

Move it or lose it: movement and mortality of sablefish tagged in Alaska

Dana H. Hanselman, Jonathan Heifetz, Katy B. Echave, and Sherri C. Dressel

Abstract: A basic step in understanding the dynamics of a fish population is to quantify movement and mortality rates. Conventional mark–recapture experiments have provided the foundation for studies on animal movement, particularly for fish. Previous studies have shown rapid mixing of sablefish (*Anoplopoma fimbria*) among fishery regulatory areas, with the pattern of movement related to fish size. Over 300 000 tag releases in Alaska and over 27 000 tag recoveries from 1979 to 2009 were analyzed. We used a Markov model to quantify annual movement probabilities among areas for three size groups of sablefish. The negative-binomial likelihood was used to model the tag-recovery data because of significant overdispersion. Annual movement probabilities were high, ranging from 10% to 88% depending on area of occupancy at each time step and size group. Overall, movement probabilities were very different between areas of occupancy and moderately different between size groups. Estimated annual movement of small sablefish from the central Gulf of Alaska had the reverse pattern of a previous study, with 29% moving westward and 39% moving eastward. Movement probabilities also varied annually, with decreasing movement until the late 1990s and increasing movement until 2009. Year-specific magnitude in movement probability of large fish was highly negatively correlated with female spawning biomass estimates from the federal stock assessment. Mean mortality estimates from time at liberty were similar to the federal stock assessment. Incorporating these tag-recovery and movement data into a fully age-structured spatial stock assessment model will inform harvest apportionment strategies to conserve spawning biomass and maximize future yields.

Résumé: Une étape fondamentale pour comprendre la dynamique d'une population de poissons consiste à quantifier les taux de déplacement et de mortalité. Les expériences classiques de marquage–recapture ont fourni les fondements pour des études sur les déplacements des animaux, particulièrement les poissons. Des études antérieures ont révélé un mélange rapide des morues charbonnières (*Anoplopoma fimbria*) entre différentes zones de réglementation de la pêche, les motifs des déplacements étant reliés à la taille des poissons. Plus de 300 000 poissons étiquetés mis à l'eau en Alaska et plus de 27 000 étiquettes récupérées de 1979 à 2009 ont été analysés. Nous avons utilisé un modèle de Markov pour quantifier les probabilités de déplacement annuel entre régions pour les morues charbonnières de trois groupes de tailles. En raison de leur dispersion significative, la loi de probabilité binomiale négative a été utilisée pour modéliser les données sur les étiquettes récupérées. Les probabilités de déplacement annuel étaient élevées, allant de 10 % à 88 % selon la région occupée à chaque pas de temps et le groupe de tailles. Globalement, les probabilités de déplacement variaient beaucoup d'une région occupée à l'autre et modérément entre les groupes de tailles. Les déplacements annuels estimés des petites morues charbonnières du centre du golfe d'Alaska présentaient un motif contraire à celui d'une étude précédente, 29 % des individus se déplaçant vers l'ouest et 39 %, vers l'est. Les probabilités de déplacement variaient aussi annuellement, les déplacements diminuant jusque vers la fin des années 1990 pour ensuite augmenter jusqu'en 2009. La magnitude de la probabilité de déplacement des grands poissons pour une année donnée présentait une forte corrélation négative avec les estimations de la biomasse de femelles reproductrices tirées de l'évaluation fédérale des stocks. Les estimations de la mortalité moyenne à partir du moment de la mise en liberté étaient semblables à celles de l'évaluation fédérale des stocks. L'intégration de ces données sur les étiquettes récupérées et les déplacements à un modèle spatial d'évaluation entièrement structuré par âge éclairera l'élaboration de stratégies de répartition des prises afin de conserver la biomasse reproductrice et de maximiser les rendements futurs. [Traduit par la Rédaction]

Introduction

Migration and movement are fundamental life-history aspects of many animal populations. A basic step in understanding the dynamics of a fish population is to quantify movement rates. Understanding these spatial dynamics greatly aids fisheries management to successfully impose catch quotas or marine closures at the correct spatial scales to prevent localized depletion, loss of productivity, or genetic erosion (Deriso et al. 1991; Palof et al. 2011). Conventional mark–recapture experiments, such as single

tag-recapture, have provided the foundation for studies on animal movement, particularly for fish, since the 19th century (Atkins 1885; Beverton and Holt 1957). Newer technologies such as satellite and archival tags have recently provided higher resolution movement data on small samples of individual animals (Nathan et al. 2008; Schick et al. 2008). However, conventional tags are still quite relevant because they are inexpensive to deploy on many animals. Since these tags have been available for many years, a long time series of release and recaptures are possible.

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One example of a particularly long tagging experiment is the conventional tagging conducted for Alaska sablefish (*Anoplopoma fimbria*) that has occurred in US federal waters, Alaska inside waters (protected waters of the Alexander Archipelago in southeast Alaska managed by the state of Alaska), and British Columbia (BC), Canada. Sablefish are a highly mobile, long-lived, demersal fish of the continental slope of the North Pacific. One of the deepest-dwelling commercially valuable species in the northeastern Pacific, sablefish have been the target of domestic and foreign fisheries since the beginning of the last century (Sasaki 1985; McDevitt 1986; Hanselman et al. 2011). The majority of sablefish biomass and catch occurs in Alaska federal waters (Hanselman et al. 2011). Since 1995, the federally managed Alaskan fishery has been prosecuted under an individual fishing quota system (IFQ) (Sigler and Lunsford 2001). Most of the catch from BC and state waters are also managed using transferable quotas or have limited entry since 1990 and 1995, respectively. These quota systems are important in the context of fish movement because these quotas are assigned to specific regional management areas. The 2010 catch of 11 900 t (Hanselman et al. 2011) from federal waters off Alaska had an ex-vessel value of over US\$100 million (Hiatt et al. 2011), making sablefish one of the most valuable and sought-after species in the region.

Conventional tag-recapture data for sablefish have been examined in a variety of contexts that have produced much of the current knowledge regarding sablefish ecology and subsequent management. Bracken (1982) conducted an analysis of a small sample size of tag releases and recoveries from southeast Alaska and suggested that sablefish undergo a counterclockwise ontogenetic migration. He proposed that the majority of the spawning occurs in the eastern Gulf of Alaska and their progeny then move west toward the Aleutian Islands and Bering Sea, but return east later in life to spawn. Beamish and McFarlane (1988) examined recoveries from over 70 000 tags released in BC and concluded that juvenile sablefish may move north, but for adult sablefish there was no relationship between length and movement pattern. Saunders et al. (1990) examined factors affecting recapture probabilities in BC by using double-tagging and oxytetracycline and estimated tag-shedding rates. Kimura et al. (1998) used tagging data to show that sablefish were divided into northern and southern stocks that divide off the coast of BC, Canada. Maloney's (2004) study tagged sablefish on seamounts far off the continental slope in the Gulf of Alaska and confirmed movement from seamounts to the continental slope, although it is not known whether movement is pelagic or along the deep sea floor. Maloney and Sigler (2008) used juvenile tagged sablefish to estimate the shape of the fishery selectivity curve and concluded it was more likely dome-shaped than asymptotic, which would mean that older fish are less vulnerable to fishing mortality. Analysis of Japanese sablefish tag returns showed that there was a relationship between mean growth increments and distance moved (Morita et al. 2012). They suggested that the further distances moved by females is a proximate cause for the larger lengths reached by females.

Previous studies have shown rapid mixing of sablefish across broad geographic areas (Heifetz and Fujioka 1991; Maloney and Sigler 2008; Morita et al. 2012). The sablefish movement rates estimated in Heifetz and Fujioka (1991) were used to evaluate management strategies for geographic apportionment of federal sablefish harvest and examine theoretical properties of migratory fish populations (Heifetz et al. 1997; Heifetz and Quinn 1998). Heifetz and Quinn (1998) concluded that sablefish spawning biomass would be resilient to different area catch apportionments as long as fishing mortality remained conservative (e.g., fishing mortality was less than natural mortality: $F < M$).

Although sablefish north of Vancouver Island, BC, have been suggested to be one population (Kimura et al. 1998), currently US federal areas (Gulf of Alaska, Aleutian Islands, and Bering Sea) are managed together as a single stock, and state-managed Chatham

Strait (CH), state-managed Clarence Strait (CL), and BC are each assessed and managed as separate stocks. The US federal assessment is a statistical catch-at-age model that uses area-weighted abundance and compositional data to determine one overall catch quota. Outside of the stock assessment model, the harvest strategy apportionments this catch quota as an exponentially smoothed 5-year mean of survey abundance and fishery catch rates by area (Hanselman et al. 2011). The state of Alaska also conducts stock assessments for areas in southeast Alaska (CH and CL) that assume closed populations, but acknowledge that some mixing with federal water occurs. The fishery in BC is also prosecuted as a separate population.

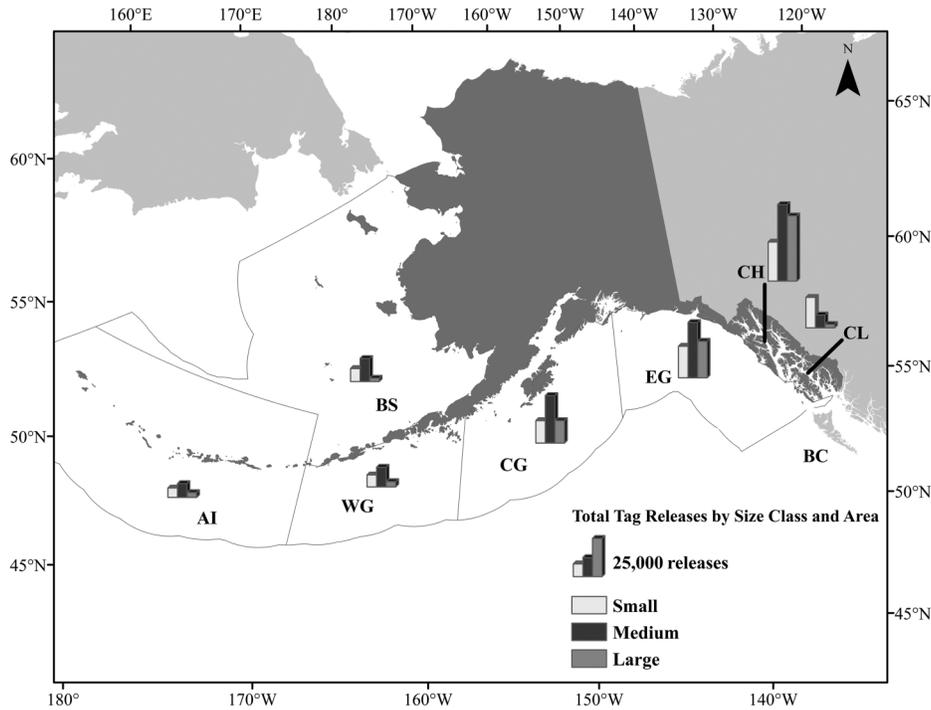
This study investigates movement of sablefish throughout these waters as a first step towards understanding how separate these areas are in terms of sablefish movement and to provide information for assessment authors with which to make appropriate assumptions in assessments regarding closure and mixing. We examine movement throughout these areas by building on previous studies that have used a Markovian model to estimate movement probabilities using conventional tag data (Ishii 1979; Hilborn 1990; Deriso et al. 1991). We quantify annual movement probabilities of sablefish among fishery regulatory areas by using the general method of Hilborn (1990) as specified in Heifetz and Fujioka (1991), hereinafter referred to as HF. We improve HF's study by incorporating an additional 22 years of tagging data, adding tag releases and recoveries from state-managed southeast Alaska inside waters, applying time-varying reporting rates, changing the likelihood formulation, and examining parameter uncertainty in more detail. We also extend the analysis of HF to include time-varying movement. In addition, we compute estimates of total mortality from time at liberty of the tagged fish and compare with federal stock assessment results. Our findings are discussed within the context of ecological hypotheses for the observed movement patterns and stock assessment.

Materials and methods

Various agencies and countries have tagged sablefish throughout the North Pacific (e.g., Kimura et al. 1998). For our study, we use the releases and recoveries of tagged sablefish from the Japanese-US cooperative and the US National Marine Fisheries Service (NMFS) longline surveys (Sigler 2000) conducted along the continental slope throughout US federal waters. We also include releases and recoveries of sablefish tagged during the Alaska Department of Fish and Game (ADF&G) surveys in inside waters of southeast Alaska (Fig. 1). We used tag releases and recoveries during 1979–2009.

As of 2009, 304 668 sablefish of exploitable size (more than 40 cm fork length) were tagged and released using the methods of Sasaki (1985). Fish were tagged with a target tagging rate of 5% for the federal longline surveys and approximately 3.5% in the ADF&G surveys. Floy anchor tags were inserted at the distal end of the dorsal fin so that the tag anchor was locked into the musculature of the fin insertion. The same methods and anchor tags have been used by Japan, USA, and the state of Alaska since 1979. Further details of the tag release methods for NMFS and ADF&G can be found in Echave et al. (2013) and Carlile et al. (2002), respectively. The number of tag releases was multiplied by 0.90 to account for immediate shedding of tags (Saunders et al. 1990). As of 2009, 27 146 tagged fish were recaptured and reported with the tag number and recovery location (longitude and latitude). Recoveries have been from the five North Pacific Fishery Management Council (NPFMC) regulatory areas, inside waters of southeast Alaska (CH and CL), and BC. The majority of tags were recovered by commercial fishing or processing operations, with a small percentage (less than 1% of the total recoveries) from research cruises. A very limited amount of Alaska sablefish are recovered on the west coast of the United States (<1%), indicating a small

Fig. 1. Sablefish tag releases by size class and area. AI = Aleutian Islands, BS = Bering Sea, WG = western Gulf of Alaska, CG = central Gulf of Alaska, EG = eastern Gulf of Alaska, CH = Chatham Strait, CL = Clarence Strait; small = <57 cm, medium = 57–66 cm, large = >66 cm. The largest bar in the legend is equal to 25 000 releases.



amount of movement from Alaska. However, we do not have the tag releases and recovery data for fish tagged on the west coast of the US. Therefore, as a simplifying assumption, we do not include areas south of BC in this analysis.

Model description and application

The movement model has three major components: (i) a population dynamics and movement model, (ii) a recovery model, and (iii) a likelihood specification. For this analysis, we used AD Model Builder (ADMB) software (Fournier et al. 2012). Following HF, we fitted separate models and compared results between different length groups of released fish: small (less than 57 cm), medium (57–66 cm), and large (more than 66 cm) sablefish. Immature fish predominate in the small length group, mature fish predominate in the large length group, and a mixture constitutes the medium length group (Fig. 2). In general, these size ranges correspond to ages 2–4 (small), 5–7 (medium), and 8 and older (large), although males grow more slowly than females; for example, a 5-year-old female may have reached “medium” size, while a 5-year-old male might still be of “small” size.

Population dynamics and movement model

This model component describes the mortality and movement of tagged fish from a release group over time. A release group is defined as fish released into area *i* in year *t*. We assume that survival is independent of movement and determined by instantaneous annual rates of natural mortality *M* and fishing mortality $\lambda f_{i,t}$. Tag loss, *H*, is assumed to occur at a known instantaneous rate. The values for *M*, *H*, and *f* are constants, where *f* is the set of the $\{f_{i,t}\}$, $\lambda \rho$ is a calibration parameter to account for selectivity and any biases in inputted values for *f* and is estimated separately for each length group. We let $S_{m,t}$ be a diagonal matrix of survival rates in each area during month *m* of year *t*, where the *i*th element of $S_{m,t}$ is described by

$$(1) \quad S_{i,m,t} = \rho \exp \left[\frac{-(\lambda f_{i,t} + \rho M + \rho H)}{12} \right]$$

Sablefish were tagged from May to September on the federal longline survey and state of Alaska longline or pot surveys. On average, these fish were vulnerable to fishing and natural mortality for half a year during the year of release. Equation 1 in the first year of release is modified to account for the proportion of fishing mortality $U_{i,t}$ that occurred after fish were released and a half a year of natural mortality *M*/2 and tag loss *H*/2. The monthly survival rate of tagged fish during this 6-month period $S_{i,m,t}$ is described by

$$(2) \quad S_{i,m,t} = \rho \exp \left[\frac{-(U_{i,t} \lambda f_{i,t} + \rho M/2 + \rho H/2)}{6} \right]$$

We let Θ be a matrix of annual probabilities of movement where the *i,k*th element of Θ , $\theta_{i,k}$, is the annual probability of movement from area *i* to area *k*. We reparameterize Θ in terms of monthly probabilities of movement Φ , such that Φ^{12} equals Θ . Movement is assumed to occur instantaneously at the end of a month. The row vector of abundance of release group *g* in each area at the beginning of a year $N_{g,t+1}$ is then the function of prior abundance $N_{g,t}$, survival $S_{m,t}$, and movement Φ :

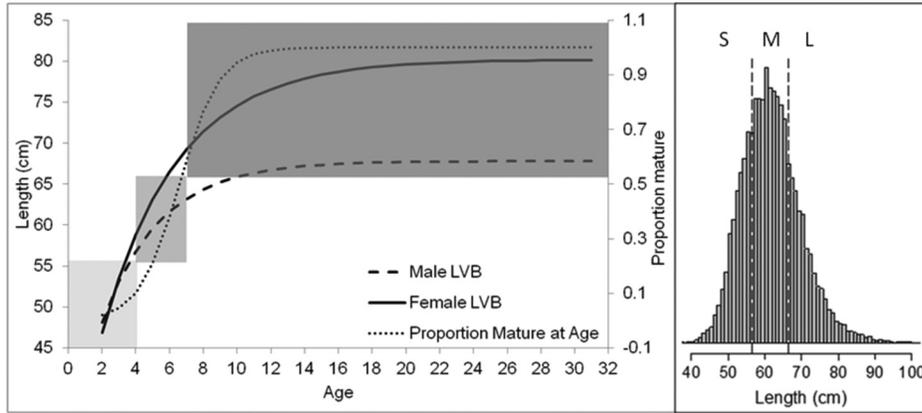
$$(3) \quad N_{g,t+1} = \rho N_{g,t} (S_{m,t} \Phi)^{12}$$

In the year of release, $S_{m,t}$ is substituted for $S_{m,t}$ and the exponent 6 is substituted for 12.

The *i,k*th element of Φ , $\phi_{i,k}$ is the probability of a fish moving from area *i* to area *k* at the end of a month *m* and is described by

$$(4) \quad \phi_{i,k} = \rho \frac{i,k}{i} [1 - \rho \exp(-\rho_{i,*})] \quad \text{for } i \neq k$$

Fig. 2. Growth and length distributions for Alaska sablefish movement model. Left panel is growth and maturity curves for Alaska sablefish. The three shaded regions correspond to the three size groups used in the movement model (small = lightest shade; medium = medium shade; large = darkest shade). Right panel is a histogram of the release length (cm) of all recoveries; the dashed vertical lines are the dividing points of the three size groups. LVB is the estimated von Bertalanffy growth curve.



$$(5) \quad \phi_{i,k} = \rho \exp(-\rho_{i,k}) \quad \text{for } i = \rho k$$

$$(6) \quad \rho_{i,k} = \rho \sum_{i \neq k} \left(\phi_{i,k} \right)$$

The $\phi_{i,k}$ values are the movement parameters to be estimated and are analogous to instantaneous rates. By constraining the $\phi_{i,k}$ values to be non-negative, this parameterization lets Φ and Θ have the properties of a Markov transition matrix; the row sums equal unity and all the elements are non-negative. A movement process is Markovian if the probability of a fish moving from area i to area k at the end of a month depends only on the area the fish is in at the beginning of the month. Thus, movement of fish is modelled as a discrete monthly event where all fish in an area have the same movement probabilities independent of their previous history.

We examined whether movement probabilities were changing over time by incorporating a model that estimated an additional year-specific parameter that conditioned the monthly movement matrix to imply more or less movement. Similar to Webster et al. (2013), this only affected the magnitude of movement probabilities, not the pattern between areas that would have vastly increased the number of parameters. Annually varying movement was estimated using a multiplicative parameter to the diagonal elements of the monthly movement matrix Φ and then normalizing it to sum to unity:

$$(7) \quad \begin{aligned} \phi_{i,k,t}^* &= \rho \tau_t \phi_{i,k,t} \\ \phi_{i,k,t}^* &= \rho \frac{\phi_{i,k,t}}{\sum_k \phi_{i,t;i \neq k}} (1 - \rho \tau_t \phi_{i,k,t;i=k}) \end{aligned}$$

where $\phi_{i,k,t}$ is the monthly probability of movement from area i to area k in year t , and $\phi_{i,k,t}^*$ are the normalized probabilities after multiplying by τ_t , the year-specific movement parameter. The τ_t parameter is estimated as a lognormal deviance vector (elements must sum to 1) with a prior distribution of $\log N(0,0.1)$. The lognormal distribution was used so that the multiplier resulted in the same proportional change in movement probability at the arithmetic scale. At the arithmetic scale, a number above 1 results in a higher probability of retention in an area, while a value less than 1 results in a higher probability of moving out of an area.

The model is formulated in terms of monthly parameters, rather than annual parameters, to reduce the number of parameters that need to be estimated and to approximate the survival and movement process with a simple formulation. Thus, at the end of a month, a fish in an area can either remain in the same area or move to a contiguous area. Description of the population dynamics and movement model in annual steps requires a more complicated formulation with more parameters to account for movement to noncontiguous areas, the possibility of returning to the previous area, and survival along the way (Hilborn 1990). We believe this assumption is approximately correct because no tag returns came from a noncontiguous area during the month after release.

Recovery model

The second model component adapts the Baranov catch equation (Beverton and Holt 1957) to describe the recovery and reporting of tagged fish. The number of tag recoveries $Q_{g,i,t}$ from a release group in an area-year stratum is obtained from the product of fishing mortality $\lambda \hat{\phi}_{i,t}$, the tag reporting rate W_i , and the mean abundance of tagged fish $\bar{N}_{g,i,t}$

$$(8) \quad Q_{g,t,i} = \rho \bar{N}_{g,i,t} \lambda \hat{\phi}_{i,t} W_i$$

From eq. 2, fishing mortality is multiplied by $U_{i,t}$ in the year of release. An approximation of $\bar{N}_{g,i,t}$ is the number of tagged fish in each area at the midpoint of a year. Equation 8 can be modified to give

$$(9) \quad \bar{N}_{g,t} = \rho N_{g,t} (S_{m,t})^6$$

The exponent 6 represents the midpoint of the year. In the year of release, $S_{m,t}$ is substituted for $S_{m,t}$, and the exponent 3 (the midpoint of the remainder of the year) is substituted for 6.

Likelihood of recoveries

The third model component specifies the likelihood (L) of the predicted number of tag recoveries Q given the observed number of tag recoveries R . Hilborn (1990) recommended the Poisson likelihood for computational efficiency. In this study, we compare the negative binomial likelihood to the Poisson likelihood. The negative binomial is preferred over the more commonly used Poisson distribution, because tagging data often exhibit more variability than can be accounted for by the Poisson as a result of non-

independence of tagged fish or other processes (Kitada et al. 1994; Hampton and Fournier 2001; Aires-da-Silva et al. 2009). Specific examples of processes that could cause overdispersion in this data set are tagged sablefish moving in groups, nonrandom fishing spatial effort, and environmental correlation in natural mortality or gear susceptibility. The negative binomial specifically accounts for this overdispersion by estimating an additional parameter. For the application of the Poisson likelihood for these data, see HF. The negative log-likelihood for the negative binomial model is

$$(10) \quad -\log L[Q_{g,i,t}|R_{g,i,t}] = -\log(R_{g,i,t} + rQ_{g,i,t}) - \log(-rQ_{g,i,t}) \\ - \log(R_{g,i,t} + 1) + rQ_{g,i,t}[\log(rQ_{g,i,t}) \\ - \log(Q_{g,i,t} + rQ_{g,i,t})] + R_{g,i,t}[\log(rQ_{g,i,t}) \\ - \log(Q_{g,i,t} + rQ_{g,i,t})]$$

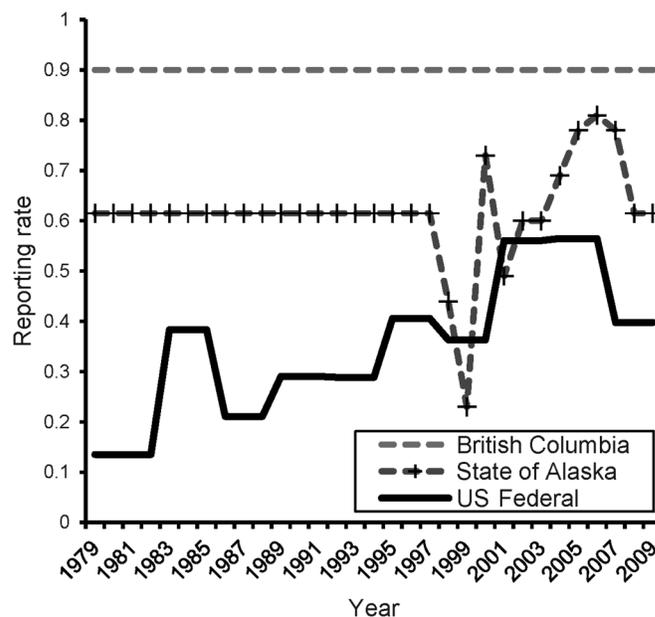
where $R_{g,i,t}$ and $Q_{g,i,t}$ are observed and predicted recoveries, respectively, from release group g in area i and year t . Γ is the log-gamma function, and r is the overdispersion parameter. We also compared the fit of a model with that obtained using the Poisson likelihood.

Parameters estimated outside the model

A key part of scaling tag-recapture data is the rate of reporting of recoveries by fishery participants (i.e., what percentage of tags recovered are actually returned). If fishing mortality and reporting rate are constant over time and space, then reporting rate can be cancelled out (McGarvey and Feenstra 2002; McGarvey 2009). If fishing mortality and reporting rate change over time and area, then reporting rate needs to be considered in any modelling application. In this analysis, we include time-varying tag reporting rates because Heifetz and Maloney (2001) showed that reporting rates have increased over time in the federal fishery, coincidental with the implementation of the IFQ system in 1995 and increased observer coverage since 1990. These estimates are based on methods described by Heifetz and Maloney (2001), and we pooled estimates across areas in blocks of 3 years. Sensitivity analyses showed that pooling data in 3-year increments generally obtained the best model fit to the release and recovery data. For inside waters, we used annual ADF&G estimates for CH (S. Dressel, unpublished data) for both CH and CL. These rates lacked a discernible pattern and varied from 23% to 81% for 1998–2007, and the mean of these rates were used for missing years (62%). CL reporting rates were unavailable, but the area shares many of the same fishermen and the majority of the tags released in CL are returned from catches in state waters. Therefore, we assumed the reporting rates were the same as those for CH. We believe the estimates for the federal and state water reporting rates (in CH) are relatively well determined because they are based on the rate of recovery on surveys versus the rate of recovery in the fishery with large sample sizes. As in HF, we assume that the tag reporting rate in BC is 0.90, based on previous research assuming that it was very high (Beamish and McFarlane 1983). In an unpublished DFO report, Haist et al. (1999) estimated BC reporting rates from 1979 to 1998 using an integrated catch-age tag-recapture model and showed variable reporting rates from ~0.4 to nearly 1 at the end of the time series and that it was generally higher than that estimated for Alaska. We continue to use the value assumed in HF, but recognize this estimate is uncertain and the BC fishery has also changed (e.g., ITQs). Therefore, we also test the sensitivity to alternative values of 0.30 and 0.60. Figure 3 shows values for reporting rates that we use in the primary model application. Natural mortality is fixed at 0.10 (Hanselman et al. 2011), and annual tag loss is fixed at 0.02 from a double tagging experiment (Saunders et al. 1990).

The estimates of fishing mortality $f_{i,t}$ used in our application of the recovery model were estimated separately for US federal,

Fig. 3. Values for tag reporting rates, $W_{i,t}$, in Alaska federal waters, state of Alaska, and British Columbia used in the sablefish movement model.



state, and BC waters. For federal waters, estimates of fishing mortality were obtained from

$$(11) \quad f_{i,t} = \rho \frac{C_{i,t}}{\bar{B}_{i,t}}$$

where $C_{i,t}$ is the catch and $\bar{B}_{i,t}$ is mean exploitable biomass in area i in year t . The exploitable biomass were obtained from

$$(12) \quad \bar{B}_{i,t} = \rho \frac{RPW_{i,t}}{q}$$

where $RPW_{i,t}$ values are the relative population weights from the federal longline survey in area i and year t , and q values are catchability coefficients for two periods of the longline survey as estimated in the sablefish stock assessment model (Hanselman et al. 2011). The values of q are 7.11 for the years 1979–1989 and 5.67 for the years 1990–2009, which corresponds to a shift from the Japanese cooperative survey to the NMFS domestic survey (Kimura and Zenger 1997; Hanselman et al. 2011). This implicitly assumes that catchability is constant across areas, which is also the way it is treated in the federal stock assessment. For fishing mortality in CH and CL, we used results from ADF&G models for CH (S. Dressel, unpublished data) and again assumed the same rates for CL. For fishing mortality in BC, we used estimates from Model C in the Canadian sablefish management strategy evaluation (Cox et al. 2010).

Mortality

The movement model presented in this study inherently estimates annual total mortality by estimating the λ parameter that is multiplied against the input fishing mortality and added to natural mortality. Single tag-recovery experiments can also provide estimates of mean total mortality (\hat{Z}) based on the time at liberty of the tagged animals in the population. Various methods for estimating \hat{Z} using time at liberty data from tag-recovery experiments have existed since the 1950s (Deemer and Votaw 1955; Gulland 1955; Chapman 1961), but have rarely been employed

in practice because of violations of assumptions of reporting rate and nonrandom recapture probabilities (Xiao et al. 1999; McGarvey 2009). These assumptions may only be mildly violated in this data set, as reporting rate and fishing mortality changes have been documented but are only moderately variable.

We examine three time at liberty models to estimate total mortality in the federal fishery during the time period of this study. The first two methods are the unbiased Chapman estimator and the truncated model from Deemer and Votaw as presented in McGarvey et al. (2009). The Chapman estimator is unbiased if the animals have been at liberty long enough that very few tagged animals would have survived. Simulations have shown that the truncated estimator has negligible bias if animals have been in the population 4–6 years since the tagging was conducted (McGarvey et al. 2009). We present an additional method that fits an exponential decay model to the time at liberty data. This method is analogous to catch-curve analysis (Thorson and Prager 2011). We compute an overall mean total mortality with release data through 2004 and recovery data through 2009 using the suggestion that the truncated bias is minimized by about 5 years at liberty (McGarvey et al. 2009).

The three methods are as follows:

$$(13) \quad \hat{Z}_{\text{Chapman}} = \frac{n_r - \rho l}{T}$$

$$(14) \quad \hat{Z}_{\text{Truncated}} = \rho \frac{\tau_{\text{max}} e^{-\hat{Z}_{\text{Truncated}} \tau_{\text{max}}}}{(1 - \rho \tau_{\text{max}} e^{-\hat{Z}_{\text{Truncated}} \tau_{\text{max}}})} - \rho \bar{\tau} = \rho l$$

$$(15) \quad N_t = \rho N_1 e^{-\hat{Z}_{\text{decay}} t}$$

where n_r is the number of tagged, recaptured, and subsequently reported animals, T is the sum of all times at liberty, τ_{max} is the length of the experiment, $\bar{\tau}$ is the mean time at liberty, N_t is the number of tagged animals at time t , and N_1 is the number of tagged animals recovered in the first year. Equation 13 is a plug-in estimator, while eqs. 14 and 15 require nonlinear least squares minimization. We implemented this in R (R Development Core Team 2012).

In addition, we computed annual total mortality estimated by the movement model for large sablefish. Large sablefish were chosen because these would be the most comparable to the stock assessment estimates of total mortality at full selection. We computed an annual mean fishing mortality for all federal areas with a catch-weighted mean of the estimate of fishing mortality in each area. This is then multiplied by the estimated λ_f for large sablefish and added to natural mortality for an annual estimate of total mortality from the movement model.

Using these methods, we show how the time at liberty estimates of total mortality change as each release year is added and compare these with the mortality estimates from the movement model and the stock assessment for that same period.

Uncertainty

By implementing the movement model in AD Model Builder, we were able to examine the uncertainty in the movement parameter estimates in several ways. First, we examined the standard errors of parameter estimates from the maximum likelihood approach derived from the Hessian matrix as in HF. While these standard errors give some measure of variability of individual parameters, the variance is often underestimated because it is assumed that the joint distribution is multivariate normal. Alternatively, we considered the movement model as a Bayesian framework (e.g., Stewart 2007). We estimated the joint posterior

distribution of parameter estimates by Markov chain Monte Carlo (MCMC) methods (Gelman et al. 1995). The movement model used noninformative priors (or nearly so, such as a uniform prior on λ_f bounded between 0.01 and 10). To remove autocorrelation from the Markov chain and to remove the early part of the chain while the jump size has not stabilized, it is necessary to “thin” the chain and remove the “burn-in.” We removed the first 400 000 iterations out of 2 000 000 and “thinned” the chain to one value out of every 400, leaving a sample distribution of 4000. Chain convergence was evaluated using the coda package (Plummer et al. 2006) in R. A sample of the chain diagnostics is included in the Supplementary Materials¹.

Results

Movement

Sablefish moved large distances throughout the 31 years of this study. Mean great-circle distance moved over all size groups was 191 km in 1 year, and 602 km over all time at liberty (up to 31 years). These distances were calculated as point-to-point, not along the coastline, bathymetry, or oceanic features, so they are minimum distances. Female sablefish moved slightly farther (16%) on average than male sablefish. There was a strong relationship between longitude of tagging and the mean distance moved; sablefish tagged in the west consistently moved much greater lifetime distances than sablefish tagged in the east (Fig. 4).

For comparisons with HF and to examine sensitivity to assumptions, we examined a range of models (Table 1). Subsequent results presented here are based on model with time-invariant movement probabilities (F.R.D.A.N.), unless stated otherwise. The magnitude of movement probabilities was more related to the area of occupancy (i.e., where the model predicts the fish is, at the beginning of each time step) than to the size group (Fig. 5; Table 2). Estimates of the annual movement probabilities varied widely across area of occupancy. The western Gulf of Alaska (WG) appears to be a transition zone for sablefish; there is an 80%–90% probability that a sablefish will move out of the WG after 1 year of occupancy. On the other hand, fish in CH (state waters) have only a 10%–14% chance of moving out of the area after 1 year of occupancy. CL sablefish, which are more geographically open to the Gulf of Alaska (GOA) than CH sablefish, show about a 30% chance of moving out of the area after 1 year of occupancy, mainly into the eastern GOA (EG) and BC waters. Fish residing in the EG, however, show relatively little movement into inside waters or BC, and mainly remain within the EG (42%–50%) or move toward the central GOA (CG, 26%–29%). Medium and large fish residing in the Bering Sea (BS) had higher annual probabilities of moving to the CG (20%–23%) than the geographically adjacent WG or Aleutian Islands (AI, 7%–15%).

Movement parameters also differed among size groups (Table 3). This was supported by a much lower Akaike information criterion (AIC) for the full model estimating 63 parameters for the three size groups (AIC = 68 198) versus a model that shared 21 parameters (AIC = 69 378) for all three size groups. The majority of the estimated movement parameters were significantly different from zero in a one-sided t test ($\square > 0$, $p < 0.05$), except for five parameters describing movement to and from the BS and AI areas (Table 3). There was not a consistent pattern for which size group showed the most movement across areas. In general, there was a tendency for the largest fish to have the highest annual movement probabilities. While the annual movement probability estimates in the BS and AI areas were relatively uncertain, they showed similar movement probabilities, and larger fish moved more than medium and small fish (Fig. 5). If we consider the CG as the centre of the distribution of Alaska sablefish, it was more likely for all size groups to move east than west (Table 4).

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0251>.

Fig. 4. Mean great circle distance (km) from release to recovery by longitude of release. Labels are the number of recoveries, line is a loess smooth. Longitude less than -180 are across the meridian (e.g., -190 = 170°E).

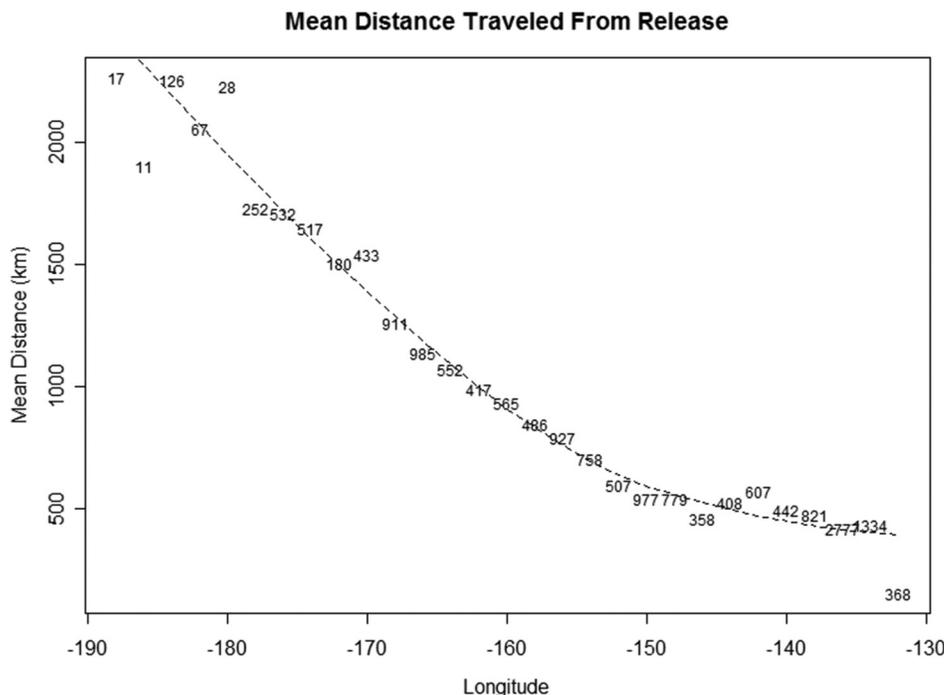


Table 1. Description of successive changes from formulation of the sablefish movement model used in Heifetz and Fujioka (HF, 1991).

Model	Description	Change in annual movement probability by area compared with HF					
		AI	BS	WG	CG	EG	Mean
HF	Original formulation and data in Heifetz and Fujioka (1991)						
F	Updated fishing mortality rates	-4%	-8%	4%	6%	-6%	5%
F.R.	Updated reporting rates	-2%	-8%	4%	5%	-5%	5%
F.R.D.	Full time series (1979–2009)	34%	-12%	12%	9%	10%	15%
F.R.D.A.	Addition of southeast Alaska inside data	32%	-10%	14%	11%	11%	16%
F.R.D.A.N.	Change from Poisson to negative binomial likelihood	79%	-2%	18%	22%	37%	31%
F.R.D.A.N.Y.	Estimate annually varying movement	—	—	—	—	—	—

Note: F.R.D.A.N. (in bold font) is the primary model used for results. Each successive change in the model also shows the percentage different from HF in the annual probability of movement out of each federal area. The mean is of the absolute values. EG, eastern Gulf of Alaska (GOA); CG, central GOA; WG, western GOA; BS, Bering Sea; and AI, Aleutian Islands.

Overall, for all size groups, sablefish are more likely to move out of an area than to stay in an area.

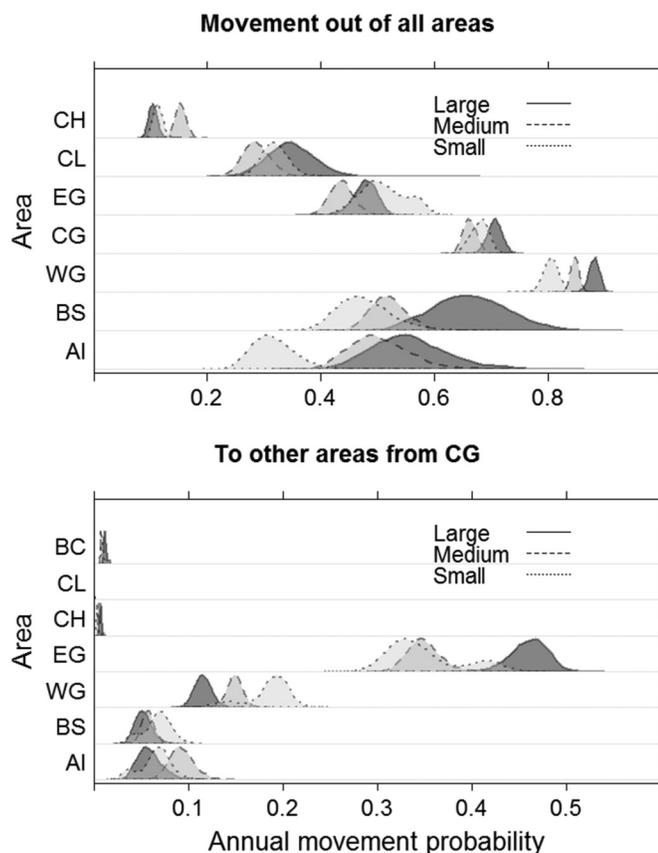
Estimates of precision derived from the inverse of the Hessian matrix had coefficients of variation (CVs) that were usually less than 25% (Table 2). For small, medium, and large fish, 84%, 86%, and 80%, respectively, of CVs were below 25%. The least precise estimates were those involving the AI, BS, and CL areas, primarily because there were fewer data from those areas. Indeed, estimated movement parameters between the BS and AI were insignificant (Table 3, $p > 0.05$, one-sided t test).

When examined with MCMC simulation, estimated posterior distributions of annual movement probabilities were generally close to normally distributed and reasonably precise with the exception of the BS and AI areas. The distribution of estimated movement probability in the EG was right skewed and slightly bimodal (Fig. 5). The uncertainty in CH, CG, and WG movement probability is low relative to other regions (Fig. 5). The distributional plots show plainly the increase in annual movement probabilities from east to west in the GOA (from CH to WG, excluding CL), which supports the strong longitudinal increase in lifetime distance moved from east to west (Fig. 4). They also illustrate that large fish often have the highest movement probability and the most uncertainty about those probabilities.

The model estimating annual movement variability (F.R.D.A.N.Y.) had a significantly better fit to the data. Even with 31 additional parameters, AIC values showed clear support (the large decrease in AIC ranging between 36 and 56 depending on fish size) that the tendency to move out of an area varied annually (Table 5). There appeared to be a temporal trend of decreasing movement across all size groups from about 1980 until the early 1990s, when the pattern reversed toward increasing movement (Fig. 6). Annual movement probability peaked at around 2005 for all three size groups. The patterns were nonrandom, so we compared the annual movement pattern to federal assessment results (Hanselman et al. 2011). We examined spawning biomass lagged over a number of years with the hypothesis that annual movement probabilities would be affected by prior abundance of adult fish. The annual movement pattern for large sablefish was highly negatively correlated ($r = -0.74$, $p < 0.01$) with female spawning biomass lagged 2 years (Fig. 7). The other two size groups were negatively associated, but less correlated with spawning biomass lagged 2 years, while small sablefish annual movement was weakly negatively correlated with recruitment with no time lag.

Overall probability of movement between areas was estimated to be greater and less directed than previous estimates had shown. Adding two release and recovery areas in southeast inside waters

Fig. 5. Posterior probability distributions of annual sablefish movement probability by size group and area. Top panel is movement probability out of each area. Bottom panel is movement probability to each area from the central Gulf of Alaska. AI = Aleutian Islands, BS = Bering Sea, WG = western Gulf of Alaska, CG = central Gulf of Alaska, EG = eastern Gulf of Alaska, CH = Chatham Strait, CL = Clarence Strait, Small = <57 cm, Medium = 57–66 cm, Large = >66 cm.



and updating the fishing mortality and reporting rates had a negligible effect on estimated movement probabilities between the federal regions estimated in HF (Table 1). Most of the change in movement probabilities was due to adding 22 years of new tagging data and estimation using the negative binomial likelihood, instead of the Poisson likelihood used in HF (Table 1). The use of the negative binomial likelihood was well supported with a substantially lower AIC value for all size groups (Table 5) and precisely estimated overdispersion parameters (Table 3). The largest relative change occurred in the AI area with an annual movement probability that was estimated to be almost 80% higher than previously estimated.

The estimated movement parameters were sensitive to the assumed reporting rate in BC of 0.9 for areas adjacent to it. In absolute annual probabilities, changes to 0.6 and 0.3 had a large effect on the movement of fish from CL to BC with a positive change of 0.02 and 0.08, respectively. These represented 67% and 420% increases in movement probability from CL to BC, respectively, because of the relatively small estimated movement in that direction. The sensitivity of movement probabilities to the specification of the BC reporting rate west of the EG area was negligible. The fishing mortality calibration parameter estimates (λ) increased as a function of fish size, but were quite similar (Table 3).

Mortality

The three different time at liberty methods of estimating mortality (Chapman, Deemer and Votaw, and exponential decay) gave similar estimates (Table 6) when computed for the whole data set. The exponential decay model gives slightly higher estimates and fits the data extremely well (Table 6). The mean annual mortality from 1979 to 2004 from the Alaska sablefish stock assessment (Hanselman et al. 2011) is slightly higher but is similar to these independently derived estimates of total mortality (Table 6). The mean total mortality estimate from the movement model is lower (22%) than the federal stock assessment but is only slightly lower than the time at liberty estimates (Table 6).

When we compare the three estimation models as each release year is added (Fig. 8), the mortality estimate from the exponential decay model increases at a slower rate than the Chapman and Deemer and Votaw estimates until 1996, but all estimates show a moderate increasing trend. These tag-based estimates are not expected to emulate the annual pattern of the stock assessment mortality estimates, because they are estimating the mean mortality of the current and prior years included. Interestingly, all of the estimators change their slope starting in 1996. According to the stock assessment, this is when the population began approaching an all-time low biomass because of low recruitment (Hanselman et al. 2011), but also when total mortality from the assessment was estimated to be relatively low and began to increase (Fig. 8).

Discussion

Movement

Our model results showed that for all size groups and areas of occupancy, sablefish are extremely mobile relative to many demersal marine fish (e.g., Hannah and Rankin 2011). The implications of our analysis are that sablefish are more mobile than previously thought, and fish originally tagged in the west have longer lifetime movements than fish originally tagged in the east. The higher lifetime movements from fish originally tagged in the west can partly be attributed to small fish comprising a larger proportion of fish tagged in the western areas that would likely have longer times at liberty (see Supplementary Table S1¹).

Our results showed that the directionality of movement has also changed since HF, particularly for small sablefish. In HF, small sablefish had a tendency to move westward. For example, HF estimated an annual movement probability of 32% for small sablefish in the CG to move westward toward the WG, BS, and AI and a 20% probability to move eastward. In our results, estimated annual movement probability of small sablefish from the CG had the reverse pattern, with 29% moving westward and 39% moving eastward. The significant difference of movement probabilities among length groups found in this study differed from Beamish and McFarlane (1988), but agreed with HF and Bracken (1982).

Since this study included many more data than HF, we evaluated whether year-specific changes in movement probabilities could be estimated and whether they were changing over time. The annual movement pattern of large sablefish was highly inversely correlated with lagged female spawning biomass. This suggests that large sablefish may move less when abundance is near its peak. Small sablefish had a different pattern that appeared to be more erratic or associated with large year classes; there was a lower probability of movement after large year classes in 1977, 1997, and 2000 and higher probability of movement during periods of low recruitment (late 1990s, and 2004–2009).

The rapid change in annual movement estimates for all sizes of fish after 2003 may indicate that when the tagged fish have not been at liberty for a sufficient number of years, movement estimates are uncertain. A future analysis might examine how many years at liberty are needed to obtain precise estimates of annual movement as a function of life history (e.g., growth rate). It is

Table 2. Annual movement probability estimates ($\theta_{i,k}$) by area (rows indicate area of occupancy), coefficients of variation (CVs, %) are below each estimate, $i \neq k$ is the total probability of moving to any other area.

Area	BC	CL	CH	EG	CG	WG	BS	AI	$i \neq k$
Small (<57 cm)									
CL	0.020 21%	0.697 3%	0.014 37%	0.186 10%	0.061 19%	0.018 17%	0.002 22%	0.002 23%	0.303
CH	0.012 18%	0.002 57%	0.896 1%	0.063 10%	0.020 20%	0.006 18%	0.001 23%	0.000 23%	0.104
EG	0.025 8%	0.001 54%	0.010 12%	0.503 7%	0.294 11%	0.127 11%	0.021 18%	0.019 19%	0.497
CG	0.010 18%	0.000 56%	0.004 20%	0.372 10%	0.325 4%	0.180 10%	0.057 18%	0.053 20%	0.675
WG	0.005 15%	0.000 56%	0.002 18%	0.271 9%	0.304 9%	0.196 7%	0.112 18%	0.110 17%	0.804
BS	0.001 18%	0.000 57%	0.000 21%	0.070 15%	0.148 16%	0.172 16%	0.567 7%	0.042 34%	0.433
AI	0.000 21%	0.000 58%	0.000 23%	0.038 18%	0.085 19%	0.105 18%	0.049 28%	0.722 4%	0.278
Medium (57–66 cm)									
CL	0.058 17%	0.723 3%	0.018 42%	0.154 11%	0.036 14%	0.008 16%	0.001 19%	0.001 20%	0.277
CH	0.023 13%	0.001 51%	0.857 1%	0.092 8%	0.021 11%	0.005 14%	0.000 18%	0.001 19%	0.143
EG	0.025 4%	0.001 29%	0.015 8%	0.584 3%	0.261 6%	0.079 9%	0.014 14%	0.021 15%	0.416
CG	0.008 9%	0.000 30%	0.005 11%	0.369 5%	0.356 4%	0.139 7%	0.049 12%	0.075 13%	0.644
WG	0.004 11%	0.000 31%	0.003 13%	0.271 7%	0.339 5%	0.151 5%	0.091 13%	0.140 15%	0.849
BS	0.001 13%	0.000 32%	0.000 14%	0.081 10%	0.200 8%	0.151 11%	0.502 6%	0.065 32%	0.498
AI	0.001 15%	0.000 33%	0.000 17%	0.073 13%	0.183 11%	0.141 13%	0.054 24%	0.548 8%	0.452
Large (>66 cm)									
CL	0.108 21%	0.678 6%	0.036 46%	0.127 19%	0.036 22%	0.011 23%	0.002 30%	0.002 33%	0.322
CH	0.016 15%	0.002 51%	0.903 1%	0.057 10%	0.016 14%	0.005 16%	0.001 24%	0.001 28%	0.097
EG	0.023 7%	0.000 59%	0.014 11%	0.550 4%	0.272 6%	0.094 9%	0.023 20%	0.024 23%	0.450
CG	0.010 11%	0.000 60%	0.006 14%	0.458 5%	0.306 5%	0.114 9%	0.050 17%	0.055 20%	0.694
WG	0.008 12%	0.000 60%	0.005 14%	0.423 6%	0.304 6%	0.117 9%	0.067 15%	0.076 18%	0.883
BS	0.002 21%	0.000 63%	0.001 22%	0.172 17%	0.227 14%	0.115 12%	0.395 16%	0.087 54%	0.605
AI	0.002 19%	0.000 62%	0.001 20%	0.153 15%	0.207 13%	0.106 12%	0.030 22%	0.501 11%	0.499

Note: BC, British Columbia, Canada; CL, Clarence Strait; CH, Chatham Strait; EG, eastern Gulf of Alaska (GOA); CG, central GOA; WG, western GOA; BS, Bering Sea; AI, Aleutian Islands.

likely that the increase in estimated movement shown in this study compared with HF is a combination of examining a much longer time series giving more accurate mean estimates, improvements in modelling assumptions (likelihood model and reporting rates), and an actual increase in movement in recent years that appears to have occurred since the end of the period examined in HF (1988; Fig. 6).

The inclusion of the tagging data from inside waters of southeast Alaska provided insights into the relationship of sablefish in federal waters to those managed by the state of Alaska in inside waters. The CH area showed lower probability of movement out of the area than CL or federal areas. The annual probability of sablefish moving from CL to federal waters and BC was considerable (~30%), but the estimated movement into CL was extremely low and lower than CH particularly for large fish (Table 2). This suggests either that CL is a source of sablefish for the GOA or that

sablefish that were not tagged in our study, such as fish from BC or larval and young fish that are smaller than those tagged, could be emigrating into CL. Future research should attempt to determine whether the adults leaving CL are from local recruitment or from immigration of larvae or juvenile sablefish. An additional caveat to the exchange with inside waters is that we do not compute absolute exchange (i.e., a small probability of moving from the large EG stock to the small CH stock could be many fish in absolute terms). Future work could attempt to estimate absolute numbers of fish and examine source-sink dynamics of inside and federal waters.

Different size sablefish have different vulnerabilities to different gear. Sablefish recaptures in this study were primarily obtained in the longline fishery, which has different selectivity by size and age (Hanselman et al. 2011). For this study, the λ parameter is essentially a proxy for gear selectivity of each size group.

Table 3. Estimated parameters for the three modelled size groups from the time-invariant negative binomial model.

Parameter	Small			Medium			Large		
	Estimate	CV (%)	<i>p</i>	Estimate	CV (%)	<i>p</i>	Estimate	CV (%)	<i>p</i>
(CL,BC)	0.002	26	0.000	0.005	18	0.000	0.011	23	0.000
(CL,CH)	0.001	42	0.008	0.002	47	0.016	0.004	49	0.020
(CL,EG)	0.027	9	0.000	0.020	12	0.000	0.018	21	0.000
(CH,BC)	0.001	20	0.000	0.002	14	0.000	0.001	16	0.000
(CH,CL)	0.000	59	0.045	0.000	54	0.032	0.000	52	0.027
(CH,EG)	0.008	9	0.000	0.011	8	0.000	0.007	9	0.000
(EG,BC)	0.003	6	0.000	0.003	4	0.000	0.003	7	0.000
(EG,CL)	0.000	54	0.033	0.000	30	0.000	0.000	61	0.050
(EG,CH)	0.001	11	0.000	0.002	8	0.000	0.002	11	0.000
(EG,CG)	0.095	29	0.000	0.062	12	0.000	0.093	21	0.000
(CG,EG)	0.131	27	0.000	0.095	11	0.000	0.198	22	0.000
(CG,WG)	0.148	42	0.009	0.137	26	0.000	0.405	17	0.000
(WG,CG)	0.257	44	0.011	0.378	28	0.000	2.042	42	0.009
(WG,BS)	0.038	18	0.000	0.046	16	0.000	0.111	40	0.006
(WG,AI)	0.033	17	0.000	0.070	20	0.000	0.104	43	0.010
(BS,WG)	0.053	15	0.000	0.064	13	0.000	0.075	22	0.000
(BS,AI)	0.001	>100	0.367	0.001	>100	0.450	0.010	>100	0.166
(AI,WG)	0.026	17	0.000	0.056	18	0.000	0.063	18	0.000
(AI,BS)	0.003	58	0.041	0.003	86	0.122	0.000	>100	0.500
<i>r</i>	2.000	2	0.000	2.318	2	0.000	3.067	3	0.000
$\lambda\rho$	0.479	2	0.000	0.532	2	0.000	0.555	3	0.000
df			2 979			4 366			2 119
-lnL			10 335			14 956			8 745

Note: -lnL is the negative log likelihood, $\lambda\rho$ is the fishing mortality rate calibration parameter, *r* is the overdispersion parameter, and (*i,k*) are the parameters of the Markov matrix used to estimate monthly movement estimates between areas *i* and *k*. BC, British Columbia, Canada; CL, Clarence Strait; CH, Chatham Strait; EG, eastern Gulf of Alaska (GOA); CG, central GOA; WG, western GOA; BS, Bering Sea; AI, Aleutian Islands. Nonsignificant *p* values are shown in bold-italic font.

Table 4. Comparison of directionality of annual movement probability for three size groups from the central Gulf of Alaska.

	East	West
Small (<57 cm)	39%	29%
Medium (57–66 cm)	38%	26%
Large (>66 cm)	47%	22%

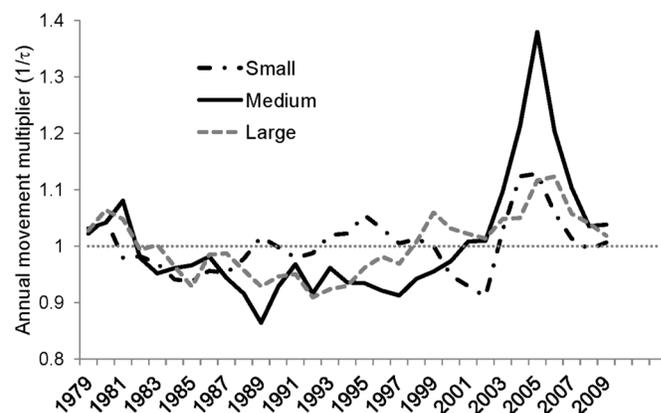
Table 5. Comparison of negative log likelihoods (-lnL) and Akaike information criterion (AIC) values among three formulations of the sablefish movement model by size group.

Model	Small	Medium	Large
Poisson (F.R.D.A.)			
-lnL	11 243	16 575	11 108
<i>k</i>	21	21	21
AIC	22 528	33 192	22 258
Negative binomial (F.R.D.A.N.)			
-lnL	10 335	14 956	8 745
<i>k</i>	22	22	22
AIC	20 714	29 956	17 534
Negative binomial with annually varying movement (F.R.D.A.N.Y.)			
-lnL	10 288	14 897	8 697
<i>k</i>	53	53	53
AIC	20 682	29 900	17 500
<i>p</i> (AIC _{min})	<0.001	<0.001	<0.001

Note: *k* is the number of estimated parameters, and *p* (AIC_{min}) is the relative probability that the best model minimized the estimated information loss.

Although $\lambda\rho$ is confounded with the assumed catchability and natural mortality, the magnitude of $\lambda\rho$ increases slightly from small to large sablefish. The pattern is what we would expect from the selectivity of a fishery conducted primarily with longline gear, which selects for large fish. However, the difference among size groups is small, implying that smaller sablefish are less vulnera-

Fig. 6. Year-specific movement multiplier (1/ τ), which increases (values > 1) or decreases (values < 1) the probability of a sablefish to move out of an area in each year.



ble for only a short period of time, probably due to their rapid growth. The parameter was lower for all size groups than previously estimated by HF. Because these parameters are substantially below unity, it may indicate that either the inputted fishing mortality or reporting rate estimates could be too high. It may be possible to estimate size selectivity directly in future models (Myers and Hoenig 1997). However, estimating selectivity with Pacific halibut tag data yielded substantially different selectivity curves than catch-at-age analysis (Anganuzzi et al. 1994). They suggested that estimating selectivity from tagging data might be feasible only in integrated age-structured models that use tagging data directly. Webster et al. (2013) estimated selectivity similarly, except they chose a size group to fix selectivity at 1, with fish of smaller size groups having a lower selectivity.

The superior fit of the negative binomial likelihood compared with the Poisson indicates that there was significant overdispersion (i.e., greater than expected variability in the data than the

Fig. 7. Scatterplot of female spawning stock biomass (SSB) lagged 2 years from Hanselman et al. (2011) and the time-varying movement parameter for large sablefish that describes the probability of moving out of or staying in an area. Dashed line is a linear regression line.

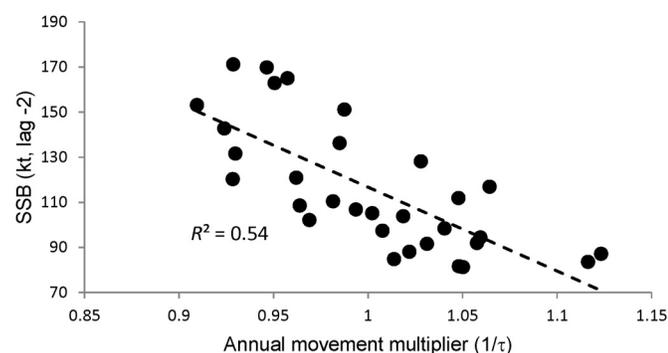


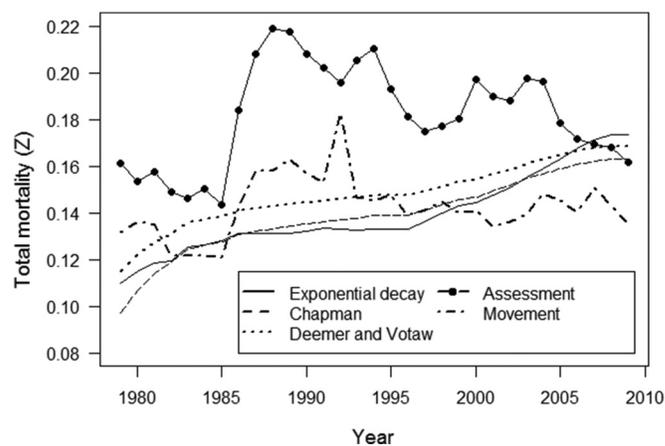
Table 6. Estimates of mean total mortality over the time period 1979–2004 (with recoveries from 1979 to 2009) based on exponential decay mortality $N_t = \rho N_t e^{-Z_{\text{decay}} t}$ (model, Chapman (1961) finite population corrected ($\hat{Z} = \frac{n_r - 1}{T}$), the truncated estimator of Deemer and Votaw (1955) from eqs. 13–15, the sablefish stock assessment (Hanselman et al. 2011), and the movement model.

	Exponential decay	Chapman	Deemer and Votaw	Stock assessment	Movement model
Z	0.163	0.165	0.157	0.184	0.143
SE	0.003	0.001	0.000	0.005	0.003
R ²	0.996	—	—	—	—

chosen model expects) in the tag-recovery data. Overdispersion can be caused by nonrandom fishing effort that is not in proportion to where the tagged animals are (Aires-da-Silva et al. 2009) or by nonindependence of tagged fish from fidelity of the tagged cohort (i.e., fish tagged together moving together; Schwarz et al. 1993). An example of the former is that the fish are tagged systematically across Alaskan waters in the federal longline survey, but the fishery focuses much of the effort near major ports, and many of the tags are returned from a small number of vessels that consistently fish similar areas. Another cause could be changes in selectivity or natural mortality caused by unmodelled environmental variability. Yet another potential cause of this overdispersion could be unaccounted for changes in detection efficiency (Lindén and Mäntyniemi 2011), which in this case would be the reporting rate. We modelled reporting rate in 3-year blocks for the federal fishery, but used some mean or dated rates for CH, CL, and BC (e.g., Fig. 3). Accurate annual estimates of the reporting rates for all areas could reduce some overdispersion. The largest change in annual movement probability was in the AI, and this was amplified using the negative binomial likelihood. The amount of releases in the AI is relatively sparse, and tags are not deployed annually, which may contribute to the overdispersion.

There are several caveats to the estimation of movement in this study. First, using size groups is not ideal. For example, fish in the small group, after several years at liberty, enter the medium and then eventually large size groups. This means some of the movement probability of the small fish was influenced by fish that were captured much later in life and were no longer small. To address this concern, we tested this sensitivity by running a model where we used only recoveries of small fish for up to 3 years at liberty, and the results were similar to including all of the data. This is likely because many recoveries happen in the first few years at liberty (52% in 3 years and 68% in 5 years; see Fig. S1 in Supplemental Materials¹). An additional confounding issue is that fish in

Fig. 8. Three time at liberty estimators of total mortality as each release year was added based on exponential decay mortality model ($N_t = \rho N_t e^{-Z_{\text{decay}} t}$; black solid line), Chapman (1961) finite population corrected model ($\hat{Z} = \frac{n_r - 1}{T}$; dashed line), and the truncated estimator of Deemer and Votaw (1955) (dotted line) from eqs. 13–15. “Assessment” are annual estimates from the sablefish stock assessment (solid line with black circles, Hanselman et al. 2011), and “Movement” (dash-dotted line) are annual estimates (for large fish) from this study.



western areas have smaller asymptotic length than those in the eastern areas (Echave et al. 2012), which is difficult to resolve with their movement patterns when estimated by size group. We could also use release and recovery lengths as covariates instead of using specific groups (Webster et al. 2013). Ideally, the model would be age-structured and incorporate growth directly, but that application has proven difficult because of the limited amount of aged recoveries (J. Heifetz, unpublished data). Second, for this model we assume that there is no movement of fish back from BC to US waters (i.e., BC is a “sink” in this model). We know this assumption is violated because previous analysis of sablefish tagged in BC showed about 12% of those fish moved into Alaskan waters (Beamish and McFarlane 1988). If tag-recovery data from the west coast of the US became available to us, these data should contribute to better estimates of movement from BC to the west coast. In the future, exchanging tag-recovery data with Fisheries and Oceans Canada and incorporating data from the west coast of the US would enable us to obtain more complete coast-wide estimates. Finally, the results of the model are sensitive to reporting rates for BC and CL, and these estimates should be refined because the BC estimate is ad hoc and the CL estimates are borrowed from CH. We expect estimates for both areas would be time-varying and different from the values assumed here. Collaboration on a coast-wide model would greatly aid in refining these important assumptions.

Our focus was to obtain the best estimates of overall sablefish movement probabilities between areas throughout the entire study period. This study shows that movement probabilities are likely changing over time. However, the dynamics of temporal change in movement probabilities were only examined for one scenario. We estimated annual year-specific movement parameters that affected all tagged sablefish of a size group in all areas each year. Many potential covariates could affect the annual pattern of movement estimated in this study. Cohort-specific movement, annually varying natural mortality, and the effect of growth on movement probabilities could also be explored. While a full exploration of time-varying parameters was outside the scope of this study, it is an important future research topic for sablefish biology and movement modelling applications. Future applications will determine if the data are informative enough to

estimate time-varying movement parameters by area, perhaps using a random walk process through time or a random effects model.

Mortality

One of the most important parameters estimated in stock assessment models is total mortality. It is instructive to ground-truth stock assessments with an independent data source (Myers and Hoenig 1997). Our mean total mortality estimates from tagging data and the mean from the federal stock assessment over the same period were similar, while having very different assumptions. While all estimates from the tagging data were lower than the stock assessment estimates, this relative concurrence provides confidence in estimates of mortality for both methods. An appealing property of the time at liberty estimators is they are relatively simple, while stock assessment models have many assumptions and confounded parameters. The exponential decay model fitted the time at liberty data extremely well, which is likely because we have a large data set.

Estimating total mortality as each release year was added provided insights into the performance of these estimators as the length of the time series increased. McGarvey et al. (2009) recommended that 4–6 years of at liberty data should minimize bias in mortality estimates for a Z of 0.5, and as a rule of thumb the number of years should be about 2–3 times $1/Z$, which would suggest 10–20 years for sablefish ($Z \sim 0.2$). Mortality estimates began rapidly changing when release years were included that have less than half the total years of the experiment of recovery information (1996 and thereafter). These estimates assume there are no fish older than 15 years ($1/2$ of the length of the time at liberty data; McGarvey 2009), which should still compose a substantial part of the population for a long-lived species like sablefish. Therefore, this rapid change starting about 1996 (Fig. 8) may be when these estimators become biased from truncation of the amount of years at liberty considered in the calculation. This result is similar to the pattern of annual movement estimates, where the estimates rapidly increased when the fish had only been recently tagged. Therefore, a longer time series of time at liberty may be required for minimizing bias in mortality estimates for longer-lived species.

Ecological mechanisms

This study clearly shows that sablefish move great distances throughout their lifetime and have movement patterns related to their size and area of occupancy. While sablefish ontogenetically move into deeper waters as they age (Beamish and McFarlane 1988; Hanselman et al. 2011), their movement patterns between areas do not seem to imply a distinct ecologically directed mechanism. Movement for other demersal fish populations such as walleye pollock (*Gadus chalcogrammus*) appears to be more directed. They are found in the northern BS as young fish, but primarily as adults in the southern BS and Aleutian basin (Bailey et al. 1999). Similarly, while not as likely to move as sablefish, Pacific halibut (*Hippoglossus stenolepis*) sometimes move great distances, but generally larvae drift into BS and then return to GOA as adults (Seitz et al. 2007; Webster et al. 2013).

This high rate of movement is likely part of a life history strategy to maximize survival and thus reproductive potential. Results from this and previous studies do not provide definitive reasons why the life history of Alaska sablefish incorporates these high movement probabilities, but other studies suggest that a number of possibilities exist. Essentially, sablefish may be (i) optimizing foraging, (ii) performing spawning migrations, and (or) (iii) reacting to competitive release or predator avoidance.

Sablefish may be moving in response to prevailing environmental conditions such as temperature or salinity gradients or other oceanographic features (Humston et al. 2004) to optimize foraging. Future studies could compare regional oceanographic indices

with time-varying movement probabilities by area and attempt to incorporate predator and prey abundance and abundance of competitor species as covariates.

The large-scale movements could also be a function of a spawning migration (Ichinokawa et al. 2008). Our annually estimated movement patterns indicated that at high levels of spawning biomass, sablefish are more likely to be retained in an area than to move. This is an unexpected result, perhaps suggesting high spawning biomass is a result of previous ecological success from movement. Since the HF study, the federally assessed sablefish population off Alaska has changed considerably — it has declined 53% since its last peak in 1986 (Hanselman et al. 2011). Since this decline, the population has remained moderately low, and its somatic growth rate has increased (Echave et al. 2012), possibly leading to the ability to move farther or faster.

Many species of fish exhibit movement throughout their life history. But for a demersal species, sablefish move frequently and have total movement ranges that are not easily explained by life history processes like spawning. Large movement ranges must allow sablefish to exploit varying prey, habitat, and bottom topography at different times during their lives, because these variables change immensely from BC to the BS. Small-sized sablefish moved the most during periods of low recruitment, suggesting that during low recruitment years, locating optimum prey was challenging, resulting in higher movement.

While interest in conventional tagging may be waning, sablefish are among several species such as tuna with large and growing tag databases that have great potential for teasing out and testing ecological movement hypotheses. In addition, newer technologies are being employed for sablefish, such as electronic archival tags and satellite pop-up tags, that provide more detailed movement data for individuals and may help locate spawning locations. As these data continue to accumulate, new insights will be gained by synthesizing these sources into one modelling framework (e.g., Jonsen et al. 2005; Nielsen 2004; Eveson et al. 2012).

Implications for fisheries management

Mark-recapture data are a valuable independent data set that can be used in concert with a statistical age-structured model or as a way to validate results from these models. This study supported that the estimates of mortality from the federal sablefish stock assessment are likely of the correct magnitude. Accounting for movement in stock assessment is a critical component for accurately depicting population dynamics. These updated results confirm previous studies that showed that Alaska sablefish in US federal waters, for the purpose of stock assessment, are likely part of the same stock because of their high mixing rates. However, without data that explicitly identifies where sablefish spawn, the stock structure cannot be determined with tag-recapture data alone. Southeast Alaska inside state waters (CH and CL) and BC appear to have less rapid exchange with US offshore waters. These rates of exchange are important to consider when choosing stock assessment methods and their inherent assumptions about population closure. As in HF, the release of tagged fish in BC was not incorporated within our analysis, so the amount of exchange between Alaska and BC remains uncertain. Cox and Kronlund (2008) conducted management strategy evaluations for BC sablefish that assumed no migration and admit that movement in and out of BC waters is a large uncertainty in the analysis that could be improved. To fully test a one-stock hypothesis among these areas, both detailed data on where spawning actually occurs and a spatially explicit stock assessment model that incorporates the BC tagging data would be necessary.

Considering how to incorporate ecosystem properties within the current stock assessment and management paradigm has become a primary goal in fisheries (Link and Browman 2014). It is likely that the movements shown in this study are partly caused by unmodelled ecosystem processes. Recent stock assessment ap-

plications have mainly considered recruitment to be the primary variable to attempt to predict with environmental covariates (Schirripa and Colbert 2006). However, these relationships once discovered and applied in a stock assessment are contentious and tend to dissipate over time (e.g., Stewart et al. 2011). Relating annual fish movement to changes in environmental conditions could also be tested directly in the sablefish stock assessment model and may be easier to link changes in movement to biological mechanisms. These relationships could potentially improve harvest forecasts, which could aid management and stakeholder planning (King et al. 2001; Shotwell et al. 2014).

The current apportionment strategy for catch among areas in US federal waters is based on incorporating results from the HF movement analysis into a simulation analysis testing different apportionment schemes (Heifetz et al. 1997). Their study concluded that under such high mixing rates, the population would be resilient to different area apportionments if fishing mortality remained low. Included in their study was evaluation of an apportionment strategy that relied on an equilibrium distribution of biomass based on movement probabilities instead of current biomass distribution. However, they did not recommend this strategy because they considered the HF movement estimates to be uncertain and possibly time-varying. In addition, their scenarios only included those that considered recruitment being equally distributed or more productive in the east than in the west. Heifetz et al. (1997) was limited in that it did not test different potential management objectives. Subsequently, a modelling framework was presented by Heifetz and Quinn (1998) that examined the dynamics of migratory fish populations and applied it to Alaska sablefish. Their study used a regional per-recruit analysis to show that fishing with a constant rate across the pooled population could detrimentally affect individual regions in terms of spawning potential when movement is occurring. Since our movement results showed differences from HF, apportionment strategies considered in Heifetz et al. (1997) and Heifetz and Quinn (1998) and alternative strategies and movement scenarios should be evaluated.

Any change to the apportionment strategy is of particular consequence for participants in the sablefish fishery, because IFQs are assigned to specific management areas. Our study should be useful in providing refined movement data for simulations and management strategy evaluations to test optimal harvest policies for Alaska sablefish (e.g., Cox and Kronlund 2008) and assess retrospective performance of the current apportionment strategy. As part of new evaluations, the tagging data should be tested directly inside the federal sablefish stock assessment model (Quinn et al. 1990; Goethel et al. 2011; Eveson et al. 2012). In addition to strengthening the connection with stock assessment results, integrating the tag-recovery data into the model should increase the precision of parameters such as mortality and selectivity. Since these data are independent of the catch-at-age data used in the assessment, they will also assist in quantifying the absolute amount of interchange among areas (Maunder 1998). This integration should enable estimation of regional recruitment strengths, help assure that regional estimates of abundance are consistent with the movement dynamics of the population, and reveal dynamic processes that would otherwise be obscured (Heifetz and Quinn 1998).

The federal tagging program is expected to continue indefinitely, as it is a fundamental part of the Alaska Fisheries Science Center longline survey sampling strategy. While these data have been only used on a limited basis for management purposes, we expect that will change as the data set continues to grow. Spatially explicit modelling of the sablefish stock is an important research goal for the federal stock assessment (Hanselman et al. 2011) and will rely on continued collection of high-quality tagging data. The state of Alaska uses their tagging data directly to estimate abundance for setting quotas, so tagging is expected to continue in southeast Alaska as well. Improved computational power as well

as integration with new tagging technologies currently being deployed should provide deeper insights into sablefish population dynamics and improve stock assessment and management. In summary, fully exploring and utilizing this large mark-recapture data set should improve future sustainable management of sablefish populations.

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