated to assess the effectiveness of marine reserves in the NWHI as a potential management tool. Using the coupled physical-biological model described above, this research would identify not only the number of reserves needed but also their placement.

## Monitoring

Monitoring is an important component of any research agenda. While annual monitoring of NWHI lobster resources using research vessels was implemented in 1983, the current survey lacks sufficient spatial resolution to promote the development of spatially structured population models. NMFS needs to implement a monitoring program that provides greater spatial resolution to facilitate model development.

## FOSTERING RESEARCH

While a suite of research topics has been suggested by workshop participants, there are a variety of ways to proceed: some, of course, more efficient and cheaper than others. The Honolulu Laboratory should take advantage of their proximity to the various colleges and universities in Hawaii and develop a partnering program with these institutions. For example, NMFS could enter into agreements with local professors to support their graduate students in exchange for students working on one (or more) of the research topics outlined above. If partnering cannot be established at the local level, NMFS should extend this arrangement to other colleges and universities. Regardless of the institution, this arrangement is a win-win scenario for all parties concerned.

Another area for NMFS to explore is cooperative research with industry. While the Honolulu Laboratory has made significant strides in lobster research (e.g., tagging and fishery-dependent monitoring), it needs to be determined if additional types of research would be best served by using industry. An obvious extension to the existing cooperative

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arrangements would be to use the commercial lobster fleet to conduct the annual NWHI lobster resource survey. This would provide for greater spatial coverage and fishing effort than using research vessels alone.

Workshop participants expressed interest in assisting the Honolulu Laboratory in the completion of this research. It was suggested that a technical working group comprised of key workshop participants be formed and regular meetings convened to review progress.

## FUNDING

The Honolulu Laboratory is responsible for conducting research on NWHI lobster populations in support of fishery management decisions. As NWHI lobster research needs have grown over the last 5 years the associated budget has decreased, and currently little funding if any is provided for lobster research. As much of the research outlined above is long term, any commitment on the part of NMFS to proceed must be matched with sufficient funding. If NMFS is not in a position to make such a commitment, the agency should explore the possibility of buying back the permits. Funds to carry out the research outlined above as well as additional research proposed in the recent NWHI lobster research and monitoring plan were outside the scope of this workshop and were not discussed. However, the workshop recommended that the Honolulu Laboratory develop a comprehensive research budget for submission to the appropriate decision makers. When developing the budget the Honolulu Laboratory should explore external funding sources to complete portions of the research, such as Sea Grant, the National Ocean Service, and the National Science Foundation, particularly when the research is conducted collaboratively with educational institutions.

## APPENDIX A

# Workshop on the Development of Spatially Structured Population Models for Northwestern Hawaiian Islands Lobster Resources 

## 4-7 December 2001

Honolulu Laboratory
2570 Dole Street
Room 112
Honolulu, Hawaii 96822
Telephone: (808) 983-5300

Tuesday, December 4, 2001, 9:00 a.m.-4:30 p.m.

| 1.Opening <br> Goals of the Workshop <br> Expected Deliverables <br> Review of Agenda <br> Appointment of Rapporteurs | G. DiNardo |  |
| :--- | :--- | :--- |
| 2. | Pre-exploitation Data: NWHI Marine Resource Surveys | G. DiNardo |
| 3. | Post-Exploitation Data <br> - Review of NWHI Commercial Lobster Fishery <br> - Fishery Dependent Programs | G. DiNardo |

Break 10:30-10:45 a.m.

- Fishery-Independent Programs

4. Current NWHI Lobster Assessment Methodologies G. DiNardo

Lunch break 12:15-1:30 p.m.
5. Population Model Shortcomings G. DiNardo

Break 3:00-3:15 p.m.
6. Recent Events Impacting NWHI Lobster Fishery
G. DiNardo

Wednesday, December 5, 2001, 9:00 a.m.-4:30 p.m.
7. Analytical Tools and Approach Methodologies

- Overview of MULTIFAN - CL
J. Hampton
- Spatial Design of Marine Reserves for Sustainability and Yield
L. Botsford

> Break 10:30-10:45 a.m.

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8. Sources of Data

- NWHI Oceanography and Available Data
D. Foley

Lunch Break 12:15-1:30 p.m.

- Lobster Sources of Data and Information Matrices

Break 3:00-3:15 p.m.
Thursday, December 6, 2001: 9:00 a.m. - 4:30 p.m.
9. Model Development and Data Collection Discussions
M. Fogarty

Friday, December 7, 2001: 9:00 a.m.-4:30 p.m.
10. Generation of Report

Workshop Participants

## APPENDIX B

## List of Participants

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Table 1. Temporal extent of NWHI lobster monitoring programs and quality of data collected.

| Data and source |  | Year |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 |
| Fisherydependent | Catch \& effort | - | - | $\bigcirc$ | - | $\bigcirc$ | - | - | - | - | - |  | - | - | - | - | $\bigcirc$ | - |  |
|  | Discards | D | - | - | D | D | - | - | D | D | D |  | - | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  |
|  | Fishing loc. | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | - | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  |
|  | Fishery size comp |  |  | $\bigcirc$ |  |  |  |  |  |  |  |  |  | - |  | - | - | - |  |
|  | Gear type |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Fishery perform. |  |  |  |  |  |  |  |  |  |  |  |  |  |  | D | D | D |  |
| Fisheryindependent | Catch \& effort |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | - | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | - | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
|  | Bycatch |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
|  | Fishing loc. |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
|  | Pop. size struct. |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
|  | Size at maturity |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
|  | Habitat map. |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
|  | Gear type |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |

Table 2. Spatial resolution of NWHI lobster monitoring programs and quality of data collected.

| Data and source |  | Bank |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Nihoa | Necker I. | FFS | Brooks | St. Rog. | Gardner | Raita | Maro | Laysan | Pioneer | Lisian. | P \& H | Midway | Kure |
| Fisherydependent | Catch \& effort | $\bigcirc$ | $\bigcirc$ | - | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | - | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | - | $\bigcirc$ |
|  | Discards | D | - | - | D | D | D | - | D | D | D | D | - | D | - |
|  | Fishing location | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
|  | Fishery size composition | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ |
|  | Gear <br> type |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | Fishery performance |  | D |  |  |  |  |  | D |  |  |  |  |  |  |
| Fisheryindependent | Catch \& effort |  | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ |  |  | $\bigcirc$ | $\bigcirc$ |  |  |  |  |  |
|  | Bycatch |  | $\bigcirc$ |  |  |  |  |  | $\bigcirc$ |  |  |  |  |  |  |
|  | Fishing location |  | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ |  |  | $\bigcirc$ | $\bigcirc$ |  |  |  |  |  |
|  | Population size structure |  | $\bigcirc$ |  |  |  |  |  | $\bigcirc$ | $\bigcirc$ |  |  |  |  |  |
|  | Size at maturity |  | D |  |  |  |  |  | - |  |  |  |  |  |  |
|  | Habitat mapping |  | D |  |  |  |  |  | - |  |  |  |  |  |  |
|  | Gear type |  | $\bigcirc$ | $\bigcirc$ |  | $\bigcirc$ |  |  | $\bigcirc$ | $\bigcirc$ |  |  |  |  |  |

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Table 3. Biological and ecological traits for spiny and slipper lobsters.

|  | Species |  |
| :--- | :---: | :---: |
| Biological/Ecological trait | Spiny lobster | Slipper lobster |
| Larval phase | $11-\mathbf{1 2 ~ M o n t h s}^{\prime}$ | $3-4$ Months |
| Spawning period | March - Dec. (May - July; D ec.) | March - Sept. (April - June) |
| Fecundity/Spawning frequency | Statistical relationship | Statistical relationship |
| Molt frequency | $?$ | $?$ |
| Size-at-age (Growth) | Von B. parameters available | $?$ |
| Natural mortality | $0.456^{\text {-yr }}$ | $?$ |
| Size at maturity | Yes | $?$ |
| Recruitment indices | Maybe | Yes |
| Habitat requirements | $?$ | $?$ |
| Source/Sinkinformation | Some | $?$ |
| Transfer rates | $?$ | $?$ |

Table 4. Details and availability of satellite data required to derive ocean surface currents.

| Model <br> input | Basic <br> measurement | Data <br> source | Spatial <br> resolution | Temporal <br> resolution | Temporal <br> availability | Spatial <br> availability |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Ekman <br> currents | Wind vectors | ERS-1 <br> ERS-2 | 1degree | 1 week | Aug. 1991- | Global |
| Ekman <br> currents | Wind vectors | Quikscat | 25 km | $1-5$ days | July 1999 - <br> present | Global |
| Geostrophic <br> currents <br> Geostrophic <br> currents | Sea surface <br> height | TOPEX | 1 degree | 10-days | Sep 1992- <br> Sea surface <br> height | JASON |

Figure 1. Transfer coefficients, $\mathrm{c}_{\mathrm{ij}}$, between three regions selected based on similarity of observed ocean dynamics.


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Figure 2. Factors affecting population size of lobsters within locations accounting for dispersal processes affecting recruitment and sources of mortality.


Figure 3. Stock recruitment relationships under two recruitment productivity regimes. The straight lines represent the effects of fishing on spawning stock biomass per recruit. The intersection of these lines with the stock-recruitment relationships represent stable equilibrium points. Under low recruitment productivity and high fishing mortality (F), a stable equilibrium point does not exist and a stock collapse is predicted.


