

Modeling spiny dogfish
population dynamics in
the Northeast Pacific

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Abstract

Modeling spiny dogfish population dynamics in the Northeast Pacific

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Spiny dogfish (*Squalus acanthias*) in the NE pacific are a long-lived, late-maturing species that appear to be particularly vulnerable to fishery impacts. Theoretical impacts of fishing are compared using the reproductive value removed by the fishery. This methodology is applied to both the short-lived Australian sharpnose shark (*Rhizoprionodon taylori*) and the long-lived spiny dogfish and found to be valuable in revealing impacts and trade-offs. A new theorem in mathematical demography is presented.

Data from two historical tagging programs for spiny dogfish in the NE Pacific (1940s and 1970s) are analyzed to obtain descriptions of movement. Similar patterns were present in both time periods, with coastal dogfish moving more than those in inside waters of Puget Sound and Strait of Georgia. Data from both time periods also indicated seasonal movement in coastal waters. A demographic analysis of spiny dogfish compared growth, maturity, and fecundity using samples from the 1940s and 2000s. This interval includes a brief but intense commercial fishery for dogfish livers and a rise in ocean temperatures in the NE Pacific of almost 1 °C. All demographic comparisons showed significant changes, with growth rate and fecundity increasing,

and age and length at maturity decreasing over the 60 year time period. Comparison with published values from intermediate years suggests that the timing of these changes make them more likely the result of fishing impacts than increasing water temperatures.

The historical tagging data and the estimated demographic parameters are integrated with multiple abundance indices and compositions of length and age into a metapopulation model for spiny dogfish in the NE Pacific. The modeled population is structured by age, sex, and spatial area, and removals are divided into two gear types. The model outputs include estimates of movement rates, changes in biomass over time, and selectivity. Biomass estimates show a wide range of possible scenarios for the combination of areas in the NE Pacific, including depletion to below 30% of the 1935 by 2006 or substantially recovered from the 1940s fishery by that time, depending on the assumptions made. The inconclusive patterns in the data and the sensitivity of the results to a variety of assumptions indicating the need for more data collection and precautionary management.

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DEDICATION

to my dear Calin,
and to the mighty dogfish

Chapter 1

INTRODUCTION

1.1 *Background*

The end of the 20th and beginning of the 21st centuries have been characterized by a concern for the conservation of sharks. Data required for stock assessments for sharks are sparse because their generally low commercial value has made them more common as bycatch than the target of directed fisheries. In some cases, data is collected, but examination of these data has not been a research priority until recently (Aires-da-Silva, 2008). Yet the life history of many elasmobranch species suggested that they would be vulnerable to fishing impacts (Hoenig and Gruber, 1990), and demographic models predict that population growth rates would be low (Smith et al., 1998; Cortés, 2002). Papers which did examine catch per unit effort (CPUE) data sometimes suggested steep declines in abundance of many sharks along with other large predatory fish (Myers and Worm, 2003; Baum et al., 2003). The severity of these declines has been debated (Burgess et al., 2005), but there is general agreement in the scientific community that shark conservation should be a priority, with improved management and a better scientific basis for future regulations (Musick et al., 2000a; Burgess et al., 2005).

These concerns have led the International Union for the Conservation of Nature and Natural Resources to classify many shark species as threatened (IUCN, 2007), and for the Convention on International Trade of Endangered Species to restrict trade in some sharks, including the Basking shark, *Cetorhinus maximus*; white shark, *Car-
charodon carcharias*; whale shark (*Rhincodon typus*, and sawfishes, *Pristidae spp.* (CITES, 2008). A variety of national and international agreements have been devel-

oped, including a U.S. National Plan of Action for the Conservation and Management of Sharks (NMFS, 2001) and an International Plan of Action for the Conservation and Management of Sharks (FAO, 1998). However, implementation of such plans presents a challenge because few quantitative estimates of the abundance or productivity of shark populations are available, making estimation of sustainable mortality difficult.

The spiny dogfish (*Squalus acanthias*) is the latest maturing and longest lived of all elasmobranchs and is estimated to be one of the least productive elasmobranch species (Smith et al., 1998; Cortés, 2002). In spite of their slow rates of population growth, dogfish may be the most abundant coastal shark, with a worldwide distribution in temperate waters. Nevertheless, the low productivity and high historic abundance in some areas is puzzling. The resilience of spiny dogfish was tested in the NW Atlantic in the 1990s, when dogfish landings increased substantially (Rago et al., 1998) at a time when cod fisheries were facing widespread closures (Hutchings and Myers, 1994). In 1998 the National Marine Fisheries Service (NMFS) declared spiny dogfish overfished in U.S. Atlantic waters. A contentious rebuilding plan has been in place since that time (Glenn, 2003; Rago and Sosebee, 2008; Fordham, 2008). Earlier declines in European waters led to fishery closures and the listing of NE Atlantic spiny dogfish as critically endangered (IUCN, 2007).

In the NE Pacific, the status of dogfish populations is less well understood. After millenia of subsistence use, commercial fisheries began operating in the Pacific coasts of the U.S. and Canada in the 1870s (Ketchen, 1986). Removals generally stayed below 10,000 mt per year until a strong demand for vitamin A from dogfish livers led to a rapid increase in catch from 1940 to 1944 with an estimated peak of more than 50,000 mt in 1944. (Ketchen, 1986). The subsequent decline in landings was as swift as the increase, and directed dogfish catch has mostly remained below 10,000 mt per year since 1950. The impact of this brief pulse of intense fishing and any subsequent changes in abundance of spiny dogfish in the NE Pacific are difficult to estimate. The only index of abundance from the time of the liver fishery was a brief time series in

Northern British Columbia (Barraclough, 1948). Little directed dogfish fishing took place from 1950 to the mid-1970s, so no catch-rate time series data exist to estimate either rebuilding or further declines to have occurred during the intervening 25 years.

1.2 Management measures in the NE Pacific

New harvest restrictions for dogfish have been implemented in NE Pacific in the last few years. The Washington Department of Fish and Wildlife (WDFW) imposed summer closures for dogfish in state waters in 2003 (Tribuzio, 2004). NMFS imposed limits in U.S. west coast waters by emergency rule in 2005 after a fishing company expressed interest in using a freezer-longliner vessel in the open access coastal dogfish fishery, which would have been the first time a vessel of this size would have been used in this fishery (NMFS, 2005). In 2006, NMFS imposed trip limits for U.S. west coast waters which varied between 45 mt and 91 mt per two months for all gears (NMFS, 2006). Rockfish conservation areas that were imposed in U.S. West Coast waters in 2002 have also limited directed dogfish fisheries and bycatch (NMFS, 2006). None of the regulations for U.S. waters of the NE Pacific are based on estimates of the productivity of the population, but are intended to limit expansion of the fishery until a better understanding of the population dynamics is available.

In U.S. waters off Alaska, there has been no historic directed dogfish fishery (Conrath and Foy, 2008). Dogfish are currently managed in aggregate as part of the “Other Species” complex in the Gulf of Alaska and the Bering Sea/Aleutian Islands areas, and recommended limits have been based on average incidental catch over the years 1997–2005 (Courtney et al., 2006). A perception that dogfish have been increasing in numbers in Alaskan waters has led to an increase in the allowable landings of dogfish bycatch in some fisheries to 35% (Alaska Department of Fish & Game, 2003; Courtney et al., 2006). A directed dogfish fishery was allowed under a commissioner’s permit in the Cook Inlet area, but no permit requests were made (Alaska Department of Fish & Game, 2006). Current research on dogfish in Alaska (Rice et al., 2008; Tribuzio,

2009) may be incorporated into future management measures.

Canada has had annual catch limits based on the population dynamics model of Wood et al. (1979) which have been in place since 1980. These limits, of approximately 3,000 mt limit for the Strait of Georgia and 12,000 mt for coastal British Columbia, have never been reached (King and McFarlane, 2008; G.A. McFarlane, pers. comm.). The parameters used in the population dynamics model included estimates of fast growth and early maturity compared to estimates that have been made since the process of ageing dogfish dorsal spines was revised and validated (McFarlane et al., 1987). Therefore, the productivity of the species was likely overestimated so the catch limits in Canadian waters of the NE Pacific may need revision.

1.3 Research in the NE Pacific

Important research on dogfish in the NE Pacific was conducted by WDFW at the time of the large liver fishery (Bonham et al., 1949; Holland, 1957). The Department of Fisheries and Oceans, Canada (DFO) Pacific Biological Station has a long history of dogfish research Ketchen (1972); Wood et al. (1979); McFarlane et al. (1987); McFarlane and King (2003). The University of Washington (UW) Shark Research Lab has also produced a number of recent dogfish-related theses (Tribuzio, 2004; Menon, 2004; Vega, 2006; Rice, 2007). In 2005, representatives from these three groups (WDFW, DFO and UW) jointly organized the “First International Symposium on the Management and Biology of Dogfish Sharks” to further focus research attention on this species. Despite this long history and recent activity, many questions remain about the dynamics of spiny dogfish in the NE Pacific.

1.4 Description of dissertation chapters

The motivation for this thesis is the need for better understanding of the population dynamics and fishing impacts on shark populations in general, and spiny dogfish in the NE Pacific specifically. It is not intended as an assessment of this stock’s status.

However, the data, methods, and results may be useful for such an assessment in the future.

Chapter 2 includes the development of a new theoretical tool to measure and compare the impacts of fishing. This is based on the amount of reproductive value removed by the fishery. It facilitates comparison of the relative impacts of different selectivity patterns or targeting methods based on the expected future contributions of different ages to the growth of the population. This methodology is applied to both the short-lived Australian sharpnose shark (*Rhizoprionodon taylori*) and the long-lived spiny dogfish and was found to be useful in both cases.

Chapter 3 is an analysis of two historical tagging programs for spiny dogfish in Puget Sound and adjacent coastal waters, one from the 1940s at the time of high landings and one from the 1970s when no directed dogfish fishery existed. The data from both tagging programs were recently made available, allowing a comparison of the results of the two programs on a common basis. Movement of tagged dogfish is considered among a set of geographic basins within Puget Sound, which are more biologically meaningful than the statistical areas used in the initial reports. Qualitative descriptions of movement among these areas made to guide the formulation of a quantitative model developed in the final chapter. The tagging data are also examined for evidence of seasonal movement of dogfish in coastal waters.

Chapter 4 is a demographic comparison of spiny dogfish using samples collected in the 1940s during the period of intense fishing and samples collected 60 years later as part of recent research. This 60 year interval has been a time of large changes in dogfish catch, raising questions about what factors may impact demography for a long-lived shark. The demographic comparison included on dorsal spines for ageing from the 1942–43. dogfish that had been held in the University of Washington Fish Collection with records of fecundity, maturity, and length measurements from the sampled dogfish. Age estimates and associated data from a sampling program conducted in 2002–03 were also available. All dorsal spines were aged using updated

methodology, making the 1940s and 2000s data comparable. This comparison allowed an estimation of demographic changes that took place over this 60 year period, which included warming ocean temperatures as well as differential fishing pressure on spiny dogfish.

Chapter 5 integrates the tagging data described in Chapter 3 and the demographic parameters estimated in Chapter 4 with multiple indices of abundance, length and age compositions, and data from Canadian tagging studies, into a metapopulation model for spiny dogfish in the NE Pacific. The modeled population is structured by age, sex, and spatial area, and removals are divided into two gear types with separate selectivities. This model is intended as an update to the work of Wood et al. (1979) to better understand historical changes in spiny dogfish abundance beginning with the 1940s fishery, as well as estimates of the current status of the population relative to previous levels.

As a whole, this thesis provides both mathematical tools for examining impacts of fishing on shark populations and new estimates of the dynamics and historic changes in a specific population, the spiny dogfish in the NE Pacific. It utilizes a range of data on movement, abundance, population structure and removals, which have never been brought together before. The analysis of these data offers new answers and raises new questions about the population dynamics of spiny dogfish in the NE Pacific.

Chapter 2

CONSERVATION AND MANAGEMENT OF EXPLOITED SHARK POPULATIONS BASED ON REPRODUCTIVE VALUE

2.1 *Introduction*

It is generally agreed that shark populations are particularly vulnerable to overexploitation due to the limited number of offspring they bear and the long periods of time before they are sexually mature (Musick, 1999). Merging this line of thought with the standard methodologies applied in fisheries stock assessment leads to a number of inconsistencies. Methods of analysis based on the use of compensatory models such as the Schaefer stock-production model (McAllister et al., 2001) assume that almost all of the life history parameters fundamental to modeling the dynamics can be represented by the two-parameter logistic model. In contrast, age-structured models (Cailliet, 1992; Cortés, 1998; Punt and Walker, 1998) allow the explicit use of the same life history parameters central to understanding why shark populations are easily overexploited. This paper builds on the use of life history parameters by the simultaneous use of the reproductive value of a given species, which is associated with Leslie matrix models (Caswell, 2001), and the application of the mathematical methodology of the Beverton and Holt (1957) yield-per-recruit (Y/R) model formulated as a function of reproductive potential removed.

This research was motivated by earlier work on multi-mesh size artisanal fisheries where juveniles of larger species were captured in mesh sizes designed for smaller species (Lai et al., 1993; Gallucci et al., 1996). In the present case, our initial interest was in sharks that use tropical bays as nurseries (V. Gallucci, personal observation),

where artisanal fishermen harvested prereproductive sizes as part of their fishing operation. Even if not targeted, sharks were a by-catch item in drift gillnet and seine gear and were either marketed or simply discarded. These harvests of juvenile sharks, which have been noted in other artisanal fisheries (Castillo-Géniz et al., 1998; Kroese and Sauer, 1998), led to research into new methods for estimating the impacts of the capture of prereproductive animals in a more generalized context. The traditional approach in stock assessment would attempt to estimate a biological reference point (Gabriel and Mace, 1999), which would be an age- or size-specific rate of instantaneous fishing mortality, such as F_{max} , $F_{0.1}$, or F_{MSY} . Occasionally these reference points are based on the spawning stock biomass of the population. The alternative approach we considered was to use reproductive value and the fraction of the reproductive potential of the population removed by harvesting any subset of the ages. This led to the derivation of a new theorem, presented herein.

Reproductive value (RV) has its roots with Fisher (1930) as a part of human demographic analysis and as a part of the ecological literature with MacArthur (1960) who considered fisheries harvests as a special case of optimal foraging theory. He phrased the predator's problem in two ways: when it knows, and does not know, the age of the prey. RV was used in the first case, which also applies to our interest as a fishery typically designs its capture gear to correspond to an initial age of capture. Our work diverges from MacArthur's, but his initial results are a basis for our approach. RV, which can be interpreted as the relative contribution of individuals at each age to the long-term growth of the population, has become a part of demographic analyses like those frequently employed for shark populations (Cailliet, 1992; Cortés, 1999; Frisk et al., 2002). Reproductive potential (RP) extends RV to the population level. RP is defined here as the sum of RVs of all individuals in a population. This measure, also called "total reproductive value" (Leaman, 1987, 1991), was also developed by Fisher (1930) and has been considered as an alternative to spawning stock biomass (Leaman, 1987, 1991; Katsukawa et al., 2002). Leaman (1987, 1991) concludes that

RP should be incorporated into monitoring programs for decision-making. Taylor and Gallucci (2005) found that the connection between RP and biomass of a species was an indicator of the degree to which surplus production models could fit biomass trends for that species.

Representing the contribution of a shark of a given age to the whole population by its RV allows the quantification of harvest strategies in terms of the removals of these contributions. This approach, used along with Y/R analysis for different exploitation strategies, allows the exploration of the long-term consequences of these harvest policies. By extension, this allows investigation of the balancing of yield, selection of juveniles, and harvest sustainability. Deterministic analyses of the type described above do not provide information on the influence of variability in life history parameters on the results, and so Monte Carlo simulations are used in a risk analysis to supplement deterministic projections.

In this paper, the comparison between short- and long-lived species allows a demonstration of the utility of RV-based measures. The above methodologies are applied to a number of practical situations representing different exploitation scenarios for sharks of two basic types: those that grow to great ages and those that do not. These short and long-lived types are represented here by the Australian sharpnose shark (*Rhizoprionodon taylori*) and the spiny dogfish (*Squalus acanthias*), respectively. These methodologies allow quantification of the consequences of harvesting prereproductive sharks from nurseries and facilitate tracking the subsequent population wave across the age structure. This analysis demonstrates the potential value of different management approaches for these two archetypes. The RP framework developed here is a valuable new tool for identifying patterns of harvest impacts across life histories and harvest strategies.

2.2 Methods

2.2.1 Matrix Formulation for harvested populations

Deterministic population dynamics were modeled using age-structured female-only Leslie matrix models (definitions of terms are provided in Table 2.1). Parameter values (Table 2.2) were taken from available published information on the Australian sharpnose shark (Simpfendorfer, 1999) and the NE Pacific population of spiny dogfish (Ketchen, 1972, 1975; Saunders and McFarlane, 1993). These species were chosen as representative of short- and long-lived species, respectively.

Natural mortality rates for the two species were assumed constant over all ages with $M = 0.561$ for the sharpnose shark (Simpfendorfer, 1999). The method of Hoenig (1983) was applied for the dogfish assuming a maximum age of 80 years (McFarlane and King, 2003) to get a value of $M = 0.0515$. The annual survivorship terms in the sub-diagonal of the Leslie matrix were calculated as $s_x = e^{-M}$.

Length was assumed to follow the von Bertalanffy growth function (Gallucci and Quinn, 1979) and average numbers of offspring per mature female was a linear function of length for both species (Table 2.2). The census for abundance was assumed to be postbreeding (Caswell, 2001) making newborn pups the first age class (age 0). The fecundity values thus include the probability of the mother surviving to pup at the end of the year, making possible the modeling of harvests on young-of-the-year pups. A sex ratio of 1:1 was assumed for both species. All sharpnose sharks were assumed to mature at age 1 and to pup every year, whereas mature dogfish were assumed to pup every 2 years. The maturity schedule for dogfish was assumed to be a logistic function of age with 50% maturity at 35.5 years (Saunders and McFarlane, 1993), so the fraction mature at age x was $(1 + e^{-0.4(x-35.5)})^{-1}$. The average number of female pups per female of age x , m_x , is the product of the function for the number of pups per mature female (Table 2.2), the maturity schedule, and the sex ratio. The fecundity terms which make up the first row of the Leslie matrix were calculated as $f_x = s_x m_x$.

Harvests were incorporated into the model as a diagonal matrix \mathbf{H} following Lefkovitch (1967) and Caswell (2001). The elements of the harvest matrix, h_x , represent the fraction of individuals of age x surviving the harvest. Thus, the usual Leslie age-structured model (Caswell, 2001),

$$\mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t, \quad (2.1)$$

where \mathbf{M} is the projection matrix and \mathbf{N}_t is the vector of numbers at each age in year t , is modified to incorporate age specific removals of individuals in a harvest,

$$\mathbf{N}_{t+1} = \mathbf{M}\mathbf{H}\mathbf{N}_t. \quad (2.2)$$

The augmented projection matrix \mathbf{MH} has the same form as the Leslie matrix but fecundity and survival of the harvested ages are reduced. The dominant eigenvalue of \mathbf{M} , λ , and, the dominant eigenvalue of \mathbf{MH} , λ' , give the asymptotic annual change in population size with and without a given harvest. Primed ('') variables are associated with a harvested population. Thus, the unharvested case (2.1) is a special case of (2.2).

Two general classes of harvest strategy were evaluated: juvenile and adult. The selection of a younger portion of the population is intended to represent harvests on the juvenile population present in nursery areas or the only sizes available to artisanal fishers. The selection of the older portion of the population matches the more common pattern of minimum size limits or the use of selective gear in commercial fisheries. For juvenile harvests the age of entry into the fishery t_c was set to 0, and for adult harvests the maximum age in the fishery t_ε was set to the maximum age for the species, t_∞ (Figure 2.1). All individuals between t_c and t_ε are considered fully recruited into the fishery.

To reduce the set of harvests considered, the fraction harvested annually from all

selected ages was equal. Thus, the harvest matrix \mathbf{H} has diagonal elements $h_i = h$ for $t_c \leq i \leq t_\varepsilon$ and $h_i = 1$ otherwise. The harvest rate, $1 - h$, associated with a stationary population size, was found by iteratively searching for the constant survival fraction h , which made $\lambda' = 1$. The term “stationary harvest” will be used for all harvests that make $\lambda' = 1$. The right and left eigenvectors corresponding to these eigenvalues give the reproductive value and the stable age distribution, respectively.

2.2.2 Reproductive value and stable age distribution

The RV vector \mathbf{v} was calculated as the right eigenvector of the projection matrix \mathbf{M} , satisfying

$$\mathbf{v}^T \mathbf{M} = \lambda \mathbf{v}^T, \quad (2.3)$$

where \mathbf{v}^T is the transpose of the column vector \mathbf{v} . The RV of the harvested population \mathbf{v}' is the right eigenvector of \mathbf{MH} , satisfying

$$\mathbf{v}'^T \mathbf{MH} = \lambda' \mathbf{v}'^T. \quad (2.4)$$

The resulting elements of \mathbf{v} , which are defined by (2.4) only up to a scalar multiplier, are proportional to those given by the discrete form of Fisher’s (1930) formula,

$$v_x = \sum_{i \geq x} \lambda^{-(i-x)} f_i \frac{l_i}{l_x}, \quad (2.5)$$

where v_x is the RV at age x , and $l_x = \prod_{i=0}^{x-1} s_x$ is the probability of survival from birth to age x . The elements of \mathbf{v}' can be calculated using (2.5) by substituting λ' , f'_x and l'_x derived from the augmented projection matrix \mathbf{MH} .

Evaluating (2.5) at $x = 0$ yields a function similar to the Euler-Lotka equation (Lotka, 1907). This similarity can be used to show that computing v_x using (2.5) is equivalent to scaling the \mathbf{v} so that $v_0 = \lambda$. Correspondingly, harvests that lead to a

stationary population size have $v'_0 = \lambda' = 1$. Under such stationary harvests (2.5) is identical to the equation for life-time egg production of an individual of age x (Quinn and Deriso, 1999),

$$R_x = \sum_{i \geq x} f_i \frac{l_i}{l_x}, \quad (2.6)$$

so that the net reproductive rate R_0 will equal the reproductive value at age 0: $R_0 = v'_0 = 1$. The scaling of the eigenvectors to make $v_0 = \lambda$ and $v'_0 = \lambda'$ has been used when comparing v_0 and v'_0 .

The stable age distribution (SAD) vectors of unharvested and harvested populations, \mathbf{w} and \mathbf{w}' , are the left eigenvectors corresponding to λ and λ' (Caswell, 2001), respectively, and satisfy,

$$\mathbf{M}\mathbf{w} = \lambda\mathbf{w}, \quad (2.7)$$

and

$$\mathbf{M}\mathbf{H}\mathbf{w}' = \lambda'\mathbf{w}'. \quad (2.8)$$

2.2.3 Reproductive potential

RP, a scalar value, is defined here as the sum of the RVs of all individuals in the population, whether at a SAD or not. It is computed following Leslie (1948) as the vector inner product,

$$P_t = \mathbf{v}^T \mathbf{N}_t = \sum_x v_x N_{x,t}, \quad (2.9)$$

where $N_{x,t}$ is the element of the population vector \mathbf{N}_t corresponding to age x . RP is a measure of the potential for the population to grow in the absence of a harvest. Thus, \mathbf{v} rather than \mathbf{v}' is used in (2.9).

The RP of the SAD vector \mathbf{w}' is given by

$$P = \mathbf{v}^T \mathbf{w}', \quad (2.10)$$

and the RP of the portion of this population which is removed by the harvest in each

year is

$$P_h = \mathbf{v}^T \mathbf{H}^* \mathbf{w}', \quad (2.11)$$

where $\mathbf{H}^* = \mathbf{I} - \mathbf{H}$, with \mathbf{I} the identity matrix, is the diagonal matrix containing the fraction of each age removed by the harvest. The ratio of these two quantities gives the fraction of the RP removed by a stationary harvest at SAD,

$$\Phi = P_h/P. \quad (2.12)$$

2.2.4 Yield per recruit

Yield per recruit (Y/R) was calculated for a range of harvest strategies as

$$Y/R = \sum_{x=0}^{t_\infty} (1 - h_x) l'_x W_x, \quad (2.13)$$

where $(1 - h_x)$ is the probability of being harvested at age x , $l'_x = \prod_{i=0}^{x-1} s_i h_i$ is the fraction of the cohort surviving to age x under the harvest, and W_x is the weight at age x given by the von Bertalanffy growth equation. The fraction surviving the harvest was also converted to a rate $F = -\ln(h_x)$ which was used in the Beverton-Holt yield-per-recruit model Beverton and Holt (1957). A comparison between (2.13) and the Beverton-Holt model found similar results, with small differences resulting from the alternative treatments of growth and mortality as discrete or continuous processes.

Y/R was calculated for adult harvests over a 2-dimensional grid of the fraction of RP removed by the harvest each year (Φ) vs. age of entry (t_c) values with the maximum age in the fishery (t_ε) fixed at the maximum age of the species (t_∞). The parameters in the grid for juvenile harvests were Φ and t_ε , with $t_c = 0$. The value of $h_x = h$ for a given range of ages $t_c \leq x \leq t_\varepsilon$ which corresponded to Φ was found using an iterative search.

2.2.5 Stochastic projections and risk

The augmented projection matrix \mathbf{MH} is a deterministic model of population dynamics under given fecundity and survival parameters, along with harvests of selected ages. The risk of depletion per harvest strategy was evaluated by including stochasticity in the survival, fecundity, and harvest parameters. Fecundity was assumed to have a lognormal distribution around a mean, f_x . The instantaneous rates $M = -\ln(s_x)$, and $F = -\ln(h)$, were also assumed lognormal. Use of the lognormal distribution for the instantaneous rates is convenient because the resulting fractions for survival and harvest will be between 0 and 1. The stochastic elements of the projection and harvest matrices for age x in year t were calculated as, $\tilde{f}_{x,t} = f_x \varepsilon_t$, $\tilde{s}_{x,t} = e^{-M\delta_t}$, and $\tilde{h}_t = e^{-F\gamma_t}$, where ε_t , δ_t , and γ_t are all lognormal random variables with mean = 1 and CV = 0.2. The same random variables were applied to all ages under the assumption that environmental effects will have similar impacts on all ages. Conditions which increased fecundity were assumed to decrease natural mortality, on average, so ε_t and δ_t were negatively correlated, with $\rho = -0.5$.

A harvest strategy is defined by specification of t_c , t_ε , and either the fraction of the total RP removed in each year, Φ , or the fraction of the total biomass removed each year, β . The harvest survival parameter h corresponding to Φ or β was calculated in each year as

$$h = \begin{cases} 1 - \Phi \frac{\sum_{x=0}^{t_\varepsilon} N_{x,t} v_x}{\sum_{x=t_c}^{t_\varepsilon} N_{x,t} v_x} & \text{when } \Phi \text{ is specified,} \\ 1 - \beta \frac{\sum_{x=0}^{t_\varepsilon} N_{x,t} W_x}{\sum_{x=t_c}^{t_\varepsilon} N_{x,t} W_x} & \text{when } \beta \text{ is specified.} \end{cases} \quad (2.14)$$

For each harvest strategy, 1000 stochastic projections were made in which an initial population at SAD, with biomass B_0 , was projected forward 50 years to determine a final biomass B_{50} . The probability that a projection ended below 20% of the initial biomass, $P(B_{50} < 0.2B_0)$, was used as an estimate of the risk of depletion associated

with each harvest strategy.

2.3 Results

2.3.1 Changes in reproductive value

Changes in RV differed under juvenile and adult harvests, and between species (Figure 2.3). These RVs may be interpreted as the relative contribution of individuals at each age to the long-term growth of the population under different harvest conditions. The bold lines refer to the RVs of the unharvested population of each species. All harvests are designed to maintain a stationary population size by constraining the removals of the selected ages so that $\lambda' = 1$. Under these harvests, the population may exhibit damped oscillations as it approaches the SAD associated with the projection matrix \mathbf{MH} , but at that SAD the population size will be constant, regardless of the initial age distribution and population size.

The changes in RV under harvests on different segments of the population were unexpected: harvests which target juveniles can increase RV above the level corresponding to no harvest. Although unexpected, an explanation is available. In all cases, harvests reduce survival of the harvested ages. Any harvest will reduce λ' below λ , but when only juveniles are selected into the fishery, survival and fecundity of adults are unaffected. Thus, if λ' , f'_x and l'_x are substituted into the summation equation for RV (2.5), the negative exponent on λ' will result in an increase in RV at all ages older than those selected into the fishery because the ratio l'_i/l'_x will be unaffected by the harvest on younger ages. The RV of some juvenile ages selected into the fishery decreases because the impact of the harvest on survival and fecundity is more influential than the changes in λ' . In general, the adult ages which are unaffected by a harvest on juveniles and are already producing offspring are relatively more valuable to the population than the juveniles being harvested.

Harvests on adults, in contrast, reduce the RV of all ages in the population. The

eigenvalue λ' is again reduced, but unlike harvests on juveniles, harvests which reduce the survival and fecundity of adults will impact the RV of all ages. Larger reductions occurred at the ages selected into the harvest, but because RV is a sum over all expected future offspring, the impact of a harvest on the last age in the population will reduce RV of all prior ages as well. The harvests associated with the greatest reductions in RV for both species considered were those targeting the smallest number of adult ages. The harvest rates associated with these harvest strategies (Tables 2.3 and 2.4) are the highest among the strategies considered under the constraint $\lambda' = 1$. Thus, the low RV associated with harvests on the oldest segment of the population may be interpreted as a measure of the high harvest rates which may be applied to the oldest fish while maintaining a stationary population size.

2.3.2 Population growth

Tables 2.3 and 2.4 give details of the harvests considered under the constraint that they will lead to a stationary population size ($\lambda' = 1$). Harvests on adults may target more ages or remove a greater fraction $(1 - h_x)$ of each targeted age while maintaining a stationary population size. The differences in sustainable harvest rates between strategies are an indication of the interdependence between selectivity and sustainable harvests. The fraction of a population's biomass that may be sustainably removed each year is a function of the ages selected by the harvest, where a greater fraction of the biomass is sustainably removed via harvests of adult ages of the two species. Unlike biomass, the fraction of a population's reproductive potential Φ which may be sustainably removed each year is independent of the ages selected by the fishery. This is demonstrated in the following theorem and lemma.

Theorem: (Taylor, Gallucci) The asymptotic annual growth of a harvested population λ' decreases linearly with the fraction of the reproductive potential harvested Φ

annually,

$$\lambda' = \lambda(1 - \Phi). \quad (2.15)$$

Proof:

$$\begin{aligned}
 \lambda' &= \lambda' \mathbf{v}^T \mathbf{w}' / \mathbf{P} && \text{multiplying } \lambda' \text{ by a fraction equal to 1 (2.10)} \\
 &= \mathbf{v}^T \lambda' \mathbf{w}' / \mathbf{P} && \lambda' \text{ is commutative under multiplication with } \mathbf{v}^T \\
 &= \mathbf{v}^T \mathbf{M} \mathbf{H} \mathbf{w}' / \mathbf{P} && \text{substitution using (2.8)} \\
 &= \lambda \mathbf{v}^T \mathbf{H} \mathbf{w}' / \mathbf{P} && \text{substitution using (2.3)} \\
 &= \lambda (\mathbf{v}^T \mathbf{w}' - \mathbf{v}^T \mathbf{H}^* \mathbf{w}') / P && \text{substituting } \mathbf{H}^* = \mathbf{I} - \mathbf{H}, \text{ and distributing} \\
 &= \lambda (P - P_h) / P && \text{definitions of } P \text{ and } P_h \\
 &= \lambda (1 - \Phi) && \text{distributing } 1/P \text{ and substituting } \Phi = P_h / P
 \end{aligned}$$

Lemma: If the fraction of reproductive potential annually removed by the harvest is $(\lambda - 1)/\lambda$ then the population size will be stationary when it reaches SAD.

Proof: Substituting $\Phi = (\lambda - 1)/\lambda$ into (2.15) gives

$$\begin{aligned}
 \lambda' &= \lambda (1 - \Phi) \\
 &= \lambda (1 - (\lambda - 1) / \lambda) \\
 &= 1
 \end{aligned}$$

If the Perron-Frobenius theorem (Caswell, 2001) applies to \mathbf{M} , then under ordinary harvests (no removal of 100% of any age class), it will apply to $\mathbf{M}\mathbf{H}$, and the population will approach a SAD. Having $\lambda' = 1$ will result in a stationary population size when the population reaches SAD. The linear relationship between λ' and Φ is shown in Figure 2.2.

The results of both the theorem and lemma are independent of the ages selected by the harvest. The only effect of the selectivity pattern is that there may be a maximum Φ associated with harvests on adults. The value $\Phi = (\lambda - 1)/\lambda$ which leads to a stationary population size for a given set of demographic parameters will be denoted $\Phi_{\text{stationary}}$. The values corresponding to the two species are $\Phi_{\text{stationary}} = 0.124$ for the sharpnose shark and $\Phi_{\text{stationary}} = 0.031$ for the dogfish. The lower level of removals that can be sustained by the dogfish are characteristic of long-lived elasmobranchs

(Hoenig and Gruber, 1990). Although the increase in population size per generation of dogfish is actually higher, their long generation time results in a very low annual increase in population size ($\lambda = 1.032$). While it is intuitive that sustainable levels of fishing pressure are related to a population's growth rate, this theorem provides a quantitative framework for calculating the fraction of a population's reproductive potential which may be sustainably harvested each year.

The theorem implies that expressing effort in terms of the fraction of RP removed from the population each year is the most accurate indicator of the impact of that harvest on the growth of the population. Because λ' is directly related to Φ , a harvest which removes a greater fraction of the RP annually will have a larger impact on λ' , regardless of the selectivity pattern of the fishery. Two instantaneous rates of fishing mortality can only be compared in this way when they are applied to the same selected age classes. For this reason, fishing effort in the following Y/R calculations was described in terms of the fraction of RP removed annually by the harvest.

2.3.3 Yield Per Recruit

Expressing fishing effort in the Y/R analysis in terms of Φ , the fraction of RP removed from the population each year, makes comparison of Y/R among sustainable harvests easy (Figure 2.4). A vertical line at $\Phi_{stationary} = (\lambda - 1)/\lambda$ indicates those harvests which lead to a stationary population size, as shown in the lemma above. Some levels of removal were not possible for some adult harvests, in which case no Y/R was calculated. If the fraction of the RP contained within cohorts of age t_c and older is less than a given Φ then no harvest on ages t_c and older can remove a fraction of RP equal to Φ . The t_c values for which no Φ above the stationary harvest rate can be removed are very conservative harvest strategies. In these ranges ($t_c \geq 3$ for sharptooth shark and $t_c \geq 40$ for the dogfish) the population will not be depleted under any amount of fishing pressure.

Considering changes in t_c or t_ϵ corresponding to $\Phi_{stationary}$, maximum Y/R from

juvenile harvests occurred when the harvest included all adult ages in addition to juveniles. Maximum Y/R from stationary adult harvests was higher than Y/R from any juvenile harvest. For the sharpnose shark, this maximum occurred when the age of entry into the fishery was as high as possible ($t_c = 3$ in Figure 2.4a). With the dogfish, Y/R for stationary harvests was highest with $t_c = 24$ years (Figure 2.4b). For both species the highest Y/R at sustainable levels of Φ was about 50% higher among adult harvests than among juvenile harvests and about 100% higher among adult harvests than among juvenile harvests that included no adults.

The short-lived sharpnose shark has a high natural mortality rate ($M = 0.561$) that is unlikely to be approached by any fishing mortality rate. Therefore, within the range of Φ considered, an increase in fishing effort applied to any range of harvested ages will increase Y/R because decreases in a cohort due to natural mortality will be faster than increases in weight. The peak Y/R occurs at the maximum possible Φ for the harvests on adults, while for juveniles, the peak Y/R occurs around $\Phi = 0.4$, when the population is declining sharply already. For this species the concern is avoiding recruitment overfishing by removing RP only from older ages which have had more time to reproduce. In contrast, natural mortality for the dogfish and other long-lived sharks is low enough that it may easily be matched or surpassed by fishing mortality. In this case growth overfishing is also a concern. That is, especially for harvests on juveniles, increasing the fraction of RP removed from any range of ages will decrease Y/R through a shift in the mean age of harvested individuals toward the age of entry in the fishery. These younger individuals, which weigh less, would have had a high probability of surviving to an older, heavier age with less fishing pressure. For dogfish, the peak Y/R from juvenile harvests is close to the stationary harvest level. Thus, in addition to indicating the advantage of adult harvests over juvenile harvests for both species, the Y/R analysis shows that for a long-lived species, in addition to decreasing recruitment, the yield per recruit will be adversely impacted by overfishing.

2.3.4 Stochastic Projections and Risk

For both species, the risk of population depletion, defined as the probability that a 50 year stochastic projection will end below 20% of the initial biomass, $P(B_{50} < 0.2B_0)$, was similar for all harvest strategies at any given removal of RP, Φ , (Figs 5a and 5b), but the risk associated with a given removal of biomass, β , was highly dependent on the range of ages harvested (Figs 5c and 5d). For the short-lived sharpnose shark (Figure 2.5a), $P(B_{50} < 0.2B_0)$ rose from less than 0.05 at $\Phi = 0.11$ to greater than 0.95 at $\Phi = 0.16$. For ages 3-7, many projections resulted in a fraction of RP contained in these ages less than Φ , so the risk presented is the result of removing all individuals from these ages in some years. In contrast, when harvests are described in terms of removals of biomass (Figure 2.5c), a harvest of only 5% from age 0 caused all projections to fall below $0.2B_0$, while three times as much biomass could be removed from ages 2-7 or ages 3-7 without causing such depletion in most of the projections.

For dogfish, the transition from low to high risk occurs over a narrower range of Φ (Figure 2.5b). The late age of maturity and long lifespan of dogfish means that stochastic fecundity will impact only one or two generations in the 50-year projections, so the impact of a series of good or bad years on the variability in the projections is reduced. This lower variability in stochastic projections for the longer lived species is also consistent with the results of Goodman (1984). None of the projections for dogfish fell below $0.2B_0$ at $\Phi = 0.05$, but at $\Phi = 0.08$, all projections fell below this level with the exception of strategies that led to removal of 100% of some ages.

When the harvest level on dogfish was based on the fraction of biomass removed from the population (Figure 2.5d), the risk was highly dependent on the range of ages selected by the harvest, as with the sharpnose shark. The risk of population depletion was again highest when harvests targeted only juveniles (ages 0-10, 0-20, and 0-30). The harvest targeting the old ages (ages 40-80) was again the most conservative and

did not lead to any populations below $0.2B_0$, even when all individuals in these ages were harvested. Harvests on age 0 likewise did not lead to depletions, indicating that if a harvest is going to take place on juveniles, then a very narrow slot limit will reduce the risk of depletion.

In this stochastic framework, Φ is the fraction of observed RP removed in each year, rather than the fraction removed at SAD. However, the connection between risk of population depletion and Φ is independent of the ranges of ages selected by the harvest, in contrast to the more complex relationship between risk of depletion and the fraction of biomass removed, further indicates the utility of using Φ as a measure of the impact of a harvest.

2.4 Discussion

RV and RP are applied to the dynamics of harvested shark populations. The argument made here is that the fraction of RP removed from a population is more representative of the impact of harvesting on a population than the traditional instantaneous rate of fishing mortality or other related management tools. This argument is supported by the results above.

MacArthur (1960) discusses RV and removals from a population in the context of optimal predation. He suggests that an optimal predator will remove individuals from the population from those ages which maximize the ratio (value to predator / reproductive value). Working with a continuous time model, he also considered the allowable rate of removals. This work was extended by a large body of literature on optimal harvests (Beddington and Taylor, 1973; Law, 1979; Brooks and Lebreton, 2001). However, the gear selectivity required for optimal harvests as defined in these papers is unrealistic in most fisheries contexts. The optimal harvest in these papers involves targeting at most two age classes. In contrast, we provide no formulae for optimizing harvest, but instead provide tools for exploring the consequences of different harvest strategies. Goodman (1982) reiterated the more generally applicable idea

of MacArthur (1960), that removals from a population should be measured in units of reproductive value lost. Almost a half century after MacArthur, this paper presents new uses of reproductive potential as a measure of fishing effort and a new theorem regarding the connection between the rate of population growth and removals of reproductive potential. It has also been suggested that the proof provides a rigorous foundation for MacArthur's (1960) paper.

The use of RV and RP and their applications comes from the use of the Leslie matrix and its augmented form with a harvest matrix. In our formulation, a harvested population projected with the augmented Leslie matrix will converge to a SAD. Asymptotic stationarity of the harvested population was accomplished by constraining the dominant eigenvalue of the augmented matrix (λ') to 1. With $\lambda' = 1$, populations will converge to a SAD, at which point the population size will be stationary.

The theorem in this paper states that the growth of a population projected by the augmented Leslie matrix is directly linked to the fraction of RP removed from the population, Φ . This holds regardless of the segment of a population that is harvested. A non-zero Φ corresponds to a range of yields, which are associated with a variety of harvest strategies. The reformulation of the Beverton-Holt yield per recruit model as a function of Φ and the age of entry into the fishery, t_c , or the maximum age in a juvenile harvest, t_ε , provides Y/R isolines that will look familiar to a stock assessment scientist. It is easy to compare Y/R for different strategies that lead to stationary harvests as they all correspond to the same value of Φ .

The approach used here shares some properties with elasticity analysis (Caswell, 2001), which has been used extensively in the elasmobranch literature (Heppell et al., 1999; Mollet and Cailliet, 2002; Cortés, 2002). Although mathematically related, RP differs from elasticity in important ways. Both make use of RV to identify the relative vulnerability of a population to impacts on different population segments. However, whereas elasticity is a measure of the Leslie matrix only, RP combines RV from the

Leslie matrix with the numbers-at-age in the population. Therefore, RP can be used to track changes in a population over time (Leaman, 1987, 1991; Katsukawa et al., 2002). Also, although elasticity can provide an approximation to the effect of a given harvest (Caswell, 2001), the theorem in this paper linking population growth directly to the removal of RP allows the use of the fraction of RP removed, Φ , as an alternative measure of fishing effort.

Two other related quantitative approaches to examining fishing impacts are spawning stock biomass per recruit, SSB/R (Gabriel et al., 1989), and spawning potential ratio, SPR (Goodyear, 1993). SSB/R is analogous to reproductive value of age zero, v_x , where x is the age of recruitment. Both are measures of the future productivity of this individual, taking into account survival. SPR, which is a measure of the spawning potential in the presence of a fishery as a fraction of the unfished level, is somewhat analogous to the measure Φ developed here. It is inverted, in that it is a measure of productivity remaining rather than productivity removed. The concepts discussed here, v_x and Φ , differ from SSB/R and SPR in that they account for the rate of change of the population size, λ . This accounting is needed to include the discount that associates different value to near-term and long-term contributions when the population size is changing. It also allows the mathematical simplicity of the matrix algebraic approach and forms the basis for the theorem proved above. The focus on potential removed, which comes from describing harvests in terms of Φ , and the insight that can come from comparing harvests along these lines, may be the most significant difference between the concepts presented here and those which came before.

Any application of this theorem and associated theory must rest upon two different aspects of the real world: density dependent effects and stochastic environments. Density dependence was not considered in this analysis for two reasons. First, the insight found in considering simpler models should provide a platform upon which to build further research as our understanding of density dependence in elasmobranchs (Smith et al., 1998) increases. Second, a population kept at a given size will have

constant survival and recruitment even in density dependent models. Therefore the problem of keeping the population stationary at any particular size in a density dependent model is equivalent to the density independent problem of maintaining a stationary population with the corresponding set of population parameters (Quinn and Szarzi, 1993). That the implications of the theorem also apply outside the deterministic framework is indicated by the results of the risk analysis in which removal of RP was directly linked to the probability of population depletion. The next two sections compare the use of RV and RP.

2.4.1 Reproductive Value

The term reproductive value has connotations of a measure that should be preserved or even maximized. Indeed the equivalence between maximizing fitness (measured by λ) and maximizing RV has been debated in a series of papers on optimal life history strategies (Schaffer, 1974; Yodzis, 1981; Caswell, 1982). All harvests in the density independent model used in this paper reduce the dominant eigenvalue, and thus reduce fitness as it is defined in the optimal life history literature. When a range of ages that includes juveniles is harvested from either species, the RV for some ages increases above the level associated with no harvest. However, when a single age is harvested, the RV of that one age is below the unharvested level, even if the RV of other ages is above. This is a consequence of both the constraint that all harvests result in a stationary population size and the strongly non-linear relationship between reproductive value and the harvest matrix parameters. These results are consistent with Yodzis (1981), that maximizing fitness is equivalent only to RV maximized with respect to the reproductive effort at a given age but not with respect to reproductive effort of all ages. In the results above, decreases in the eigenvalue of the augmented matrix correspond to decreases in the RV of a single harvested age, but not decreases in RV of all ages simultaneously.

The contrast between changes in RV associated with juvenile harvests and those

associated with adult harvests suggests that changes in RV, especially for the older ages, are not good indicators of the effect of a harvest on the potential for growth of a population. Without more information than RV, such as the age distribution of the population, the effect of a harvest cannot be evaluated. Two harvests which are constrained to maintain stationary population sizes may lead to opposite effects on the RV of some ages. It follows that RP, as a sum of the unharvested RV over all individuals in the population has the potential to be a better indicator of the impacts of a harvest, because it includes information about the age distribution.

2.4.2 Reproductive Potential

The framework presented in this paper is applicable to a wide variety of species. We focused on shark populations because they are harvested, they range greatly in longevity, and they are the object of considerable conservation interest. The RP framework was used here to demonstrate that the short-lived Australian sharpnose shark was more susceptible to recruitment overfishing than growth overfishing, while the long-lived spiny dogfish is susceptible to both growth overfishing and recruitment overfishing, especially when juveniles are selected into the fishery. For both species, juvenile harvests lead to a greater risk of depletion than harvests which remove the same fraction of the population's biomass from adults (Figure 2.5). This pattern holds for both species and is likely to be characteristic of shark populations in general. Thus, the intuitive guideline that harvesting of juveniles endangers a population has here been given a mathematical foundation. These results also highlight one concern over the use of surplus production models, because the impacts of a suggested harvest rate may be highly dependent on the range of ages harvested.

Although only two species were considered here, and the knife-edged selectivity functions considered in the paper are only an approximation to true selectivity patterns, the benefits in yield and reduction in risk associated with harvesting the oldest possible segment of the population likely apply to many shark fisheries. Exceptions

to this general rule may occur when the range of ages selected by a juvenile fishery is very narrow. In such gauntlet fisheries (Simpfendorfer, 1999), only high levels of effort would remove too much reproductive potential from the population. Likewise, for species where the oldest individuals are found to be the most successful spawners, the reproductive value would reflect this and lower fishing pressure on these oldest ages might be preferred. However, when a fishery, either artisanal or commercial, does harvest juveniles, any concurrent harvest of adults likely imperils the population.

In addition to demonstrating the benefits of avoiding harvests on juvenile sharks, the analyses in the paper have shown the utility of measures based on RP. Although survival and fecundity rates for an individual species are required to compute RV and RP, the analysis of long- and short-lived shark species identified similar trade-offs between sustainable yield and the selection of juveniles. These patterns may be used to guide the management of fisheries on species for which less information is available.

2.5 Tables

Table 2.1: Definition of terms

| | |
|---|--|
| \mathbf{M} | Leslie matrix |
| \mathbf{H} | Harvest survival matrix with diagonal elements h_x |
| h_x | Fraction surviving harvest at age x |
| $\mathbf{H}^* = \mathbf{I} - \mathbf{H}$ | Diagonal matrix containing fraction harvested at each age with diagonal elements $1 - h_x$ |
| λ | Dominant eigenvalue of \mathbf{M} giving the annual multiplicative increase of the unharvested population at stable age distribution (SAD) |
| λ' | Dominant eigenvalue of \mathbf{MH} giving the annual multiplicative increase of the harvested population at SAD |
| \mathbf{w} | SAD for \mathbf{M} , satisfying $\mathbf{Mw} = \lambda\mathbf{w}$ |
| \mathbf{w}' | SAD vector for \mathbf{MH} , satisfying $\mathbf{MHw}' = \lambda'\mathbf{w}'$ |
| \mathbf{v} | Reproductive value vector for \mathbf{M} , satisfying $\mathbf{v}^T \mathbf{M} = \lambda \mathbf{v}^T$ |
| \mathbf{v}' | Reproductive value vector for \mathbf{MH} , satisfying $\mathbf{v}'^T \mathbf{M} = \lambda' \mathbf{v}'^T$ |
| v_x | Reproductive value at age x |
| $P_t = \mathbf{v}^T \mathbf{N}_t$ | Reproductive potential of the population in year t |
| $P = \mathbf{v}^T \mathbf{w}'$ | Reproductive potential of the SAD vector \mathbf{w}' corresponding to \mathbf{MH} |
| $P_h = \mathbf{v}^T \mathbf{H}^* \mathbf{w}'$ | Reproductive potential of the fish harvested from \mathbf{w}' each year |
| $\Phi = P_h / P$ | Fraction of the reproductive potential removed by the harvest at SAD |
| \mathbf{N}_t | Vector of numbers at each age in year t |
| $N_{x,t}$ | Number of individuals of age x in year t |
| t_c | Age of entry into the fishery |
| t_ε | Maximum age selected by the fishery |
| t_∞ | Maximum age of the species |

Table 2.2: Parameter values used for each species. Note: TL, total length; A_{50} is age of 50% maturity; L_∞ , k , t_0 standard von Bertalanffy growth function parameters. See Table 2.1 for other definitions.

| Species | Common name | Pups per mature female (TL in cm) | A_{50} | t_∞ | \mathbf{M} | L_∞ | k | t_0 |
|-------------------------------|----------------------------|-----------------------------------|----------|------------|--------------|------------|--------|--------|
| <i>Rhizoprionodon taylori</i> | Australian sharpnose shark | $0.19TL - 7.919$ | 1 | 7 | 0.561 | 73.2 | 1.013 | -0.455 |
| <i>Squalus acanthias</i> | spiny dogfish | $0.20TL - 13.24$ | 35.5 | 80 | 0.0515 | 114.94 | 0.0437 | -3.557 |

Table 2.3: Details of stationary harvests for *Rhizoprionodon taylori*. Note: F , fishing mortality; R_0 , net reproductive rate; Y/R, yield per recruit; β , fraction of the total biomass removed each year. See Table 2.1 for other definitions.

| Type of harvest | t_c | t_ε | Harvest fraction ($1 - h_x$) | F | λ' | R_0 | Y/R | Φ | β | Fraction of numbers harvested |
|-----------------|-------|-----------------|-----------------------------------|-------|------------|-------|-------|--------|---------|-------------------------------|
| No harvest | — | — | 0 | 0 | 1.141 | 1.572 | 0 | 0 | 0 | 0 |
| Juvenile | 0 | 0 | 0.364 | 0.452 | 1 | 1 | 0.018 | 0.124 | 0.029 | 0.199 |
| Juvenile | 0 | 1 | 0.202 | 0.226 | 1 | 1 | 0.052 | 0.124 | 0.079 | 0.153 |
| Juvenile | 0 | 2 | 0.155 | 0.168 | 1 | 1 | 0.070 | 0.124 | 0.102 | 0.135 |
| Juvenile | 0 | 3 | 0.137 | 0.147 | 1 | 1 | 0.078 | 0.124 | 0.113 | 0.128 |
| All ages | 0 | 7 | 0.124 | 0.132 | 1 | 1 | 0.087 | 0.124 | 0.124 | 0.124 |
| Adult | 1 | 7 | 0.174 | 0.191 | 1 | 1 | 0.120 | 0.124 | 0.162 | 0.090 |
| Adult | 2 | 7 | 0.311 | 0.372 | 1 | 1 | 0.139 | 0.124 | 0.183 | 0.079 |
| Adult | 3 | 7 | 0.731 | 1.313 | 1 | 1 | 0.148 | 0.124 | 0.193 | 0.076 |

Table 2.4: Details of stationary harvests for *Squalus acanthias*. Note: F , fishing mortality; R_0 , net reproductive rate; Y/R, yield per recruit; β , fraction of the total biomass removed each year. See Table 2.1 for other definitions.

| Type of harvest | t_c | t_ε | Harvest fraction ($1 - h_x$) | F | λ' | R_0 | Y/R | Φ | β | Fraction of numbers harvested |
|-----------------|-------|-----------------|-----------------------------------|-------|------------|-------|-------|--------|---------|-------------------------------|
| No harvest | — | — | 0 | 0 | 1.032 | 4.892 | 0 | 0 | 0 | 0 |
| Juvenile | 0 | 0 | 0.7956 | 1.588 | 1 | 1 | 0.019 | 0.0314 | 0.0026 | 0.1656 |
| Juvenile | 0 | 10 | 0.1344 | 0.144 | 1 | 1 | 0.117 | 0.0314 | 0.0149 | 0.0926 |
| Juvenile | 0 | 20 | 0.0728 | 0.076 | 1 | 1 | 0.239 | 0.0314 | 0.0267 | 0.0623 |
| Juvenile | 0 | 30 | 0.0500 | 0.051 | 1 | 1 | 0.328 | 0.0314 | 0.0309 | 0.0464 |
| Juvenile | 0 | 40 | 0.0389 | 0.040 | 1 | 1 | 0.378 | 0.0314 | 0.0309 | 0.0375 |
| All ages | 0 | 80 | 0.0314 | 0.032 | 1 | 1 | 0.432 | 0.0314 | 0.0314 | 0.0314 |
| Adult | 10 | 80 | 0.0397 | 0.041 | 1 | 1 | 0.533 | 0.0314 | 0.0353 | 0.0182 |
| Adult | 20 | 80 | 0.0547 | 0.056 | 1 | 1 | 0.593 | 0.0314 | 0.0327 | 0.0117 |
| Adult | 30 | 80 | 0.0935 | 0.098 | 1 | 1 | 0.587 | 0.0314 | 0.0281 | 0.0083 |
| Adult | 40 | 80 | 0.7059 | 1.224 | 1 | 1 | 0.620 | 0.0314 | 0.0261 | 0.0071 |

2.6 Figures

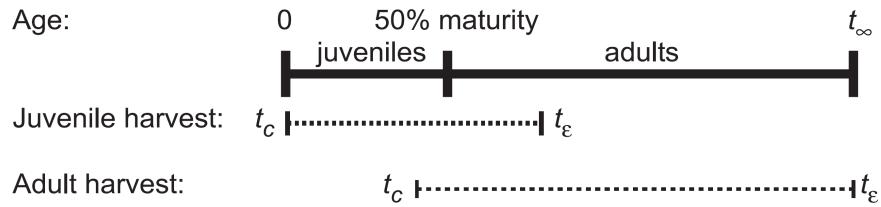


Figure 2.1: Example of juvenile and adult harvests showing that both types may include some juveniles and some adults.

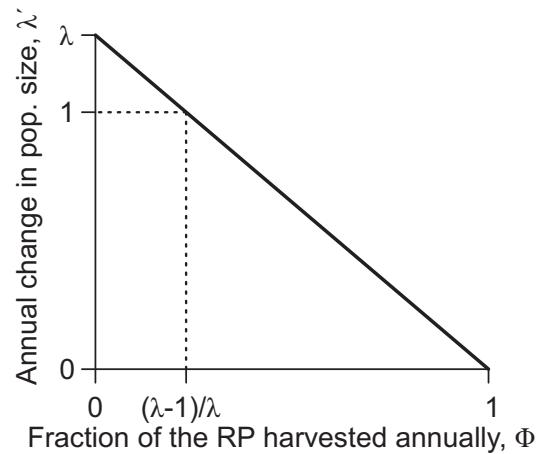


Figure 2.2: The relationship between λ' and Φ as given by the theorem and lemma. Pop., population; RP, reproductive potential.

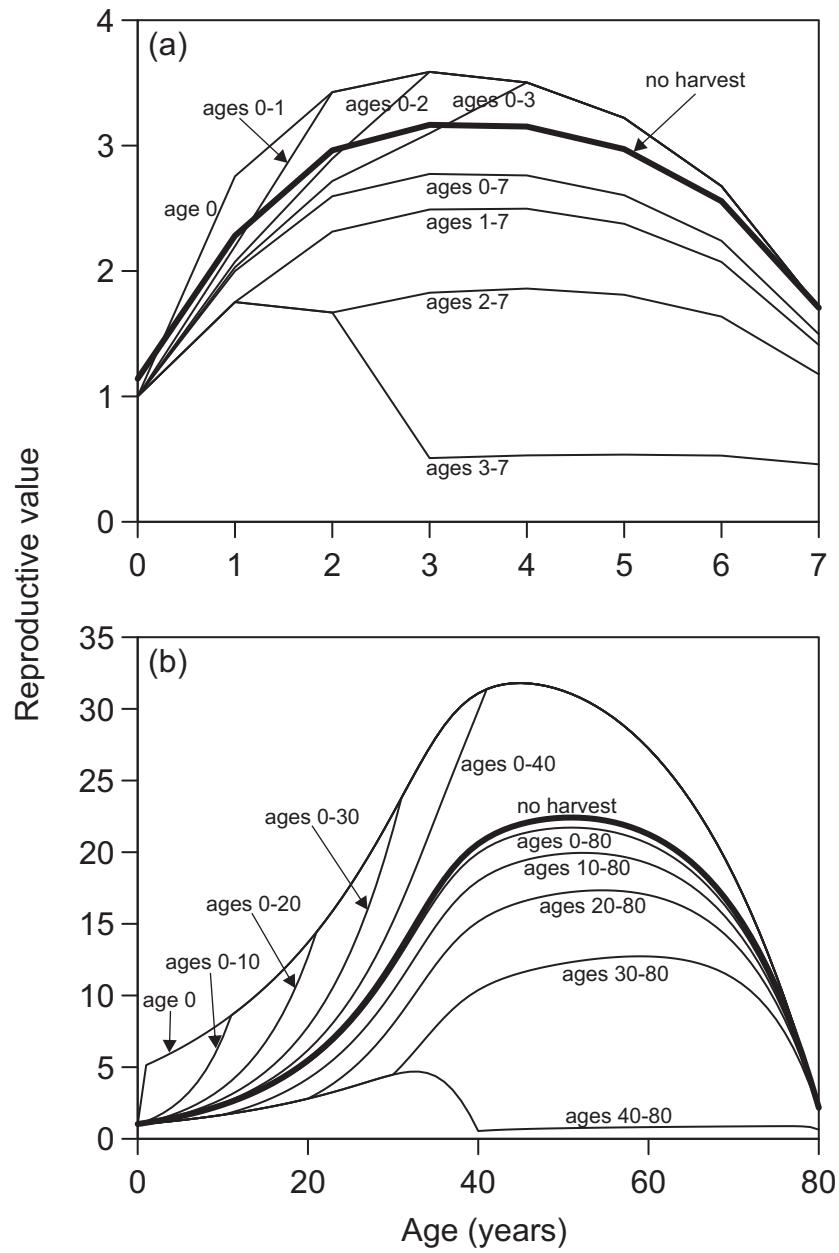


Figure 2.3: Reproductive value vs. age for (a) *Squalus acanthias* and (b) *Rhizoprionodon taylori* under harvests that maintain a stationary population size and under no harvest. Labels denote the range of ages selected into the harvest for each curve.

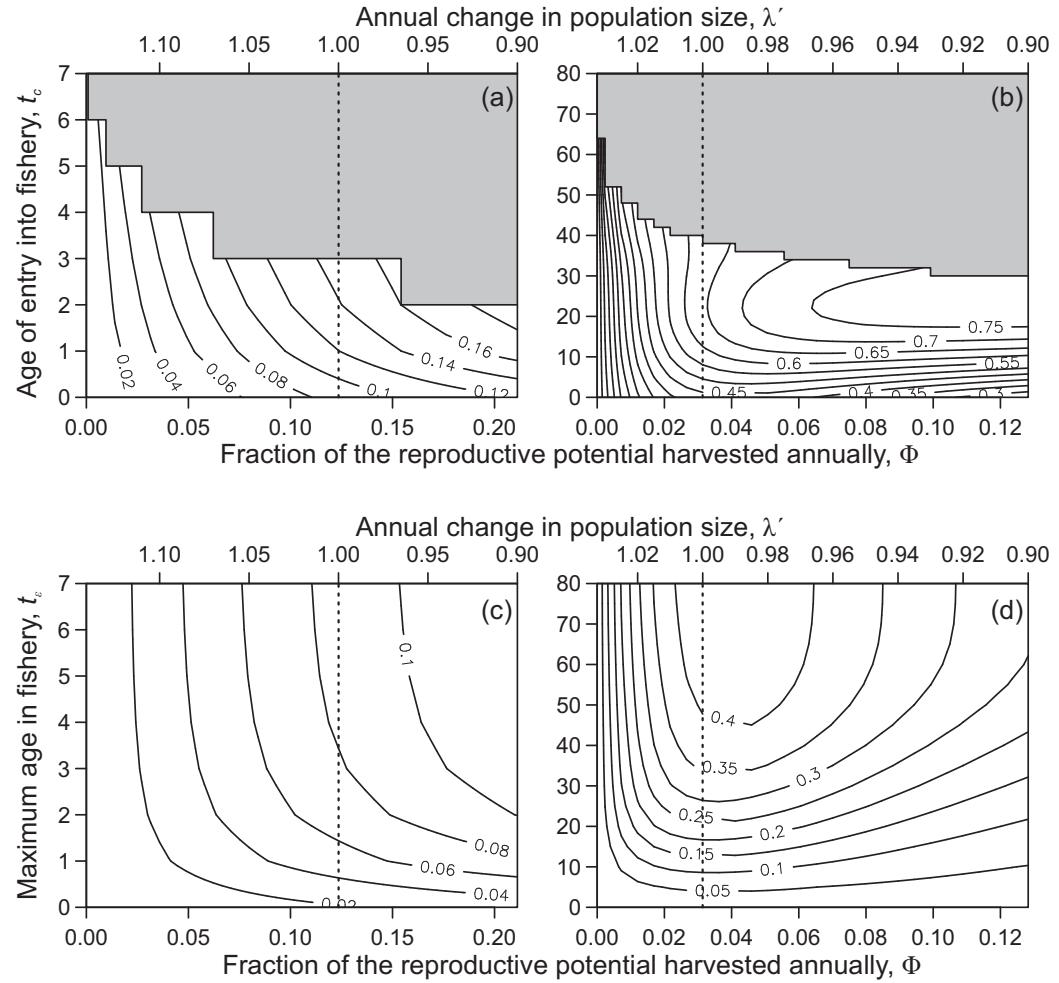


Figure 2.4: Isopleths of yield per recruit as a function of selectivity parameters and fishing pressure expressed as Φ , the fraction of reproductive potential (RP) harvested each year. The corresponding annual change in population size λ' is shown at the top of each figure. (a) Adult harvests on *Rhizoprionodon taylori*; (b) Adult harvests on *Squalus acanthias*; (c) Juvenile harvests on *Rhizoprionodon taylori*; (d) Juvenile harvests on *Squalus acanthias*. The vertical lines mark $\Phi_{\text{stationary}} = (\lambda - 1)/\lambda$, the value of Φ that leads to a stationary population in a deterministic projection. Shading indicates the fraction of RP in selected ages is less than Φ .

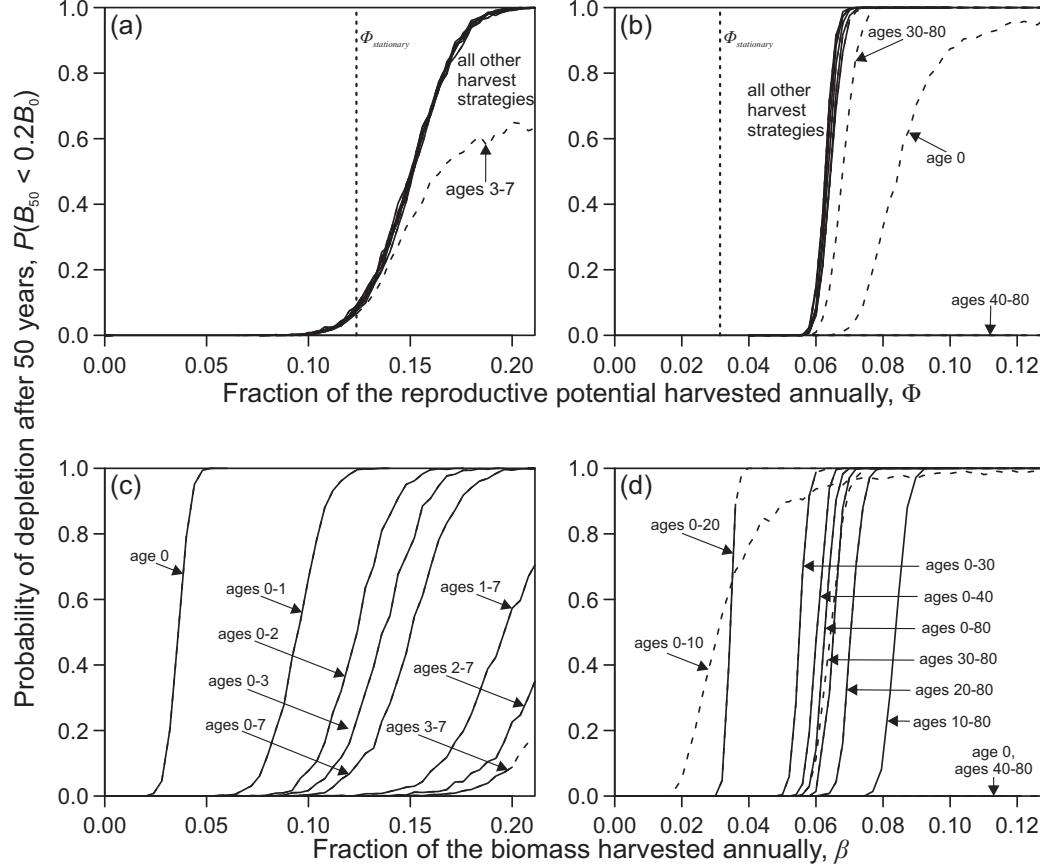


Figure 2.5: Risk of severe depletion associated with different levels of harvest, as a function of harvesting (a) reproductive potential from *Rhizoprionodon taylori*, (b) reproductive potential from *Squalus acanthias*, (c) biomass from *Rhizoprionodon taylori*, and (d) biomass from *Squalus acanthias*. Labels denote the range of ages selected into the harvest for each curve. Dashed sections of the risk curves indicate that over 90% of the projections led to complete removal of some ages classes. The vertical lines in (a) and (b) mark $\Phi_{\text{stationary}} = (\lambda - 1)/\lambda$, the value of Φ that leads to a stationary population in a deterministic projection. Arrows pointing to figure boundaries indicate risk curves that are constant at 0.

Chapter 3

MOVEMENT PATTERNS OF SPINY DOGFISH FROM HISTORICAL TAGGING EXPERIMENTS IN WASHINGTON STATE

3.1 *Introduction*

The spiny dogfish has been studied extensively in the NE Pacific, with interest driven alternately by its commercial value, a perception that it is a detriment to other fisheries, and an interest in the ecology of this long-lived shark. Tagging experiments on dogfish began in 1940 and were carried out in three phases in the NE Pacific. From 1940 to 1946, during the peak of the dogfish fishery in this area, approximately 9,800 dogfish were tagged. Dogfish were tagged primarily in the inside waters of the Puget Sound and the US part of the Strait of Georgia, but about 2,000 tags were also released along the Coast of Washington State and the West Coast of Vancouver Island (Bonham et al., 1949; Holland, 1957). From 1969 to 1972, a larger experiment was conducted, consisting of approximately 24,200 tagged dogfish, again primarily in inside waters, but including about 6,800 on Swiftsure Bank in coastal waters (Fujioka and DiDonato, 1974; Fujioka, 1978). These two experiments in Puget Sound will hereafter be referred to as the 1940s and the 1970s studies. Another large tagging experiment was conducted in British Columbia from 1978 to 1988 and included approximately 70,800 tagged dogfish (McFarlane and King, 2003). Similar patterns were found in all tagging experiments, notably that most dogfish were recovered close to the point where they were released, that coastal dogfish exhibited greater movement than those released in inside waters (defined here as all waters of the Strait of Juan de Fuca, Strait of Georgia, San Juan Archipelago, and Puget Sound), and that

movement between coastal and inside waters was relatively rare.

The two tagging programs in Washington State took place during very different patterns of commercial fishing. The first tagging program coincided with the period of the highest landings in the history of the fishery, when annual landings of dogfish in the NE Pacific (including the US and Canada) grew to over 50,000 mt (Ketchen, 1986). By the commencement of the second tagging program, landings in the NE Pacific had fallen below 500 mt, their lowest level in over 50 years (Ketchen, 1986). This difference in commercial fishing effort meant that a greater fraction of the tag returns from the second study were from bycatch in sport fisheries.

Although the tagging experiments in the 1940s and the 1970s included releases in some of the same regions within Puget Sound, the statistical areas used to report the recoveries differed. Holland (1957) also plotted movement of tagged dogfish up and down the coast from the point of release as a function of the time of recovery as evidence for seasonal movement of coastal dogfish, but such results were not reported for the 1970s study (Fujioka and DiDonato, 1974; Fujioka, 1978). In spite of these differences, the results of the both Puget Sound experiments were recorded with enough precision to allow the current reanalysis. This reanalysis was conducted with three goals: to compare rates of recovery of dogfish released in Puget Sound using a common set of geographical areas, to estimate seasonal movements of coastal dogfish, and to aid the design of a metapopulation model for dogfish in the NE Pacific that will incorporate the tagging data from these studies. Potential differences in fishing effort and landings are not included in this analysis, so the recapture rates only provide qualitative information about movement patterns which may be used to guide more quantitative modeling efforts in the future.

3.2 Methods

3.2.1 Tagging experiments

Tagging experiments in US waters took place during the intervals from April 2, 1940 to May 28, 1946 and then again from May 28, 1969 to December 7, 1972. The tags used in the 1940s tagging experiment were celluloid Petersen-type disks tied with a variety of wire types including nickel, silver, and monel steel. Dogfish were obtained opportunistically on a variety of commercial vessels, most of which used trawl gear. From February to April, 1945, however, 3,425 dogfish were tagged at a herring trap in Holmes Harbor, in the Whidbey Basin. Tags used in the 1970s were plastic “spaghetti-type” dart tags. In the later study, the releases were again carried out primarily on commercial trawlers, but with fewer trips than the previous study, and more releases per trip. The later study also concentrated the releases in a smaller set of fishing grounds. Tagged dogfish were recaptured by a variety of fishing gears, with commercial trawl gear the most common (Holland, 1957; Fujioka and DiDonato, 1974). Recoveries in both studies were generally close to the point of release but include some long distance movements (Figure 3.1), including two returns from Japan, the first in 1945 after 622 days at liberty, and the second in 1972 after 729 days at liberty. Both tags returned from Japan had been released in coastal waters.

Only length at release has been considered in this reanalysis, to avoid uncertainty associated with the measuring methodology at recapture. Total lengths were recorded for most tagged dogfish in both studies, and these were assumed to be with the tail extended, but some variation associated with the positioning of the tail may remain. In some cases, fork length was recorded, and this was converted to total length using the allometric relationship, $TL_{extended} = 1.124 \times FL$, ($n = 54$, $R^2 = 0.9997$), estimated from dogfish collected in Puget Sound in the 2000s for which both measurements were taken.

3.2.2 Basin Determination

Releases and recaptures in inside waters were assigned one of nine established basins (Ebbesmeyer et al., 1984; Puget Sound Water Quality Action Team, 2002), or to outside waters (Figure 3.2). Records of releases and recaptures from both tagging experiments included statistical areas and fishing ground codes. Approximate latitude and longitude were assigned to the release and recapture point at an arbitrarily chosen central point within the fishing ground. Any recorded notes related to recapture locations were used in assignment of latitude and longitude values. Recorded distance traveled and the cardinal or ordinal direction of travel were used to refine the location of recapture points. Recapture records for 15 dogfish were insufficient for basin determination and were excluded from the results.

3.2.3 Seasonal Movement of Coastal Dogfish

Movement north or south along the coast from release to recapture as a function of the calendar date of recapture was examined for dogfish that were both released and recaptured in coastal waters following Holland (1957). Estimated latitude and longitude of release and recapture were used to compute the distance traveled north or south from release to recapture. Only dogfish recaptured more than 60 days after release were considered. After 60 days at liberty, no clear trend remained in the total distance traveled as a function of time at liberty (Figure 3.6). A sinusoid with three parameters for date of maximum value, range (distance from minimum to maximum), and mean value, was fit to the data from the two tagging experiments using maximum likelihood assuming a normal error distribution. A four parameter piecewise linear model was also considered but did not fit the data as well as the sinusoidal model. The average daily sea surface temperature from 1989 to 2005 at the Cape Elizabeth buoy 45 nm northwest of Aberdeen, WA, and length of day from sunrise to sunset at that same location were used as indicators of seasonal changes

along the coast to which the sinusoid estimates were compared.

3.3 Results

3.3.1 Inter-basin movement

The fraction of recaptures that occurred in the basin of release was 81% for the 1940s study and 65% for the 1970s study. The largest number of dogfish moving between basins was between Central and South Puget Sound in the 1970s study (Table 3.1). When these two areas were combined in this study, the percentage of the recaptures in the basin of release for the 1970s increased to 79%. Most dogfish that were recaptured outside of the basin of release had moved into neighboring basins (Figure 3.3). However, dogfish moving out of the Strait of Georgia in the 1940s were more often recaptured in outside waters than the other basins. This is most likely the result of differences in fishing effort in that time period.

3.3.2 Length distributions and sex ratios

A comparison of length distributions indicates that more small dogfish were released in inside waters than in outside waters in both the 1940s and the 1970s (Figure 3.4). The dogfish released in outside waters were dominated by males (69% in the 1940s and 76% in the 1970s), and included fewer small fish. This differs from the dogfish observed in NMFS groundfish trawls in coastal waters which have a more even sex ratio and include more small dogfish, but often take place later in the year than much of the tagging, and include deeper waters (unpublished data). Bottom trawl gear was the primary collection method in the tagging trips, and there is no indication that size-based targeting or discarding occurred, so these distributions are likely to be representative of the available population on the fishing grounds where tagging took place, taking into account the selectivity of the trawl gear.

The largest deviation from the typical fishing patterns were the dogfish captures

in the herring trap in Holmes Harbor in 1945. The herring trap releases included few large dogfish with only 13% over 600 mm compared to 44% of the dogfish tagged elsewhere in inside waters in the 1940s. This difference, combined with the selectivity of the fishery may have contributed to a lower recapture rate compared to other release areas: in the 1940s study, the recapture rate for Whidbey Basin releases (99% of which were from the herring trap) was only 5% versus 11% of Strait of Georgia releases. Dogfish in inside waters in the 1970s included more mature females, based on a length at 50% maturity of 939 mm (Saunders and McFarlane, 1993), and more of the first few year classes (less than 400 mm.) than were tagged in the 1940s. The length distribution of the recaptures includes fewer small dogfish than the releases, which is likely the result of commercial fishers focusing on areas where they find larger dogfish.

3.3.3 Seasonal Movement of Coastal Dogfish

Dogfish released on the coast show evidence of seasonal movement (Figure 3.7, Table 3.2). Sinusoids fit to the distance traveled north or south from release to recovery vs. the calendar day of recovery have similar maxima: June 27 for the 1940s study and June 12 for the 1970s study. The magnitude of the estimated movement from the 1940s was higher, with an estimated north-south seasonal shift of 603 km which explained about 1/4 of the variability in return position ($r^2 = 0.23$). The estimated north-south seasonal range for the 1970s covered only 202 km and explained less of the variability in return position ($r^2 = 0.07$). For both time periods, the low r^2 values indicate that the seasonal shift is only one component of more complex movement patterns. Releases in the 1940s took place in a variety of places along the coast while releases in outside waters in the 1970s took place only on Swiftsure Bank at the entrance to the Strait of Juan de Fuca (Figure 3.1). Similar analysis for dogfish tagged in inside waters showed no clear indication of seasonal movement.

3.3.4 Trans-boundary movement

Among dogfish tagged in US inside waters in the 1940s, 32% were recaptured in Canada. However, the vast majority of these recaptures were released in the Strait of Georgia basin, which is mostly located in Canadian waters, and where the releases were close to the international boundary. Among dogfish released in the Strait of Georgia in the earlier study, 46% were recaptured in Canadian waters compared to 6% for all other basins combined.

In the 1970s, the number of recaptures in Canadian waters was far lower, at 4% of dogfish tagged in US inside waters. Again these trans-boundary migrations were dominated by releases in the Strait of Georgia basin, 15% of which were recaptured in Canadian waters, while less than 1% of releases in other basins were recaptured in Canada.

3.4 Discussion

Although the two tagging studies on dogfish in Washington State differed in major ways, the similarity of some of their results, analyzed using the same methodology, supports the idea that these the observed patterns are more than artifacts of a given study design or fishing regime.

The fraction of recaptures in the basin of release was higher than the equivalent rates for the statistical areas reported in Fujioka and DiDonato (1974). The average size of the basins was similar to that of the statistical areas, so the larger fraction remaining in the basins, which were delineated using geographic and oceanographic features (Ebbesmeyer et al. 1984), is evidence that they are more descriptive of the typical range of dogfish movement or habitat use than the statistical areas.

Recaptures showing movement between inside and outside waters were relatively infrequent in both studies, which is similar to the results of the large tagging program in Canadian waters (McFarlane and King, 2003). Nevertheless, an increased under-

standing of the impact the small amount of exchange has on the stock structure and population dynamics is important to the successful management of this species.

The differences in length distributions and sex ratios between inside and outside waters was similar between the two tagging experiments, although this may be more representative of the patchiness of the dogfish population than differences in stock structure. The absence of smaller dogfish in coastal waters in the tagging studies compared to coastal NMFS trawl surveys indicates that segregation by size and sex in habitat selection is a possibility that warrants further investigation. Dogfish dorsal spines collected by Bonham et al. (1949) are being aged using updated methods (Saunders and McFarlane, 1993) and will complement the length data and improve understanding of the population structure during the period of the first tagging experiment. Investigations into the demographic and genetic connections between inside and outside waters are currently underway (Vega, 2006; Franks, 2006), and should shed light on questions of stock structure and population dynamics.

Seasonal movement of dogfish may be partly confounded with seasonal patterns of fishing effort. However, the similarity between the results for the two tagging experiments, which took place at times when commercial and recreational fishing patterns differed, is some indication that this pattern has a biological basis. Seasonal movement patterns have been noted for dogfish in the NE Atlantic (Holden, 1965) and the NW Atlantic (Jensen, 1965), in addition to the NE Pacific (Holland, 1957; Ketchen, 1986), but in general the descriptions have been qualitative. The sinusoid curves presented above, while only explaining a small fraction of the variability in north-south movement of dogfish tagged in coastal waters, provide evidence that, on average, dogfish in coastal waters move seasonally hundreds of kilometers to the north and south, reaching their most-northward position near the summer solstice. This pattern, combined with the large abundance of dogfish near the international boundary at the mouth of the Strait of Juan de Fuca, demonstrates the value of developing a co-management system for coastal dogfish. Seasonal movement in coastal

waters also raises questions about the impacts of climate variability and change on the range of dogfish in the NE Pacific.

The frequency of releases in US inside waters that were recaptured in Canadian waters differed between the two studies, but in both cases, they were primarily the result of dogfish both released and recaptured in the Strait of Georgia basin. Likewise, McFarlane and King (2003) showed that most of the dogfish that were tagged in the Canadian portion of the Strait of Georgia and recaptured in US waters remained in the Strait of Georgia basin. In many cases, the recaptures were a considerable distance away from the release point, so it is possible that this pattern is not just the result of the proximity of the release to the international boundary, but also an indication of possible stock differences between dogfish in inside waters north or south of the San Juan Archipelago. Thus, co-management of dogfish by the US and Canada is also important for dogfish in the Strait of Georgia basin.

The amount of movement of tagged dogfish between basins is sufficient to warrant modeling the spiny dogfish in the NE Pacific as a metapopulation rather than separate stocks. Wood et al. (1979), in the first population dynamics model of spiny dogfish in the NE Pacific, assumed separate stocks in the inside and outside waters. However, they also suggested that the incorporation of movement between these areas would be a valuable addition to future models. Differences in length distributions between regions and between released and recaptured fish also indicate that incorporating fisheries selectivity will be important in trying to model the observed recapture patterns. Although the majority of recaptures occurred in the basin of release, many of the basins had too few releases to warrant modeling population dynamics at this scale. However, the preponderance of the Strait of Georgia as the basin of release for Canadian recaptures indicates that separating the US inside waters into Northern and Southern components would be a valuable improvement to a population dynamics model, and for management of dogfish in general.

Although the length measurements include some uncertainty, the absence of large

females tagged in inside waters in the 1940s compared to the 1970s is likely a measure of the impact that the early fishery had on the dogfish at its peak, and the degree to which the population was able to recover over 25 years of reduced fishing. Thus, data from these tagging studies are likely to provide valuable information about changes in population status as well as patterns of movement.

3.5 *Tables*

Table 3.1: Releases and recaptures by basin for the two tagging studies. Recaptures in basin of release are shown in bold. No releases occurred in West Strait of Juan de Fuca basin (WSJF).

Table 3.2: Maximum likelihood parameters for sinusoids fit to north-south distance from release to recovery for dogfish tagged and recaptured in outside waters (Figure 3.6). Date of maximum is the calendar date at which the sinusoid is at its peak. Mean is the average value of the sinusoid, which is found midway between the maximum and minimum values, and range is the total north-south distance between the maximum and minimum points on the sinusoid. r^2 is the fraction of variability in the data explained by the model. Standard deviations are given in parentheses.

| Tagging period | Date of maximum | Mean | Range (min to max) | r^2 |
|-----------------------|------------------------|------------------------------|---------------------------|-------|
| 1940s | June 27 (14 days) | 159 km S. of release (54 km) | 603 km (156 km) | 0.23 |
| 1970s | June 12 (36 days) | 53 km S. of release (45 km) | 202 km (115 km) | 0.07 |
| combined | June 22 (14 days) | 122 km S. of release (37 km) | 430 km (100 km) | 0.16 |

3.6 Figures

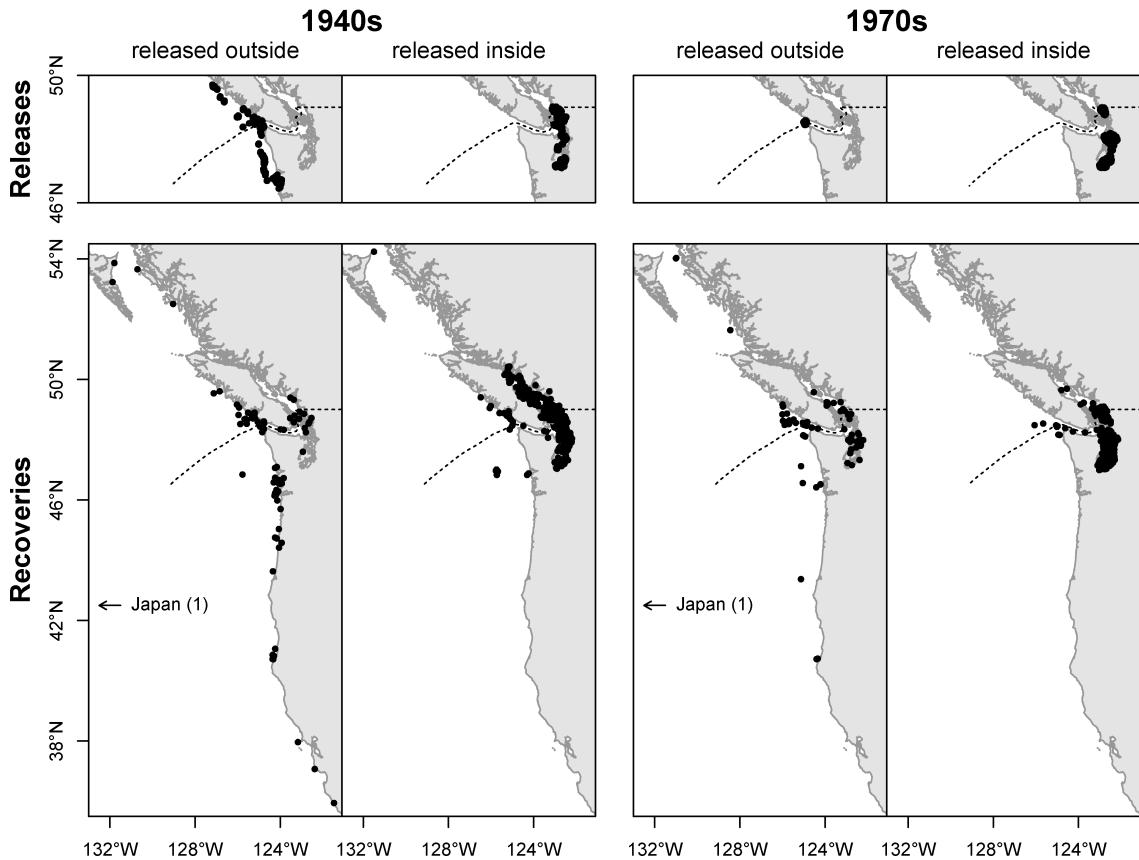


Figure 3.1: Approximate location of releases and recoveries from the tagging programs in the 1940s and 1970s separated into tags released in outside and inside waters. Points have been jittered to improve visibility of multiple tags in one location.

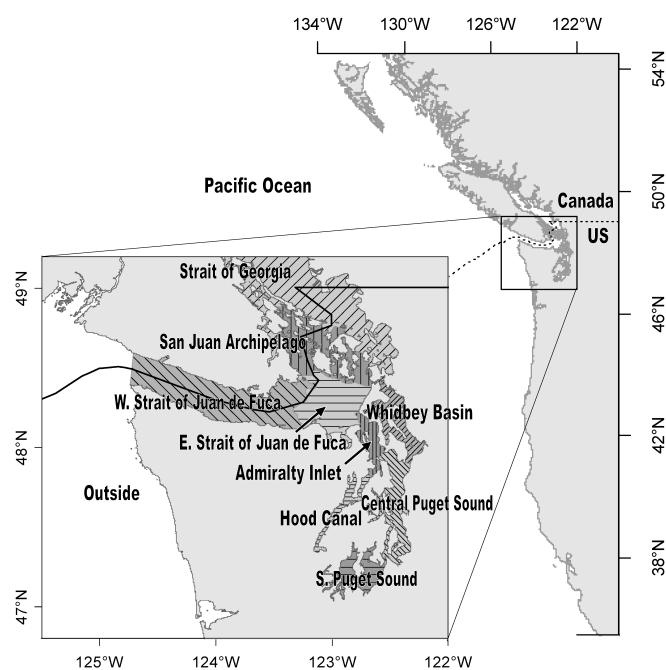


Figure 3.2: Basins in inside waters of Puget Sound and the Strait of Georgia.

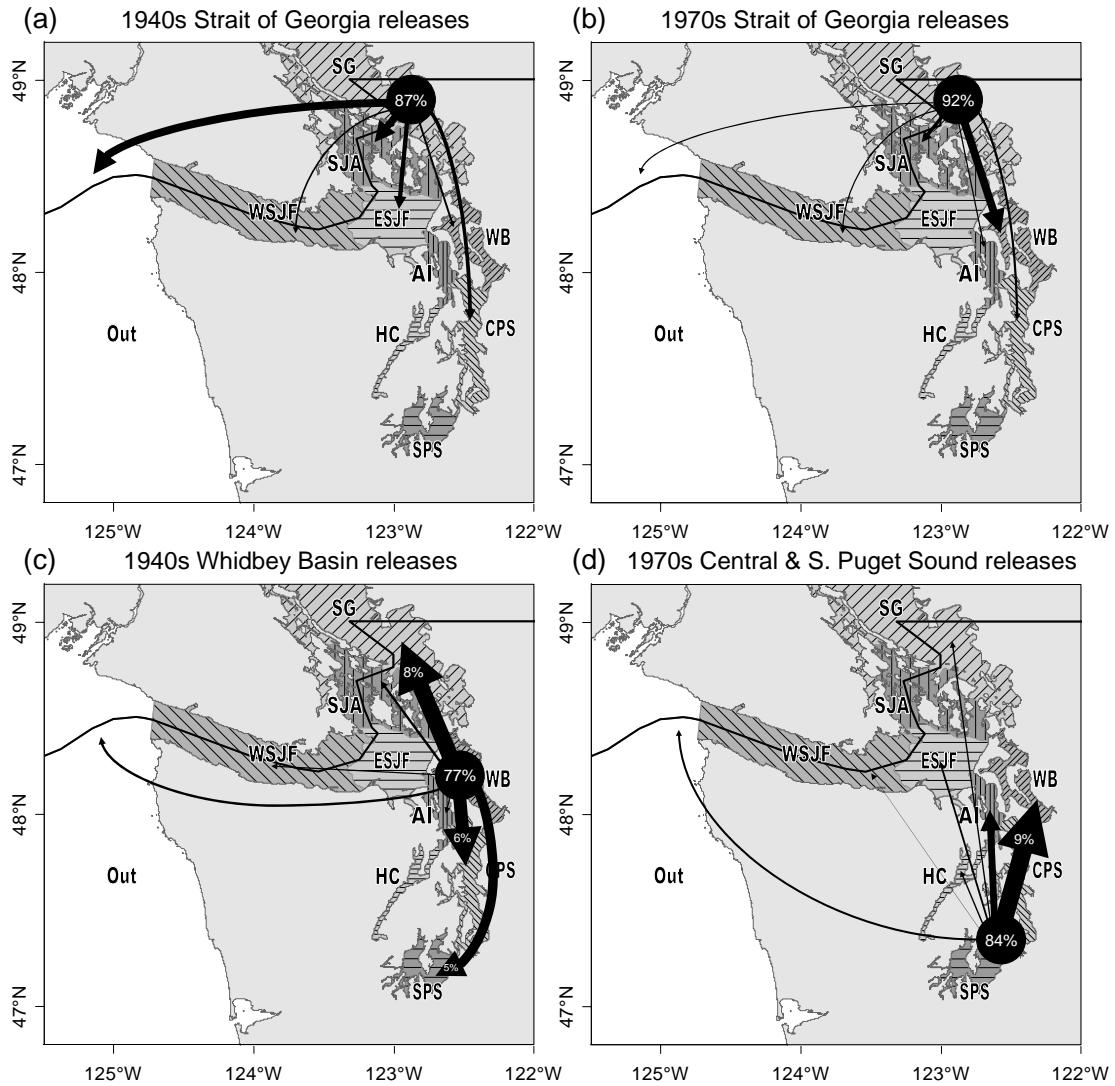


Figure 3.3: Recovery patterns for the largest release areas from the two studies. Black dots with percentages refer to release basin and fraction of recoveries in basin of release. Arrows represent movement of tagged dogfish with line width proportional to fraction recovered in each basin. Release basins and periods are (a) Strait of Georgia in 1940s, (b) Strait of Georgia in 1970s, (c) Whidbey Basin in 1940s, and (d) Central and South Puget Sound combined in 1970s.

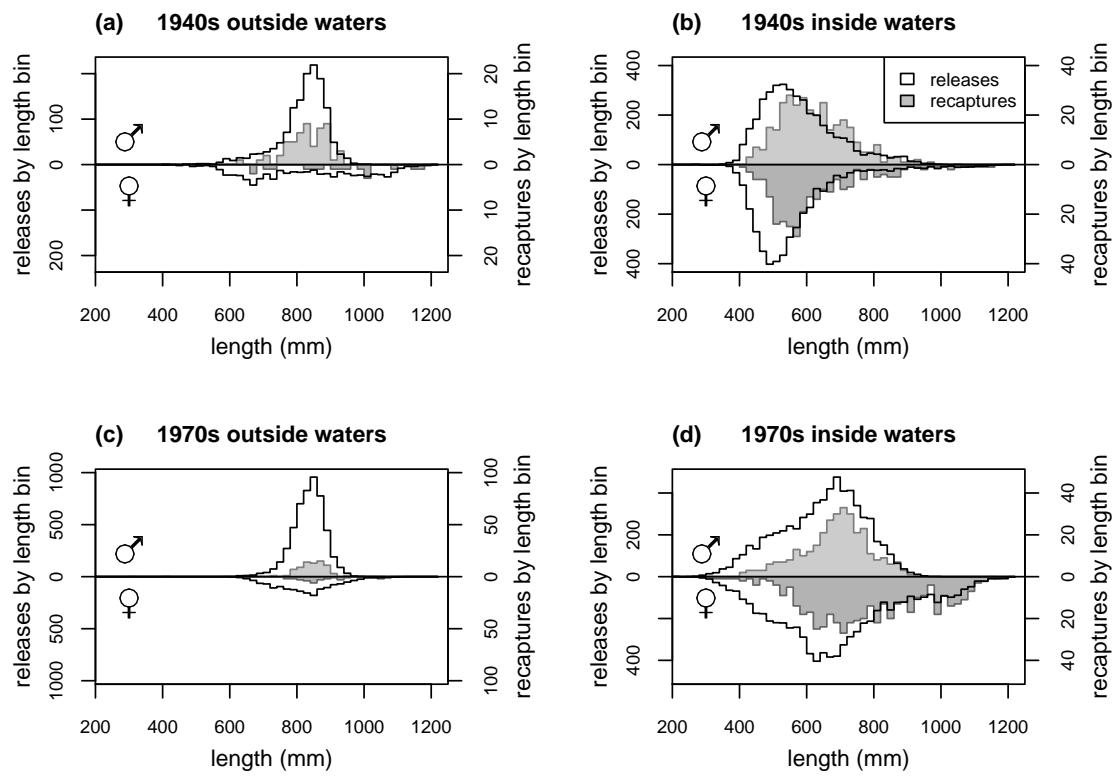


Figure 3.4: Distributions of length at release, grouped by 20 mm length bin, for releases (white) and recaptures (gray) for males (upper) and females (lower).

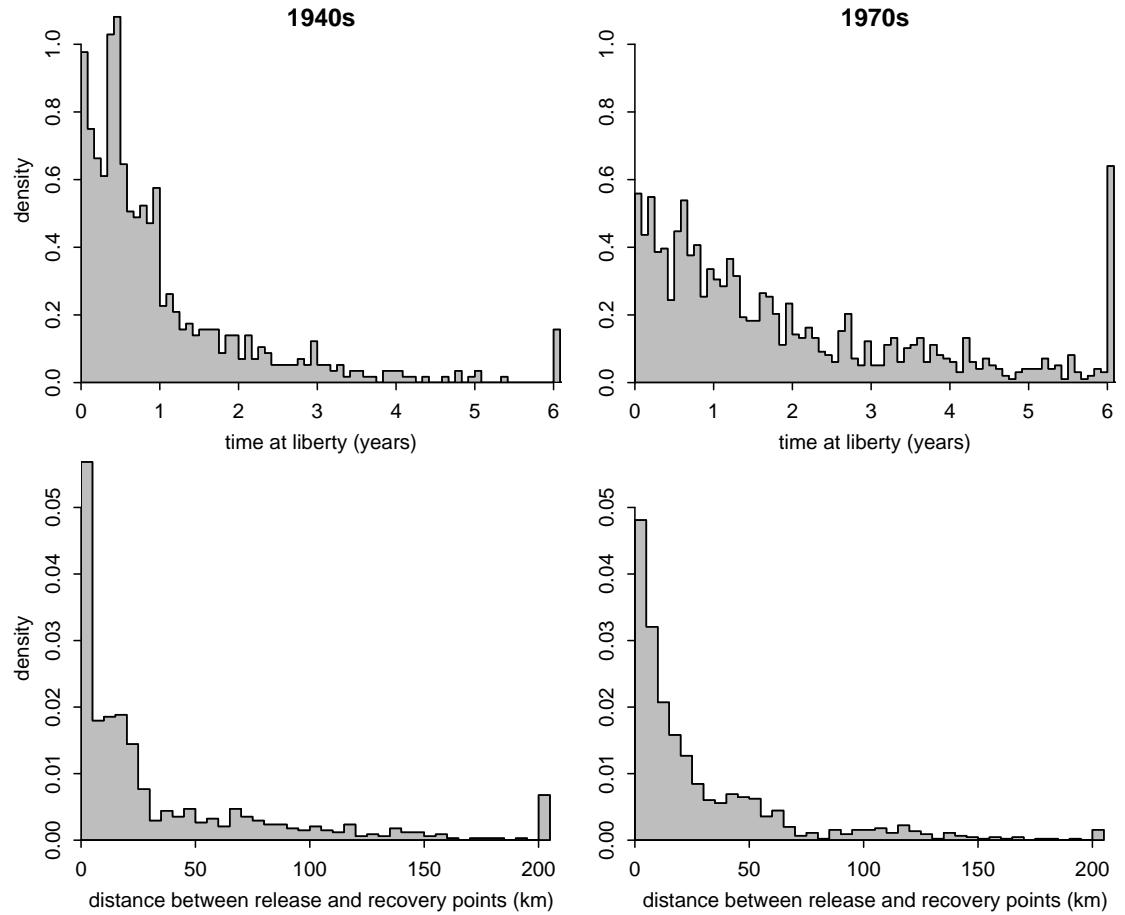


Figure 3.5: Distributions of time at liberty and straight line distance between release and recovery. Time at liberty is binned by month and distance binned by 5 km intervals. Final bins for time at liberty include all values greater than 6 years. Final bins for distance include all values greater than 200 km.

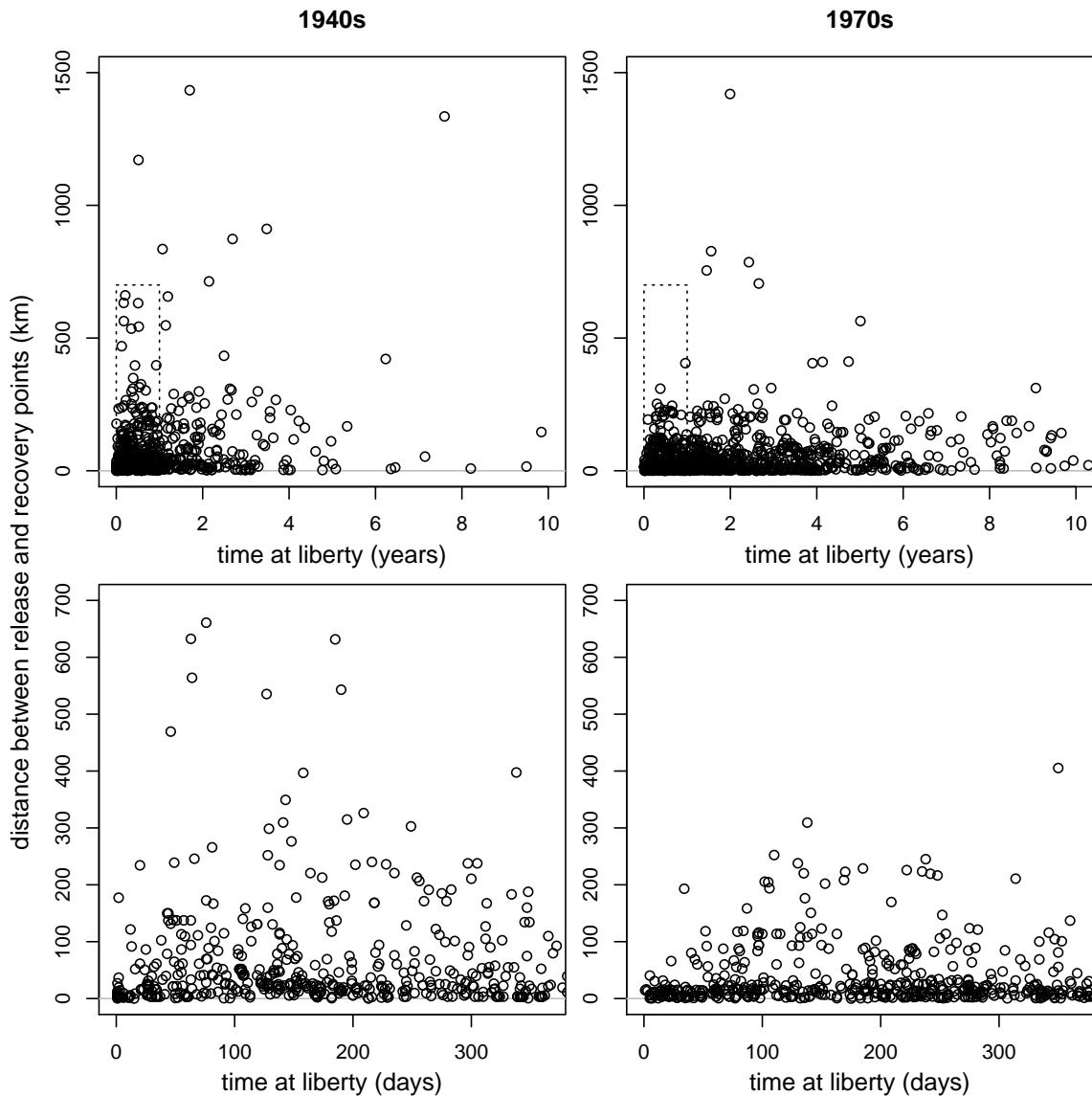


Figure 3.6: Plot of time at liberty vs. straight line distance between release and recovery. Upper plots show all recaptures within 10 years except recaptures from Japan. Dashed boxes indicate subset of time and distance shown in lower plots.

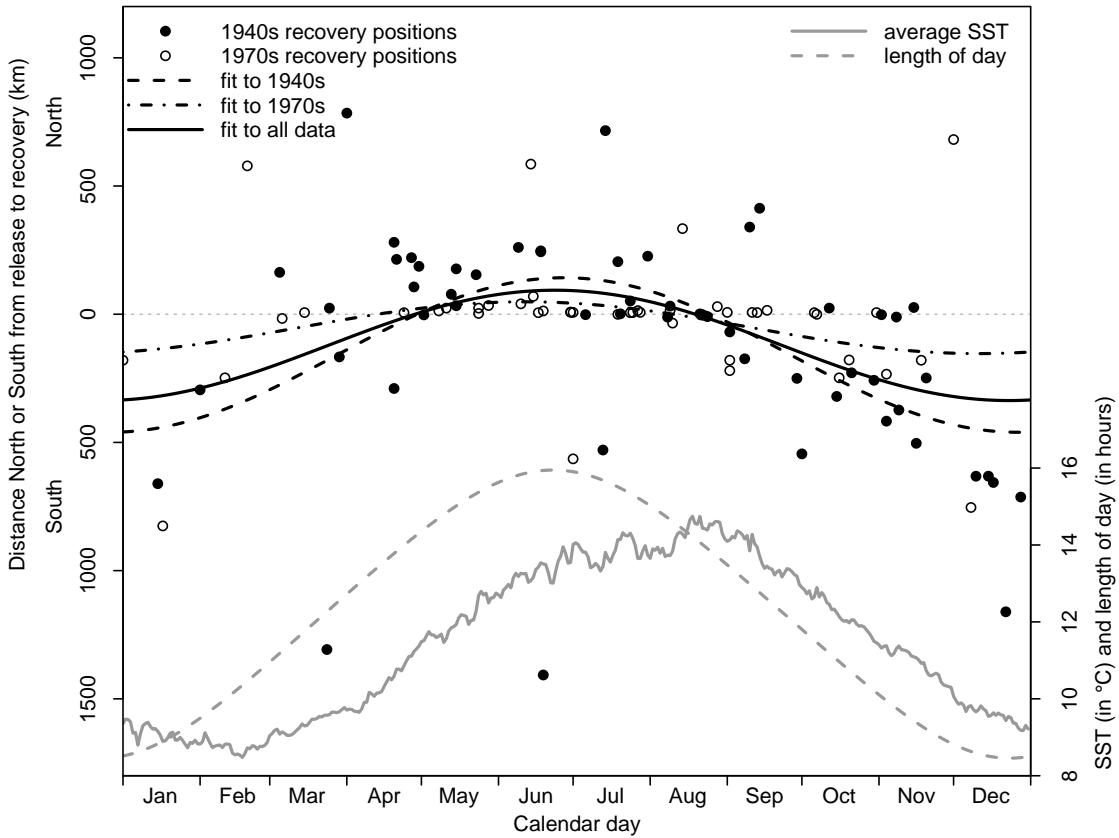


Figure 3.7: Distance north or south from release to recovery for dogfish tagged and recaptured in outside waters, with best fit sinusoids for each tagging study, and the combined data from both studies. The solid gray line gives the average daily sea surface temperature from 1989 to 2005 at the Cape Elizabeth buoy, 45 nm northwest of Aberdeen, WA. The dashed gray line is the length of day from sunrise to sunset at that same location. Parameter estimates are provided in Table 3.2.

Chapter 4

UNCONFOUNDING THE EFFECTS OF CLIMATE AND DENSITY-DEPENDENCE ON THE SPINY DOGFISH OVER A 60 YEAR PERIOD

4.1 *Abstract*

The confounded effects of changes in climate and density on a population's demography are hard to separate for long-lived species because demographic traits are usually the aggregated result of conditions faced over years. Demographic parameters are compared for spiny dogfish (*Squalus acanthias*) in the NE Pacific, the longest lived and latest maturing of all sharks, using samples from the 1940s and 2000s. This 60 year interval has seen ocean temperatures rise by almost 1 °C and dogfish harvests peak above 50,000 mt and then drop below 50 mt per annum. Over this period, the age at 50% maturity for dogfish declined from 45 years to 34 years, while the estimated average number of embryos per litter for a 100 cm dogfish increased from 5.9 to 6.7. Growth parameters changed significantly, with faster growth to a smaller size. Leslie matrix analysis showed that these changes could lead to an increase in population growth rate of about 1%. Comparison with published demographic parameters from the 1970s and 1980s indicated that the greatest change in demographic parameters occurred between the 1940s and 1970s, prior to the largest changes in ocean temperatures. The implications for fishing on long-lived populations during times of rapid environmental change are explored.

4.2 Introduction

Long-lived marine fish are often the most vulnerable to overfishing as a result of low rates of population growth (Musick, 1999). Declines in shark populations, in particular, have been attributed to their life-history strategy, which typically includes a late age at maturity and small numbers of offspring (Burgess et al., 2005), although exceptions exist, such as the blue shark (Aires-da-Silva and Gallucci, 2007). These and other demographic parameters may be density dependent and respond accordingly to depletions, but the extent of such responses is not understood, so the potential for recovery of the depleted populations is difficult to predict. The decline in shark populations over the last half century (Myers and Worm, 2003; Burgess et al., 2005) has also coincided with an increase in global ocean temperatures (Hansen et al., 2006). Thus, the impacts of reduced intra-specific competition in harvested shark species may be confounded with impacts of changing ocean temperatures. Changes in growth and maturity have been observed for a few shark species (Silva and Ross, 1993; Sminkey and Musick, 1995; Carlson et al., 2003; Cassoff et al., 2007) but generally assumed to be density dependent.

The long life-span of many sharks (Cortés, 2002) makes maturity, growth, or fecundity the integrated result of conditions faced over years or decades rather than the immediate response to short-term changes in abundance or environment. An extreme example of a biological integrator is the spiny dogfish (*Squalus acanthias*), a small, slow-growing demersal shark with a lifespan greater than 80 years (McFarlane and King, 2003). Spiny dogfish live longer and mature later than any other shark species for which estimates are available (Saunders and McFarlane, 1993; Cortés, 2002). Dogfish in the NE Pacific are longer lived and later maturing than those in the Atlantic (Campana et al., 2006).

Changes in demography of spiny dogfish over a 60 year period are examined in this study. Samples were collected from the Puget Sound basin of the NE Pacific in 1942-43

and 2002-03. This is the longest time period over which any demographic comparison has been made for a shark species. During the 60 year period spanned by this study, spiny dogfish in the NE Pacific have faced both variable fishing pressure and warming water temperatures. Demand for vitamin A, combined with the cessation of cod liver oil imports from Europe due to World War II, led to a 10 year period of intense fishing for dogfish in the NE Pacific, beginning in the early 1940s (Bonham et al., 1949; Ketchen, 1986). During the 1960s and early 1970s, dogfish were considered a nuisance that interfered with fishing gear and preyed on or competed with more valuable species (Ketchen, 1969, 1986). Incentives were considered to promote removals during this period (Fujioka, 1978). Since 1975, dogfish exports to Europe have supported a small commercial fishery in the NE Pacific (Ketchen, 1986; McFarlane and King, 2003). Coincident with changes in fishing patterns for dogfish, the sea surface temperatures (SST) in the NE Pacific in general, and Puget Sound in particular, increased by almost 1°C from 1942 to 2003 (Strom et al., 2005; Snover et al., 2005). The simultaneous changes in environmental conditions and fishing pressure on dogfish in the NE Pacific are confounded in their impacts on dogfish demography.

Rose (2004), addressed the separability of fishing and environmental pressure for cod in the NW Atlantic and demonstrated that changes in abundance were due to both environment and fishing using centuries of climate data and an index of abundance spanning 100 years. The confounding of intrinsic and extrinsic effects on biology and population dynamics has not been addressed for sharks, for which indices of abundance and time series of catch are often short. The primary environmental effect that has been considered for sharks is the effect of temperature on distribution. SST explained 56% of the variability in the number of basking sharks recorded off southwest Britain each year from 1988 to 2001 (Cotton et al., 2005) and spiny dogfish in NW Atlantic bottom trawl surveys were found to be associated with a relatively narrow temperature range (Shepherd et al., 2002). A study of climate impacts on fish distribution in the North Sea (Perry et al., 2005) showed significant poleward shifts

in mean latitude for 15 species, although dogfish and the other long-lived species in the study did not show significant changes in distribution over the 25 years covered in the study.

Spiny dogfish in the NW Atlantic were declared overfished in 1998 and have been covered under a rebuilding plan since that time (Rago et al., 1998; NEFSC, 2006). This history, combined with depletions in the NE Atlantic and NW Pacific, has contributed to spiny dogfish being listed by IUCN as “Vulnerable” globally and “Critically Endangered” in the NE Atlantic (Fordham et al., 2006). Spiny dogfish have been proposed for listing in CITES Appendix II (CITES, 2006), which would restrict international trade of dogfish products. Although dogfish in the NE Pacific appear to be relatively abundant (Wallace et al., 2008; Taylor, 2008), information on the potential for population growth in this region is needed so that appropriate management measures may be taken to avoid a repeat of the Atlantic experience. The possibility of demographic changes in response to the combined pressure of density dependence and environmental change has powerful implications for the management of all dogfish populations, and sharks in general, particularly at a time when they are under such extreme pressures (Baum et al., 2003; Burgess et al., 2005).

4.3 Methods

4.3.1 Age and growth

Spiny dogfish were sampled in Puget Sound and adjacent coastal waters during the years 1942-43 and from Puget Sound waters in 2002-03 (Bonham et al., 1949; Tribuzio, 2004). These sampling periods are hereafter referred to as “1940s”, and “2000s.” The term “Puget Sound,” is used to describe all inside waters of the Puget Sound, the Straits of Juan de Fuca, the San Juan archipelago, and the southern part of the Strait of Georgia which is within U.S. waters (Figure 4.1). Records of length, maturity, and fecundity were available for the sampled dogfish from both time periods. The term

demography is here used to described the combination of characteristics associated with fecundity, maturity, and growth.

Dorsal spines collected from 1940s dogfish (576 females, 579 males) were aged using validated methodology (Saunders and McFarlane, 1993; Campana et al., 2006; McFarlane and King, 2008b). The ageing methodology includes counting annuli under a dissecting microscope, estimating the relationship between the annuli counts of unworn spines and their base diameter, and using this relationship to estimate the number of missing annuli beyond the last readable point on worn spines (Appendix B). Age estimates for the 2000s dogfish were taken from results of a previous study (Tribuzio, 2004). Different age readers were used for the two sets of spines, but all readers were tested using a reference set of spines that had been read by a number of other readers (Rice et al., 2008). The readings of the reference set of spines showed no evidence of bias between the readers whose results were used in this study.

The von Bertalanffy growth curve,

$$L(x) = L_{\infty} \left(1 - e^{-k(x-t_0)}\right), \quad (4.1)$$

was fit to the values for length and estimated age from the 1940s and 2000s. Length at age was assumed to be normally distributed and age to be known without error. Tests for differences in growth between dogfish collected the 1940s and the 2000s were made using the ω -test (Gallucci and Quinn, 1979), which is a χ^2 test on the parameter $\omega = L_{\infty}k$, and the likelihood ratio test (Cerrato, 1990).

4.3.2 Maturity

Logistic regression (Neter et al., 1996) was conducted to estimate length and age at maturity. The proportion mature is given by,

$$m(x) = \left(1 + e^{-\log(19)(x-x_{50})/\delta}\right)^{-1}, \quad (4.2)$$

where x is either age or length, x_{50} is the age or length at 50% maturity, and δ is the difference in age or length at 95% maturity and that at 50% maturity (Appendix A; Punt and Walker 1998). Randomization (Dwass, 1957) was used to test for differences in the age or length at 50% maturity between 1940s and 2000s because these derived quantities (Appendix A) could not be directly compared using a simpler test.

4.3.3 Fecundity

Counts of embryos per litter were available for 168 pregnant females sampled in the 1940s and 106 from the 2000s. A linear model was used to relate the number of embryos per litter to maternal length, as

$$f(\text{TL}) = \alpha + \beta_1 \text{TL} + \beta_2 \text{P} + \beta_3 \text{L} + \beta_4 (\text{TL} \times \text{P}) + \beta_5 (\text{TL} \times \text{L}), \quad (4.3)$$

where TL is maternal length, P is the sampling period (1940s or 2000s), and L is location (Puget Sound or coastal waters). $\text{TL} \times \text{P}$ and $\text{TL} \times \text{L}$ are the interaction terms for length with period and location. Analysis of covariance was used to estimate the significance of the covariates and the interaction terms, following standard practice for such linear models.

4.3.4 Environmental variables

Annual mean sea surface temperature (SST) was computed using daily measurements from the Race Rocks Lighthouse at the southern end of Vancouver Island (Figure 4.1). SST and values of the Pacific Decadal Oscillation (PDO) were compared for the 20 year intervals prior to the 1940s and 2000s sampling events (1923–42 and 1983–2002). Trends in SST were estimated by fitting a linear model to the annual average SST values for these 20 year intervals. This allowed a consideration of differences in the rate of change in SST between the two periods when the demographic characteristics would have been developing prior to the sampling events.

4.3.5 Population growth

A Leslie matrix was constructed for each of the two time periods considered in this study: 1940s and 2000s. A third matrix was constructed for the Strait of Georgia in the 1970s and 1980s using published parameter values (Ketchen, 1972; Saunders and McFarlane, 1993).

All matrices were females-only. The fecundity terms in the first row of the Leslie matrix were computed as,

$$fec(a) = s(x)m(x)f(L(x))/4, \quad (4.4)$$

where $s(x)$ is the assumed annual survival rate for age x , $m(x)$ is the fraction of females mature at age x given by (4.2), and $f(L(x))$ is the number of embryos per litter given by (4.3) at the length associated with age x in the growth curve (4.1). Division by 4 accounts for the assumed 1:1 sex ratio of the pups and the pupping in alternate years resulting from the 2 year gestation period of spiny dogfish (Jones and Geen, 1977b).

Age 0 was the initial age under the assumption of a post-breeding census (Caswell, 2001), and ages ≥ 85 were grouped as an accumulator age (plus-group). Annual survival rates of spiny dogfish are unknown. The survival rate which resulted in a stationary population size ($\lambda = 1$) for the Puget Sound 1940s matrix was chosen under the assumption that the 1940s demography represents an equilibrium population state (Caswell, 2001). This survival rate was used in all three matrices for all ages under the simplifying assumption that survival has been constant over time and constant over the life of the dogfish. This focused the comparison on the effect on population growth of changing maturity, fecundity, and growth. The dominant eigenvalue λ was computed for the 1970s-80s Strait of Georgia and 2000s Puget Sound matrices and compared to the value of 1.0 assumed for 1940s Puget Sound. No external estimates of survival are available to indicate that it has remained constant, so the λ estimates

are for comparative purposes only.

4.4 Results

4.4.1 Age and growth

After extrapolation for missing annuli on worn spines (Appendix B), the range of estimated ages from the 1940s dogfish was 1.0 to 71.5, with a median of 30.0 years. The dogfish collected in coastal waters covered a smaller size and age range than those collected in the inside waters of Puget Sound. The coastal dogfish were larger and older, on average, than those from Puget Sound, with 79% of female dogfish from coastal waters estimated to be over 40 years old (Figure 4.3). The age range of the coastal dogfish was not considered adequate to estimate growth and maturity. However, coastal dogfish were included in the estimates of fecundity because these estimates are derived only from mature females.

Female dogfish from Puget Sound in the 1940s had a slower growth rate ω and higher asymptotic length (L_∞) than those from Puget Sound in the 2000s and those observed in the Strait of Georgia in the 1980s (Saunders and McFarlane, 1993) (Figure 4.4, Table 4.1). The likelihood ratio test (Cerrato, 1990) indicated that separate growth curves fit to the 1940s and 2000s Puget Sound female length at age data had a significantly better fit than a single curve fit to both data sets ($p < 0.0001$). The ω -test (Gallucci and Quinn, 1979) indicated that the growth rates ω for the two time periods were likewise significantly different ($p < 0.0001$).

4.4.2 Maturity

The age at 50% maturity was estimated to be 44.8 years for 1940s Puget Sound females and 33.5 years for the 2000s Puget Sound females (Figure 4.5, Table 4.1). The 2000s Puget Sound value was not significantly different from the 35.5 year age at 50% maturity estimated by Saunders and McFarlane (1993) for female dogfish

sampled in 1980-81 in the Strait of Georgia.

Length at 50% maturity for females was estimated to be 94.0 cm for the Puget Sound in the 1940s and 88.2 for Puget Sound in the 2000s. The 1940s value corresponds closely with later estimates from the Strait of Georgia of 93.5cm (Ketchen, 1972) and 93.9cm (Saunders and McFarlane, 1993).

Randomization tests indicated that both the 11.3 year change in age at 50% maturity the 5.8 cm change in length at 50% maturity from the 1940s to the 2000s were statistically significant ($p < 0.0001$)

4.4.3 Fecundity

No significant differences were found in fecundity at length between 1940s dogfish collected in inside waters of Puget Sound and outside waters of the coast ($p = 0.67$), so all 1940s dogfish were pooled for comparison to the 2000s. In the analysis of covariance for the linear model of fecundity at length, the difference in slopes for the two periods (1940s vs. 2000s) was not significant at the 0.05 level, but the difference in intercepts was found to be significant, with $p = 0.0069$ in the reduced model (Table 4.2). The estimated relationships for the two time periods (Figure 4.6) were

$$0.214 \cdot \text{TL} - 15.5, \quad (4.5)$$

for the 1940s and,

$$0.214 \cdot \text{TL} - 14.7, \quad (4.6)$$

for the 2000s, where TL is the total length in cm measured with the tail extended. For a 100 cm dogfish, the predicted mean litter counts are 5.9 pups for the 1940s and 6.7 pups for the 2000s, a 12% increase. The relationship estimated for the Strait of Georgia in the 1970s (Ketchen, 1972), $0.20 \cdot \text{TL} - 13.24$, was similar to the estimate for the 2000s over the observed range of maternal lengths, with 6.8 pups estimated

for a 100 cm dogfish compared to 6.7 for the 2000s.

4.4.4 Environmental variables

SST at the Race Rocks Lighthouse rose from 9.0 °C averaged over all daily measurements in 1942 and 1943 to 9.8 °C for 2002 and 2003 (Figure 4.7). Linear models fit to the annual averages for the two decades prior to each sampling period (1923–1942 and 1983–2002) indicated that the temperature had been warming in each of those periods at a similar rates, 0.027 °C/year and 0.024 °C/year, respectively. From 1940s to the 1970s, the temperature does not have a clear trend. The pattern of an increase in temperatures beginning in the 1970s is mirrored in the growth rings of Puget Sound geoducks (Strom et al., 2005) and the air temperatures in the Puget Sound region (Snover et al., 2005). Water temperatures in Puget Sound show considerable coherence both vertically within the water column and horizontally throughout the Sound (Moore et al., 2008), indicating that rising surface temperatures represent changes faced by dogfish in the demersal zone. The PDO had been primarily in warm phases during these same 20 year periods, although it was in a cool phase for four years just prior to the 2000s sampling, from mid-1998 to mid-2002.

4.4.5 Population growth

An annual survival rate of 0.931 (equivalent to an instantaneous natural mortality rate of $M = 0.0715$) resulted in a stationary population size ($\lambda = 1$) for the Leslie matrix based on the growth, maturity at age, and fecundity estimates for 1940s Puget Sound female dogfish. Using this survival rate in the Leslie matrices based on the estimated relationships for the Puget Sound from the 2000s resulted in a population growth parameter of $\lambda = 1.013$. A Leslie matrix for the 1970s and 80s Strait of Georgia resulted in a population growth parameter of $\lambda = 1.012$ using published relationships for fecundity at length (Ketchen, 1972) and length and maturity at age (Saunders

and McFarlane, 1993), with the same survival rate as the Leslie matrices for Puget Sound.

4.5 Discussion

4.5.1 Causes of the observed changes

Dogfish in Puget Sound waters of the NE Pacific had statistically significant declines in both length and age at 50% maturity (Figure 4.5, Table 4.1), and a statistically significant increase in fecundity from the 1940s to the 2000s (Figure 4.6, Table 4.1). Growth curves fit to data from the two time periods (Figure 4.4, Table 4.1) indicated that the initial growth rate ω had increased significantly from the 1940s to the 2000s, but that the asymptotic size had declined. The long lifespan of dogfish (the oldest estimated age in this study was 84 years) implies that any changes in dogfish demography, either intrinsic or extrinsic, will likely be the integrated result of decades of abundance or environmental conditions. This biological integration dampens the relation between cause and effect and makes the confounding of density dependence and environmental effects more difficult to unravel. Three general hypotheses for the causes of the observed demographic changes are considered individually below: observation error (in measurement, estimation or sampling); extrinsic effects (environmental effects); and intrinsic effects (density dependence).

Hypothesis 1: observation error

Under this hypothesis, the observed changes in demographic parameters do not characterize the true population, but are caused by differences in measurement technique, statistical estimation, or the selection of the population that was sampled.

Comparisons of maturity and fecundity as a function of length depend on the consistency of the measurement techniques between time periods. Records associated with the spines of the 1940s dogfish described the length measurement as “the length from the tip of the snout to the tip of the extended, but not stretched, tail.” This

matches the methodology used in the 2000s for measuring total length with the tail extended (Tribuzio, 2004). For dogfish measured with the tail in the natural position, the allometric relationship used to convert between measurement types is strong ($R^2 = 0.9999$, Appendix B). Differences in measurement techniques are therefore unlikely to account for the observed changes in length at age, fecundity at length, or length at 50% maturity.

The ageing methodology includes multiple sources of uncertainty. First, some error is inherent in the process of visually counting the annuli, especially in older dogfish with indistinct banding (McFarlane et al., 1987; Rice et al., 2008; McFarlane and King, 2008b). Second, the statistical extrapolation to account for missing annuli is an approximation that naturally includes uncertainty. Third, the measurement of spine diameter for use in extrapolation for worn spines was found to be an additional source of uncertainty in the age estimates (McFarlane and King, 2008b).

Although uncertain, there is no evidence that the age estimates are biased. The spines from the 1940s and 2000s were examined by different people, but all readers separately examined a reference set of 100 spines (Rice et al., 2008), and got similar annuli counts. Analysis of 1940s dogfish spines that were re-read by the same or different readers showed no bias or uncertainty of a magnitude that could explain the observed differences in demographic parameters. Both length and age at 50% maturity independently showed significant decreases from the 1940s to 2000s, providing further evidence that these patterns are not the result of measurement or estimation error.

Sampling error would be present if differences in gear between time periods caused greater or lesser selection of large or small fish, introducing biases in length at age. However, the majority of both the 1940s and 2000s samples were collected using trawl gear. The range of ages and lengths from the two time periods was also similar (Figure 4.4). Ketchen (1972) also reported the use of trawl gear for sampling, but the samples collected in 1980-81 described by Saunders and McFarlane (1993) were collected using longline gear. Thus, if differences due to gear selectivity are present,

they are most likely to occur in the comparisons with the 1980s dogfish described by Saunders and McFarlane (1993). However, length compositions indicate that dogfish are selected by both trawl and longline gear before they reach the age or length at 50% maturity, so sampling error due to gear selectivity is unlikely to account for the observed differences in demography.

Hypothesis 2: extrinsic effects

Under this hypothesis, the observed changes in demographic parameters are the result of changes in the environment that dogfish inhabit in the NE Pacific, independent of any changes in abundance of dogfish.

The rise in SST at the Race Rocks lighthouse from 9.0 °C in 1942-43 to 9.8 °C in 2002-03 brings the temperature above the 9.2 °C upper 90% quantile for observed temperatures utilized by dogfish in the NW Atlantic (Figure 4.7; Shepherd et al., 2002). SST also approaches the upper limit of the 7.0 – 10.0 °C range that characterized the water temperature in areas of commercial fisheries for dogfish in the NE Pacific (Ketchen, 1986). Both of these published temperature ranges are just reported correlations, but approaching the boundaries of these ranges may indicate that some impact of temperature on the dogfish is taking place.

It is not known whether the observed temperature increase toward the limits of the observed range for dogfish would have a direct physiological impact on dogfish or an indirect impact through changes in the food web, but both could cause changes in maturity, fecundity, or growth. For example, Pacific herring (*Clupea pallasii*), one of the most common dogfish prey items (Bonham, 1954; Jones and Geen, 1977a), has declined in abundance in the Puget Sound by about 50% from 1985 to 2000 (Stout et al., 2001). Although the causes of this decline are not well understood, changing temperatures may play a role, and the decline in herring could contribute to the environmental pressures on dogfish.

A potential impact of these environmental pressures is a shift in distribution of

spiny dogfish away from Puget Sound toward the Strait of Georgia or coastal waters. Movement of dogfish between these areas is known to occur (McFarlane and King, 2003; Taylor et al., 2008), but the distribution of releases of tagged dogfish may not be sufficient to estimate changes in movement rates (Taylor, 2008). Nevertheless, water temperatures in the Strait of Georgia have not risen at the same rate as those in Puget Sound (Beamish et al., 2007), and herring abundance has been stable (DFO, 2005), so this area may be attracting dogfish. A northward shift in dogfish distribution could contribute to both the observed declines in Puget Sound dogfish abundance (Palsson, 2008) and the observed stability of dogfish abundance in the Strait of Georgia (King and McFarlane, 2008). A northward movement would likewise be consistent with the observed increases in some indices of abundance for dogfish in Alaskan waters (Menon, 2004; Courtney et al., 2006). The dogfish remaining in Puget Sound under such a large-scale change in distribution might be different enough from the population 60 years ago to partially explain the changes in demographic parameters observed in this study, even in the absence of density dependent change.

Hypothesis 3: intrinsic effects

Under this hypothesis, the observed changes in demographic parameters are the result of density-dependent responses to decreased abundance of dogfish due to fishery removals.

The estimated changes in demographic parameters from the 1940s to the 2000s (Figure 4.8) are all consistent with the patterns expected from a compensatory response to a reduced density of dogfish in Puget Sound: fecundity and growth rate increasing, age and length at 50% maturity decreasing. A decrease in length at 50% maturity and increase in fecundity were also observed in NW Atlantic spiny dogfish over a 20 year period and assumed to be density dependent effects (Silva and Ross, 1993; Sosebee, 2002).

The 1940s samples considered in this study are representative of the demography

of dogfish prior to the intense liver fishery. The fishery expanded rapidly in 1941 (Ketchen, 1986; Figure 4.2), just prior to the sample collection in 1942 and 1943. However, the observed maturity of the sampled dogfish likely reflect processes that had been in place for decades, not just the conditions at the time of sampling. Likewise, the two year gestation period of dogfish means that the number of embryos per litter in 1942-43 is likely to be representative of conditions at the start of the fishery. Therefore, it may be assumed that the intense liver fishery for dogfish had only a minor effect on the observed patterns of maturity and fecundity for the 1940s dogfish.

Conversely, the dogfish collected in the 2000s would reflect conditions in Puget Sound that may include lingering effects of the liver fishery. Many of the mature dogfish in the 2000s would have been born during a period of reduced abundance due to the liver fishery of the 1940s. Furthermore, the harvest of dogfish from 1975 onward (Figure 4.2), may have been sufficient to prevent the population from rebuilding to its former abundance.

The hypothesis of density dependence is based on the assumption of a decline in abundance of dogfish in Puget Sound due to the liver fishery in the 1940s. Commercial CPUE data from Puget Sound is only available from 1970s onward and surveys of fish abundance in Puget Sound began in the late 1980s (Palsson, 2008). Although both indices show declines in abundance during the 1990s, they cannot be used to directly measure of the impact of the 1940s fishery. The population dynamics model of Wood et al. (1979) predicted significant declines in abundance due to the liver fishery, followed by rebuilding to near their virgin biomass by the 1970s. A more recent population dynamics model, (Taylor, 2008) showed similar declines, but less rebuilding. In both models, the dogfish population experienced reduced abundance in the 1950s and 1960s that could have caused the observed changes in fecundity, maturity, and growth between the 1940s and 1970s.

4.5.2 Comparison with previous studies

Demographic analyses have been conducted in recent years for dozens of elasmobranch populations, allowing comparisons of life-history patterns across species (Smith et al., 1998; Cortés, 2002; Gallucci et al., 2006). These studies have established both the inter-specific variability in shark demography and the vulnerability of many species to overfishing, as indicated by low rates of population growth, especially those which are long-lived and late to mature like spiny dogfish (Cortés, 2002).

Few studies have had sufficient data to make spatial or temporal comparisons of demographic traits within a shark species. Cope (2006) examined intra-specific differences in life-history patterns between ocean basins and Vega (2006) compared demographic differences for spiny dogfish across a latitudinal gradient. Temporal differences have been observed in growth of the sandbar, Atlantic sharpnose, and porbeagle sharks in the NW Atlantic (Sminkey and Musick, 1995; Carlson et al., 2003; Cassoff et al., 2007). Changes in length at maturity have been observed for the spiny dogfish and Atlantic sharpnose shark, also in the NW Atlantic (Silva and Ross, 1993; Sosebee, 2002; Carlson et al., 2003). Changes in fecundity were observed for spiny dogfish in the NW Atlantic, but not found to be statistically significant (Silva and Ross, 1993; Sosebee, 2002). These species all experienced declines in abundance over the study periods and the observed changes were all in the direction expected from density-dependent responses to reduced abundance. That is, all observed changes in growth have been increases (Sminkey and Musick, 1995; Carlson et al., 2003; Cassoff et al., 2007), and all observed changes in size at maturity have been decreases (Silva and Ross, 1993; Sosebee, 2002; Carlson et al., 2003).

All of the previous temporal comparisons of shark demography used samples collected only 10-20 years apart, with the exception of 40 years for Cassoff et al. (2007). Environmental changes in these short time periods were small compare to presumed changes in abundance, so in each case the authors attributed the observed differ-

ences in demographic parameters to density dependent causes. In contrast, the 60 year period considered in this study has been long enough to include both large-scale environmental changes and fishery impacts in the NE Pacific ecosystem.

Comparison of the 1940s and 2000s estimates from this study with the published 1970s and 1980s estimates (Ketchen, 1972; Saunders and McFarlane, 1993) divides the 60 year period considered here into two phases, the first from the 1940s to the 1970s/80s and the second from the 1970s/80s to 2000s (Figure 4.5, Table 4.1). If all estimates are assumed to be comparable, then this comparison allows a consideration of the timing of the changes relative to potential causes. The biggest changes in age at 50% maturity, fecundity, and the three von Bertalanffy growth parameters all occurred in the first phase when SST was relatively stable. Only length at 50% maturity changed more in the second phase than in the first, during the period when SST was increasing, a pattern that may be attributed to the combination of faster growth and earlier age at maturity. The predominance of the changes having occurred in the first phase suggests that depletion resulting from the 1940s fishery removals was a larger factor in the demographic changes that took place than changing ocean temperatures, which primarily occurred in the second phase, after the period of greatest demographic change.

4.5.3 Conclusions and implications

The evidence favoring density dependence over climate as the dominant cause of the observed changes in demographic parameters is not definitive and may require years of further study to confirm. Nevertheless, some implications are clear. If the demographic changes are indeed an intrinsic effect, then the potential for dogfish in the NE Pacific to rebuild after fishery removals is low. The increase in population growth associated with the faster growth, earlier maturity, and greater fecundity associated with the 2000s compared to the 1940s is just over 1%. This is a small change compared to the magnitude of the changes in demographic parameters, with

the age of 50% maturity having decreased by more than 11 years (25%) and the fecundity having increased by almost 1 pup per litter (12% for a 100 cm dogfish). The impact of the change in maturity is dampened by the slope of the fecundity at length relationship (Figure 4.6), where younger, smaller dogfish will have few pups, even if they mature earlier.

The resulting 1% increase in population growth is also small compared to the potential rebuilding rates of the spiny dogfish population in the NW Atlantic, which can increase at 7% per year in the absence of fishing (NEFSC, 2006). The higher rates of population growth in the Atlantic are expected due to their earlier age at maturity (12-15 years), but did not prevent the population there from being overfished (NEFSC, 2006). If survival is also density dependent, then the NE Pacific dogfish population could grow faster than 1%, but could not expand at rates similar to the Atlantic population unless natural mortality fell to 0, which is biologically unfeasible.

If the observed changes in demography are instead the result of environmental effects, then managers may be faced with the need to manage a population which would not return to its virgin state even in the absence of fishery removals. If the warming of Puget Sound waters in recent decades has caused a northward shift in distribution of dogfish, the division of catch between the United States and Canada would become more complex, and the potential for a sustainable commercial fishery at an economically viable level in Puget Sound may be reduced.

The changes observed in demographic parameters over 60 years for the longest lived shark population provide insights into changes that could have occurred or will occur in other spiny dogfish populations throughout the world. Indeed, similar changes may have occurred in many long-lived species, and samples held in museum collections, such as those that formed the basis of this study, may yet provide information covering sufficient time scales to make the necessary comparisons. Understanding changes in growth, fecundity, and maturity, like those observed for spiny dogfish in this study, will be crucial to fully understanding the global decline of many sharks and

other long-lived species. This understanding will surely also play a role in managing their recovery.

4.6 Tables

Table 4.1: Estimated parameters and quantities of interest with CVs and sample sizes. 1940s and 2000s values are from this study and 1970s values are Ketchen (1972) and Saunders and McFarlane (1993).

| | 1940s | 1970s | 2000s | p-value |
|-------------------------------------|----------------|---------------|----------------|----------------|
| Age at maturity | $n = 299$ | $n = 3068$ | $n = 499$ | |
| Age at 50% maturity (yrs) | 44.8 (2.7%) | 35.5 (0.7%) | 33.5 (2.5%) | < 0.0001 |
| δ -age (yrs) | 16.0 (7.3%) | 17.0 (*) | 24.3 (6.7%) | |
| Length at maturity | $n = 430$ | $n = 3068$ | $n = 516$ | |
| Length at 50% maturity (cm) | 94.0 (1.0%) | 93.9 (0.3%) | 88.2 (0.6%) | < 0.0001 |
| δ -length (cm) | 10.3 (8.6%) | 12.6 (*) | 10.9 (5.3%) | |
| Fecundity | $n = 168$ | $n = 190$ | $n = 106$ | |
| Slope (embryos \cdot cm $^{-1}$) | 0.214 (8.6%) | 0.20 (6.5%) | 0.214 (8.6%) | |
| Intercept (embryos) | -15.5 (12.6%) | -13.24 (9.6%) | -14.7 (12.6%) | 0.0069 |
| Embryos per litter at 100cm | 5.87 (3.4%) | 6.76 (1.3%) | 6.70 (3.4%) | |
| Growth | $n = 299$ | $n = 3068$ | $n = 499$ | |
| L_∞ (cm) | 140.2 (6.4%) | 114.9 (*) | 109.3 (2.5%) | |
| k (yr $^{-1}$) | 0.0230 (14.9%) | 0.04 (*) | 0.0476 (11.6%) | < 0.0001 |
| t_0 (yrs) | -5.04 (33.1%) | -3.56 (*) | -2.044 (90.7%) | |
| ω (cm \cdot yr $^{-1}$) | 3.237 (7.1%) | 5.02 (*) | 5.208 (6.9%) | |

Note: CVs are in brackets where (*) indicates CV couldn't be determined from published literature. δ -length and δ -age represent the differences in length and age between 50% and 95% maturity (Appendix A). Growth parameters (L_∞ , k , t_0 , and ω) are standard parameters associated with von Bertalanffy growth function(Gallucci and Quinn, 1979). P-values are for the two-sided test of whether 1940s and 2000s values are significantly different from each other. Tests are described in the methods.

Table 4.2: Results of the analysis of covariance for fecundity as a function of length, time period, and sampling location.

Full model:

| Variable | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|-------------|-----|---------|---------|---------|-----------------------|
| TL | 1 | 690.54 | 690.54 | 127.73 | 1.8×10^{-24} |
| Period | 1 | 39.87 | 39.87 | 7.37 | 0.0070 |
| Location | 1 | 0.99 | 0.99 | 0.18 | 0.6691 |
| TL×Period | 1 | 3.29 | 3.29 | 0.61 | 0.4363 |
| TL×Location | 1 | 6.57 | 6.57 | 1.22 | 0.2712 |
| Residuals | 268 | 1448.88 | 5.41 | | |

Reduced model:

| Variable | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|-----------|-----|---------|---------|---------|-----------------------|
| TL | 1 | 690.54 | 690.54 | 128.20 | 1.4×10^{-24} |
| Period | 1 | 39.87 | 39.87 | 7.40 | 0.0069 |
| Residuals | 271 | 1459.72 | 5.39 | | |

Note: TL is the continuous variable for total length. Period is a factor for the time period of the sampling (1940s or 2000s), and Location is a factor for the sampling location (either coastal or Puget Sound waters).

4.7 Figures

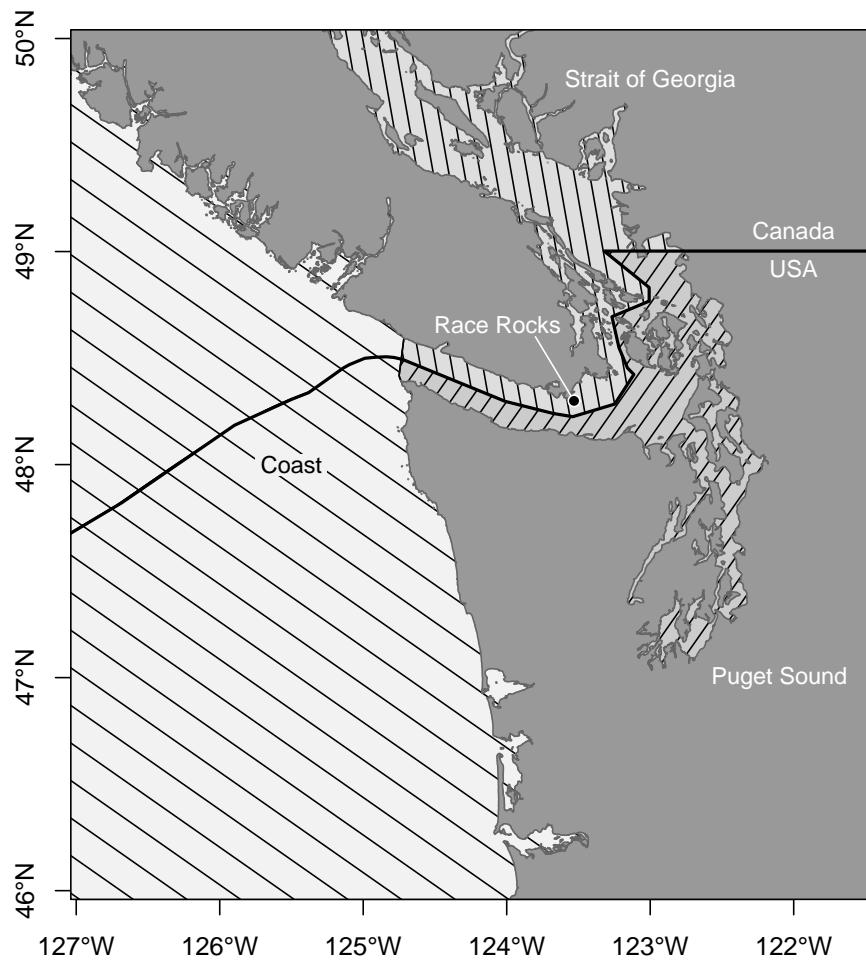


Figure 4.1: Map of areas described in the analysis. Dark grey areas indicate approximate sampling locations for the three time periods combined. Coast locations were only used in the 1940s and Strait of Georgia locations were only used on the 1970s/1980s.

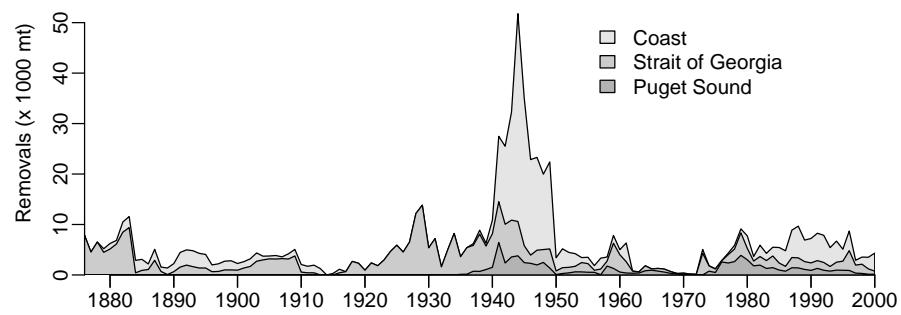


Figure 4.2: Estimated removals due to directed fishing of spiny dogfish in the NE Pacific corresponding to the areas in Figure 4.1.

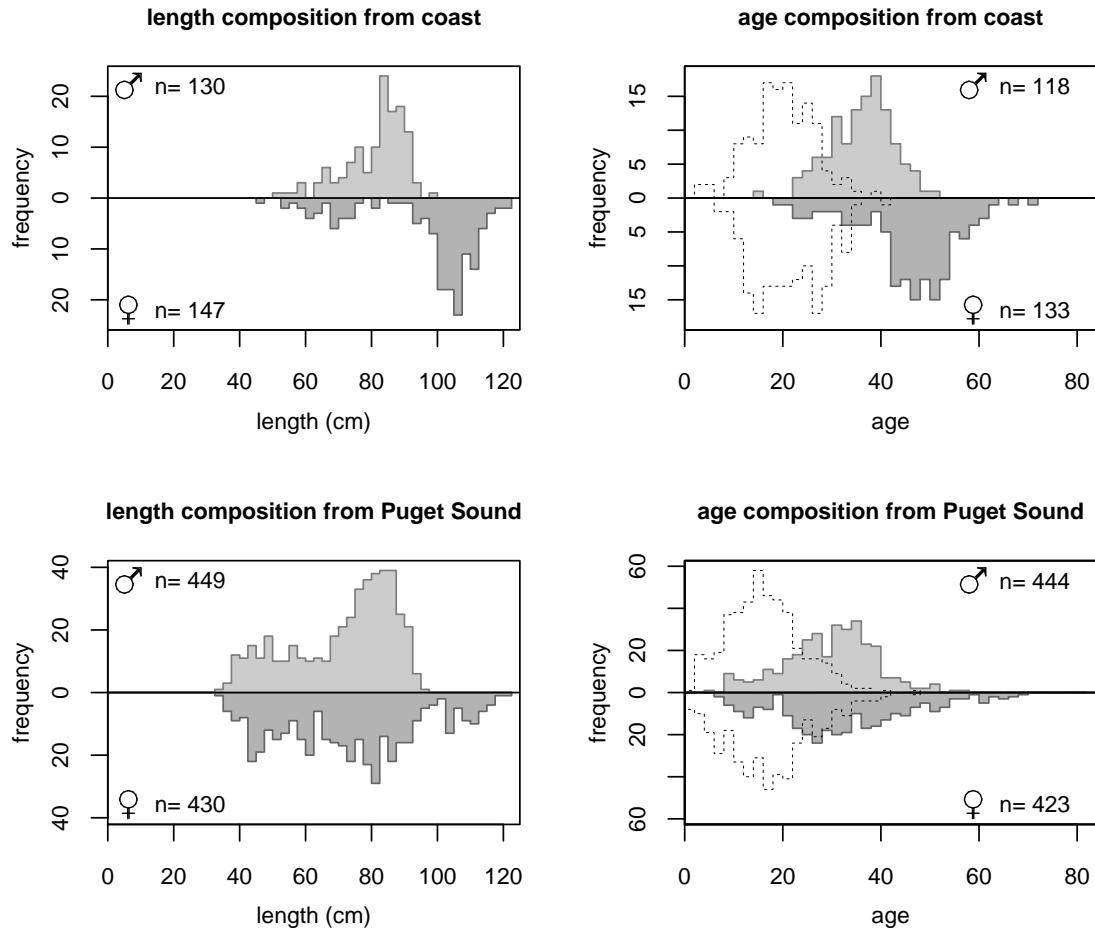


Figure 4.3: Histograms of length and age compositions from coastal and Puget Sound dogfish sampled in the 1940s. Males are shown above the zero line, and females below. Open polygons on right panels show composition of annuli counts before extrapolation for worn spines and shaded polygons show composition of estimated ages after extrapolation.

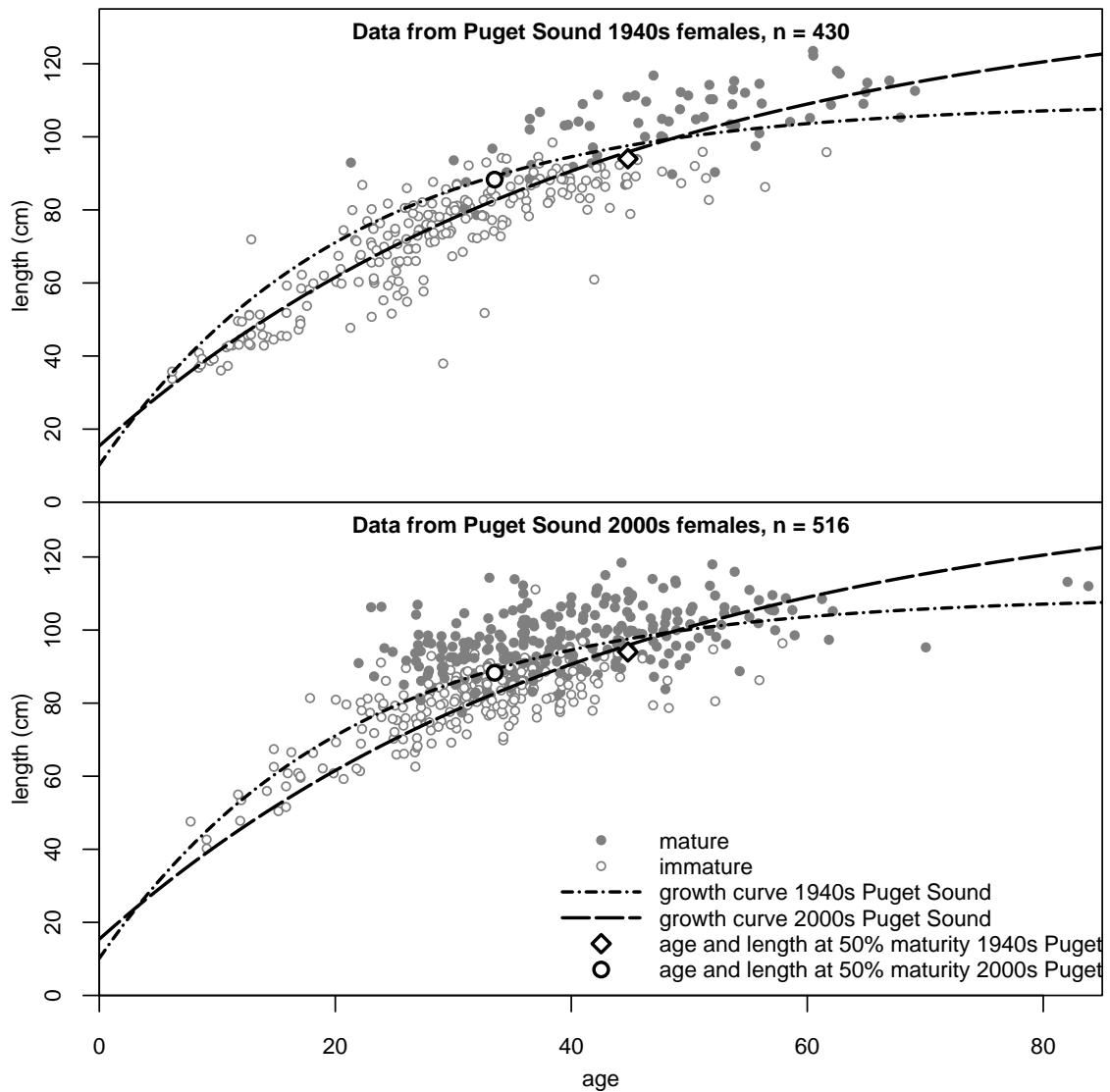


Figure 4.4: Estimated growth curves and maturity parameters for female dogfish sampled in Puget Sound in the 1940s and the 2000s. Length and age values for samples from the 1940s are shown in the top panel and from the 2000s in the lower panel, with mature dogfish designated by filled circles.

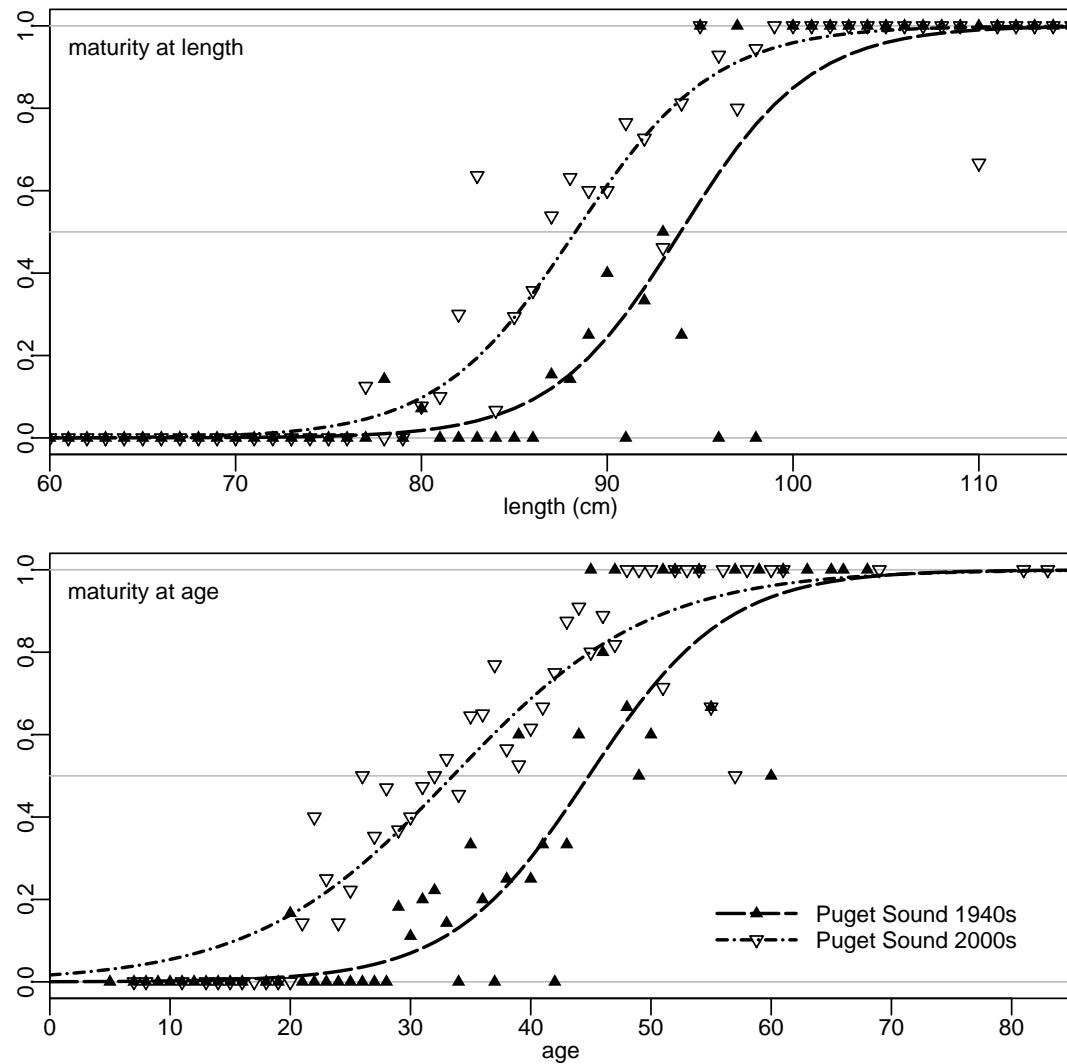


Figure 4.5: Fraction mature by length and age with results of logistic regression. Fraction mature is displayed for age estimates rounded to the nearest year, and lengths in 2cm bins, but regression is applied to individual observations.

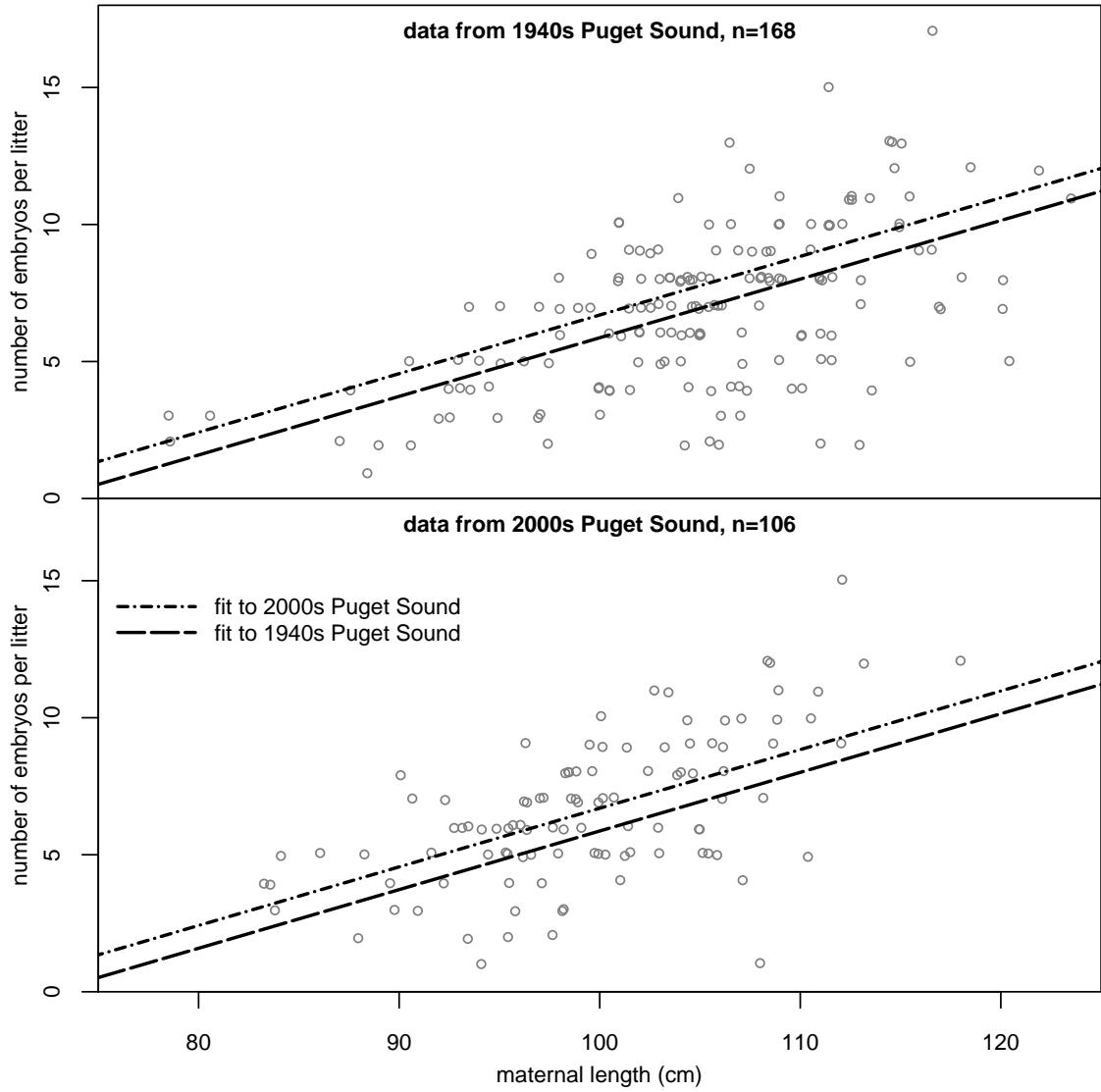


Figure 4.6: Relationship between maternal length and embryos per litter. Data from the 1940s are shown in the top panel and from the 2000s in the lower panel. The same linear models are shown in both panels to facilitate comparison.

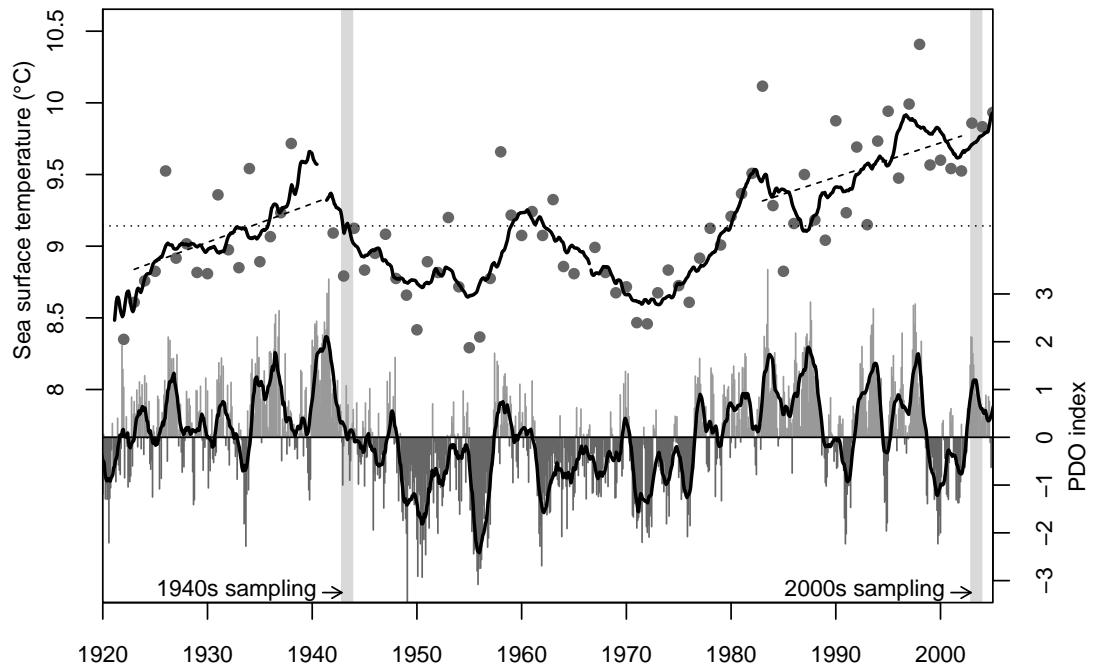


Figure 4.7: Annual mean sea surface temperature (SST) from the Race Rocks Lighthouse with 5 year moving average (top) and monthly Pacific Decadal Oscillation index with 1 year moving average (bottom). Grey vertical bars designate the two sampling periods, and dashed lines show linear fit to SST values for 20 years prior to each sampling period.

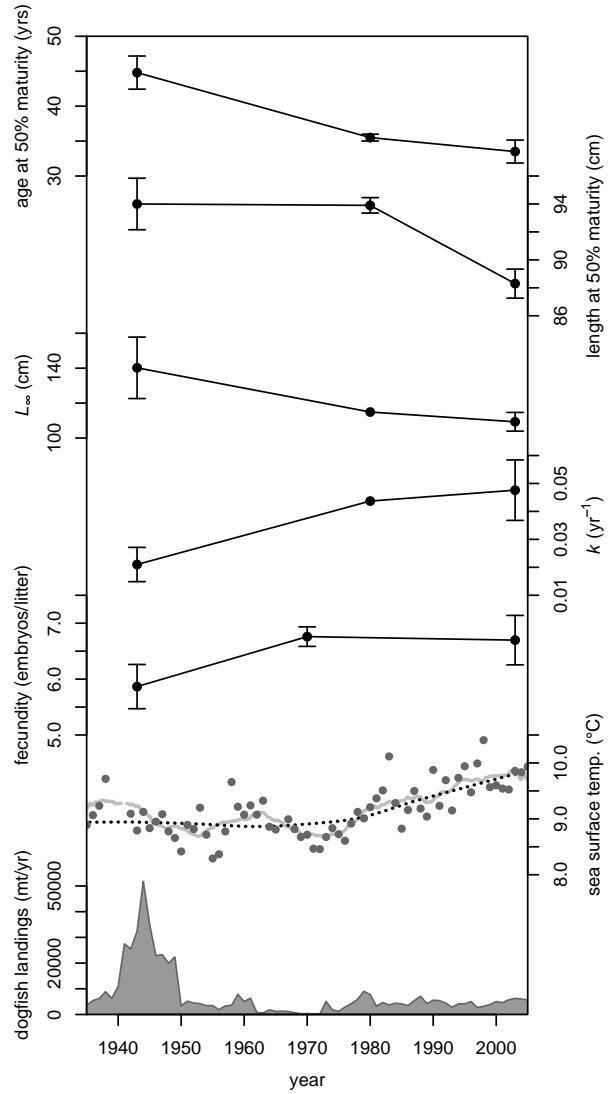


Figure 4.8: Summary of parameter estimates with comparison to sea surface temperature and landings in Puget Sound. Values from 1940s and 2000s are estimates from this study based on samples from Puget Sound. Values from 1970s and 1980s are from and, Ketchen (1972) and Saunders and McFarlane (1993) based on samples from Strait of Georgia. No CVs were available for growth parameters (L_∞ and k) from Strait of Georgia. SST values (in $^{\circ}\text{C}$) are from Race Rocks Lighthouse. Grey line is 5 year moving average of the daily SST values and dotted line is Loess Curve (Cleveland, 1979) fit to the annual averages.

Chapter 5

A METAPOPULATION MODEL FOR SPINY DOGFISH IN THE NORTHEAST PACIFIC

5.1 *Introduction*

The spiny dogfish, *Squalus acanthias*, is a small demersal shark with a worldwide distribution in temperate waters. Records of commercial harvest of dogfish in the NE Pacific date back to 1876, and archaeological evidence indicates dogfish were harvested for thousands of years prior to this time (Ketchen, 1986). In the early 1940s, an increase in demand for vitamin A, combined with the cessation of cod liver oil imports from Europe due to World War II, led to an intense fishery for dogfish livers in these waters (Bonham et al., 1949; Ketchen, 1986). While market reasons were an important factor influencing the decline of this fishery, an index of abundance derived from a sunken gillnet fishery in Northern British Columbia, Canada showed a 60% decline over 3 years from 1943 to 1946 (Barracough, 1948). Since 1975, exports of dogfish to Europe have supported a small commercial fishery for dogfish in the NE Pacific. Spiny dogfish have been listed by IUCN as globally “vulnerable” and “critically endangered” in the NE Atlantic (Fordham et al., 2006). In the NW Atlantic, the U.S. declared dogfish overfished in 1998 and they have failed to rebuild at the expected rate since then (Rago et al., 1998; NEFSC, 2006).

The first population dynamics model for spiny dogfish in the NE Pacific (Wood et al., 1979), was also the first age-structured population dynamics model applied to any elasmobranch population. This model considered two areas: inside waters (including the Strait of Georgia and Puget Sound), and outside waters (including the coastal waters of Canada and the U.S.). Although movement between these areas

was not included in the model, Wood et al. (1979) noted that anecdotal reports of large increases in abundance in the 1950s may have been the result of immigration from less exploited populations. In the time since this model was developed, the ageing methodology was revised and validated, (McFarlane et al., 1987; Saunders and McFarlane, 1993; McFarlane and King, 2008b), leading to the conclusion that in the N. Pacific, dogfish were slower growing and later maturing than in any other part of their worldwide distribution, and longer lived and later maturing than any other elasmobranch population. These age estimates and the differences between dogfish in the N. Pacific and the N. Atlantic that they reveal, were further validated through the use of bomb radiocarbon dating of dorsal spines (Campana et al., 2006).

The understanding of the long life-span of dogfish in the NE Pacific and the increasing demand for seafood products contribute to the need for an updated model of the population dynamics of spiny dogfish in the NE Pacific. Several challenges inhibit this effort. First, no index of abundance spans the full geographic range of spiny dogfish in the NE Pacific, which extends from Mexico to Alaska (Ketchen, 1986). Second, the indices of abundance cover relatively short time periods compared to the history of commercial exploitation of the species. Third, dogfish bycatch is one of the largest components of discards in commercial fisheries on the U.S. west coast (Hastie and Bellman, 2006), so landings data form an incomplete picture of dogfish mortality. The volume of dogfish bycatch also indicates that the status of the dogfish population is important not just for commercial fisheries targeting dogfish, but the many commercial fisheries with dogfish bycatch which would be impacted by any required reductions in dogfish mortality.

Analysis of tagging data (Chapter 2; McFarlane and King, 2003) indicates that movement rates among areas within the NE Pacific are neither so low compared to the potential population growth of the species as to be ignored, allowing the areas to be treated separately, nor so high as to allow the NE Pacific to be treated as a single homogeneous unit stock. Thus, each abundance index may provide information

about local changes in abundance that could be partially, but not totally, connected to the changes in abundance in other areas.

A spatially structured metapopulation model is the best choice in this context for both making use of available data and attempting to capture sufficient complexity of the population dynamics of spiny dogfish in the NE Pacific. Here the term metapopulation is used in the general context of Kritzer and Sale (2004), to describe a set of sub-populations, each with their own population dynamics, that are connected through movement or dispersal.

The integration of tagging data into such a population dynamics model (Hilborn, 1990; Maunder, 1998; Punt et al., 2000) has the benefit of both providing estimates of movement rates among areas, and also utilizing an additional source of information on abundance through the comparison of the observed numbers of recaptures with the number that might be expected for a given set of parameters combined with the catch history.

Although this metapopulation model accounts for age- and spatial-structure of the dogfish population in the NE Pacific, it is acknowledged that this remains a simplification of the true population dynamics of this long-lived, unique species, which may include a variety of elements that are not considered here.

5.2 Methods

5.2.1 Overview

The population dynamics model is structured by age, sex, area, and tag group. Recruitment is deterministic and survival is density dependent. The model was assumed to start at an equilibrium state in 1935, and the final year of the model was 2006. Prior distributions were assumed for all estimated parameters and Bayesian posterior distributions were calculated for these parameters and other quantities of interest.

5.2.2 Designation of Areas

Five areas were considered in the analysis (Figure 5.1): Puget Sound (PS), the Strait of Georgia (SG), the U.S. Coast (USC), the West Coast of Vancouver Island (WCVI), and Northern British Columbia (NBC). These areas were chosen primarily based on the level of detail in the historic landing records (Ketchen, 1986). They also corresponded to the areas where tags had been released and allowed estimation of rates of movement between U.S. and Canadian waters and between coastal waters and the inside waters Puget Sound and the Strait of Georgia. The divisions among areas are formed by the U.S.-Canada border, and the Bonilla-Tatoosh line at the mouth of the Strait of Juan de Fuca, a common boundary for statistical areas (Evans, 1998).

Dogfish in Alaskan waters are the subject of ongoing studies (Rice et al., 2008), but were not considered in this analysis. The connection between dogfish in Alaska and waters to the south is poorly understood due to the lack of historical tagging experiments in Alaskan waters and the absence of a directed dogfish fishery during periods of the tagging experiments in other areas. Extension of the metapopulation model to include Alaskan waters and the results of the ongoing studies is a goal for future research. Although dogfish tagged in the NE Pacific have been recaptured in the waters of Mexico and Japan (McFarlane and King, 2003; Taylor et al., 2008), such events are infrequent and these areas have also been excluded from the model.

5.2.3 Data Sources

Catch history

Directed fishing for dogfish had taken place as early as 1876, but had remained fairly steady below 10,000 mt per year. 1935 was chosen as the start to speed up the computation of the model under the assumption that the population would have been at an equilibrium at that point, although below the level that would have been

associated with the non-commercial fishing that had taken place for millenia in the NE Pacific (Ketchen, 1986). The directed catch of spiny dogfish from 1935–2006 (Figure 5.2) was compiled from data in Ketchen (1986), McFarlane and King (2003), Palsson (2008), and the PacFIN database (Sampson and Crone, 1997). Bycatch of spiny dogfish was estimated using data from the West Coast Groundfish Observer Programs Hastie and Bellman (2006) and the At-Sea Hake observer program (Dorn, 1998). An explanation of the sources and computation of catch and bycatch values is given in Appendix C.

Indices of abundance

Indices of abundance were available for all areas (Table 5.1). Both standardized surveys and fishery CPUE were assumed to be proportional to the biomass in that area selected by the particular gear type. In cases where variances of the indices were unavailable, CVs of 0.4 were assumed for fishery independent surveys and 0.6 for fishery dependent CPUE. The survey CV was consistent with the surveys with known CV, and the higher CV for catch rate was chosen to account for the belief that fishery dependent catch rate data are not standardized to the extent that fishery independent survey data are standardized. It is recognized that this issue is distinct from observation error, but this higher CV was a simple way to reduce the influence of the fishery CPUE data relative to the fishery-independent surveys.

Age and length comps

Length compositions of dogfish catch were available from a variety of sources (Table 5.5). Total length with the tail extended (in cm) was used as the standard form of length. When length records were known to be measured with a different measurement technique, lengths were converted using allometric relationships fit to dogfish that had been measured multiple ways (Chapter 3; Tribuzio, 2004). The sample size used in the statistical fit to the age and length comps was assumed to be 1/10 the

observed number of sharks measured to partially account for the intra-haul correlation of the samples (Pennington and Vølstad, 1994). The NMFS surveys in the USC area, one of the few data sources for which the number of hauls was available, had an average of 40 fish sampled per haul, so the 1/10 value reduces the statistical sample size to 4 per haul.

Tagging data

Tagging data from three studies were incorporated into the model. Approximately 9,800 dogfish were tagged in the NE Pacific from 1940 to 1946, during the peak of the dogfish fishery in this area (Bonham et al., 1949; Holland, 1957). The tagging was primarily conducted in the inside waters of the Puget Sound and the U.S. part of the Strait of Georgia. About 2,000 tags were also released along the Coast of Washington State and the West Coast of Vancouver Island during the 1940–1946 period. A larger experiment with approximately 24,200 tagged dogfish, was conducted from 1969 to 1972. The majority of these releases were again in inside waters, but about 6,800 tags were released on Swiftsure Bank in coastal waters (Fujioka and DiDonato, 1974; Fujioka, 1978). The largest tagging experiment in the NE Pacific was conducted in British Columbia from 1978 to 1988. Approximately 70,800 tagged dogfish were released in the Strait of Georgia, the West Coast of Vancouver Island, and Northern British Columbia (McFarlane and King, 2003). The data from these tagging experiments were divided into 8 tag groups covering all combinations of tagging experiment and release area (Table 5.3).

5.2.4 Population dynamics

The population dynamics were all assumed to be discrete events for computational convenience. The growth and maturation of dogfish take place on such long time scales, and the natural mortality is so low, that the order of these events, and their treatment as discrete rather than continuous, are unlikely to make large differences in

the results. The population dynamics were assumed to occur in the following order: census, tagging, movement, harvest, natural mortality, tagging, pupping, growth, maturation. Tagging occurs twice because half the tags were assumed to be released prior to harvest and recapture and half after. This is an approximation to the true pattern of tagging sporadically throughout the year, and allows the model to match the observed pattern of some tags moving and/or being recaptured in the year of release without making all the tags available for movement or recapture in the year of release. The elements of the population dynamics are described in greater detail below and illustrated in Figure 5.3.

Maturity and fecundity

Maturity was assumed to be a logistic function of age, with the proportion of females mature at age x given by,

$$m_{yx} = \left(1 + e^{-\log(19)(x-x_{50,y})/\delta_y}\right)^{-1}, \quad (5.1)$$

where $x_{50,y}$ is the age at 50% maturity in year y and δ_y is the difference between the ages at 95% maturity and 50% maturity in year y (Chapter 3 Appendix B; Punt and Walker, 1998).

The number of pups per litter for mature females was assumed to have a linear relationship, with the number of pups per litter for a female of length l (Chapter 3; Ketchen, 1972), given by

$$pups_l = pups_y^{100cm} + (l - 100) pups_y^{slope}, \quad (5.2)$$

where $pups_y^{100cm}$ is the number of pups per litter for a mature 100 cm dogfish in year y , and $pups_y^{slope}$ is the change in litter size associated with a 1 cm change in maternal length in year y . Half of all mature females were expected to give birth each year,

based on the two year gestation period Ketchen (1972).

Combining equations (5.1) and (5.2) and the distribution of lengths at a given age gives the fecundity for a female of age x as

$$fec_{yx} = m_{yx} \sum_l \phi_{lx} pups(l)/2, \quad (5.3)$$

where ϕ_{lx} is the proportion of females of age x in length bin l . A 1:1 sex ratio was assumed and all pups were initially assigned to the area in which they were born.

Previous analysis (Chapter 3) indicated that maturity and fecundity of dogfish in the NE Pacific changed significantly between the 1940s and the 2000s. Maturity and fecundity parameters used in the model (Table 5.5) were taken from this analysis, which included samples collected in the Puget Sound in the 1940s and 2000s (Chapter 3), and from published values (Ketchen, 1972; Saunders and McFarlane, 1993). To include this temporal change in the model, parameters describing fecundity and maturity were assumed to change linearly over time between estimated values and remain constant before and after the available estimates. The previous analysis (Chapter 3) found that time of changes in maturity and fecundity took place prior to observed warming ocean temperatures. This indicated that the changes were more likely to be density dependent effects than the result of extrinsic environmental forces. Under this hypothesis, the fecundity estimates from the 1970s and 1980s (Ketchen, 1972; Saunders and McFarlane, 1993) are likely to be the result of the 1940s removals (Figure 5.2) and would have developed sometime between the 1940s fishing and the sampling events of the 1970s and 1980s described by Ketchen (1972) and Saunders and McFarlane (1993). An arbitrarily intermediate year, 1955, was chosen as the date associated with these parameters in this model (Table 5.5). The time varying maturity and fecundity were assumed to be constant across all areas in each year.

Growth

Growth was assumed to follow the von Bertalanffy growth curve and be uniform across areas but vary over time for females. The changes in growth for female dogfish described in Chapter 4 were treated in the same way as the maturity and fecundity parameters described above (Table 5.5). Growth parameters for males were assumed constant over time at the value estimated for the combined data from the 1940s and 2000s.

Growth was assumed to be constant across all areas for simplicity. Significant differences in growth rates have been found between northern and southern areas within U.S. coastal waters (Vega, 2006), but the growth rate of dogfish in Northern Puget Sound is similar to that of northern U.S. coastal waters and those estimated for BC (Saunders and McFarlane, 1993; Vega, 2006). The southern U.S. coastal waters where smaller maximum sizes were observed by Vega (2006) have lower dogfish densities than the northern part of the USC area and therefore represent a small fraction of the population in this area.

A CV of 0.13 was used for the observed lengths around the predicted values for each year. This CV was based on an empirical estimate of the combined 1940s and 2000s samples (Chapter 4) and used to compute a matrix of normally distributed length at age values for each year as described in Methot (2006). Changes in the proportion of length at age due to fishery removals were not considered.

Age 60 was used as an accumulator age, with all dogfish beyond 60 years included as a plus-group. Although dogfish have been aged over 80 years (McFarlane and King, 2003), they are close to their asymptotic size by age 60 and the reduction in age classes improved computation speed.

Survival

Annual survival was assumed to be constant across all ages in the population within each area and year, but allowed to change in response to changes in the density of the population in each area. For simplicity, the annual survival rate was assumed to decrease linearly as a function of the biomass (Figure 5.4), as,

$$S_{ya} = S^{\text{eq}} + S^{\text{frac}} (1 - S^{\text{eq}}) \left(1 - \frac{B_{ya}}{K_a} \right), \quad (5.4)$$

where S^{eq} is the survival rate that would result in an equilibrium population in the absence of movement and S^{frac} is a parameter controlling the limit of survival as the population becomes fully depleted, represented as a fraction of the difference $1 - S^{\text{eq}}$. B_{ya} is the biomass in year y in area a , and K_a is the equilibrium biomass in area a in the absence of movement. Survival is undefined for an exterminated population, but the limit of survival as the population approaches 0 comes directly from (5.4), as,

$$\lim_{B_{ya} \rightarrow 0} S_{ya} = S^{\max} = S^{\text{eq}} + S^{\text{frac}} (1 - S^{\text{eq}}). \quad (5.5)$$

The equilibrium survival rate S^{eq} was fixed at the value which resulted in a stationary population size at the maturity and fecundity values used in the initial year of the model, 0.931, which is equivalent to an instantaneous rate of natural mortality of 0.071.

This implementation of survival is similar to that used by Wood et al. (1979). A traditional stock recruit curve could also be used, but density dependent fecundity and maturity have already been included as described above. Therefore, a stock-recruit relationship would be describing density dependent survival of pups only. Their large size at birth suggests that any density dependent survival may be spread over more age classes.

Movement

Movement among areas was assumed to be a constant fraction of all ages in the population, and constant across years. Movement was assumed to take place between all pairs of adjacent areas, but no direct movement within a single year was assumed to take place between non-adjacent pairs. Thus, in the five area model, no movement occurred within a single year between Northern B.C. and the two areas in the U.S. waters (Figure 5.1). Movement between these non-adjacent pairs within a single year was rare in the tagging experiments, so the complexity of adding additional movement parameters was assumed to be of little benefit to the fit of the model to the majority of the tagging data. The probability of remaining within a given area in a given year was calculated as 1 minus the sum of the movement parameters associated with moving to other areas. The matrix of movement parameters for the 5 area model is,

| | | <i>From</i> | | | | |
|-----------|------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | | USC | PS | SG | WCVI | NBC |
| <i>To</i> | USC | $1 - \sum p_1.$ | p_{21} | p_{31} | p_{41} | 0 |
| | PS | p_{12} | $1 - \sum p_2.$ | p_{32} | p_{42} | 0 |
| | SG | p_{13} | p_{23} | $1 - \sum p_3.$ | p_{43} | p_{53} |
| | WCVI | p_{14} | p_{24} | p_{34} | $1 - \sum p_4.$ | p_{54} |
| | NBC | 0 | 0 | p_{35} | p_{45} | $1 - \sum p_5.$ |

where p_{ij} is the fraction of all dogfish moving from area i to area j in each year, and $\sum p_i.$ represents the sum of the p_{ij} over all j such that $j \neq i$, so that the columns of the matrix sum to 1.

Of the 25 cells in this matrix (5.6), the 5 diagonal elements are derived quantities and 4 values are fixed at 0, leaving 16 values to be estimated. Attempts to estimate all 16 values as independent parameters led to biologically unreasonable results, including estimates of movement showing that almost all dogfish from one area moved to the

next in a given year. This indicated that the available data may not be sufficient to reliably estimate so many movement rates. To reduce the number of estimated movement parameters, it was assumed that no areas in the model were sources or sinks, so the number of dogfish moving from area i to area j at equilibrium was equal to the number moving from j to i . This simplifying assumption requires,

$$B_{0i}p_{ij} = B_{0j}p_{ji}. \quad (5.7)$$

Under this strong equilibrium assumption, as long as two areas have the same level of depletion, there will be an equal exchange of biomass between them in a given year. If two adjacent areas have different levels of depletion, then there will be a net flow of biomass from the less depleted to the more depleted area. This assumption allows for the reduction of the number of movement parameters from 16 to 8. Rather than estimate half of the movement parameters as functions of the other half, each pair p_{ij} and p_{ji} were derived from a single, neutral parameter $p_{i\leftrightarrow j}$, which was their average,

$$p_{i\leftrightarrow j} = \frac{p_{ij} + p_{ji}}{2}. \quad (5.8)$$

Using equations (5.7) and (5.8) to solve for p_{ij} as a function of the neutral parameter and the equilibrium biomass values for two areas gives,

$$p_{ij} = p_{i\leftrightarrow j} \frac{2B_{0i}}{B_{0i} + B_{0j}}. \quad (5.9)$$

Gear selectivity

Selectivity was assumed to be a logistic function of age for all harvests,

$$\beta_{fx} = \left(1 + e^{-\log(19)(x - a_{50,f})/\delta_f}\right)^{-1}, \quad (5.10)$$

where $x_{50,f}$ is the age at 50% selectivity and δ_f is the difference between ages at 95% and 50% selectivity for fishery or survey f . Length-based selectivity was considered but had a worse overall fit to the data, indicating that selectivity may be due in part to an ontogenetic shift in availability to the gear (Ketchen, 1986).

All gear types were grouped as either trawl or non-trawl (Appendix C), with a separate pair of selectivity parameters estimated for each group. The grouping of all non-trawl gear together was necessary because of lack of length or age composition data from gillnet and recreational fisheries. Selectivity was assumed constant across all years in all areas for both gear groupings.

Tagging

All tagged dogfish were assigned an age in the model. This allowed the incorporation of the changes in selectivity that occurred as the tagged dogfish grew beyond their size at release. Tagging data available from the 1940s and 1970s experiments included the length and sex of each individual. A predicted age at release was estimated under the assumption that all tagged individuals grew according to the von Bertalanffy growth curve for their gender. Lengths greater than L_∞ or associated with ages greater than 60, the accumulator age, were all assigned to age 60. Tagging data from the 1980s did not include data on individual lengths, so the tagged population was assumed to have the age composition for dogfish sampled in the SG area in 1980, as described by Saunders and McFarlane (1993). A 1:1 sex ratio was assumed for these 1980s releases.

The tags were aggregated into groups associated with each combination of release area and tagging study (Table 5.3). The dogfish in these groups, which were structured by age, sex, and area, were projected in the model according to the same population dynamics as the untagged dogfish. To speed computations, the tag groups were only projected in the model for 15 years beyond the last tag release for that group. After 15 years, the remainder of the group were reassigned to the untagged population. This 15 year period encompassed all observed recaptures. Individuals estimated to

have lost tags due to tag shedding during this 15 year period are also reassigned to the untagged population.

The three tagging studies (1940s, 1970s, and 1980s) each used a separate tag type and were each assumed to have a separate rate of annual tag retention, S_g^{tags} . In the 1940s tagging experiment, a range of wire types were used to attach Peterson disk tags, and some differences in corrosion levels of recaptured tags was observed (Holland, 1957). However, the recapture rates associated with each wire type are confounded by the differences in fishing patterns over the periods of use for each type. Thus, for simplicity, a single tag retention rate was applied to all wire types from the 1940s experiment.

Loss of tags that occurs at the time of tagging due to either initial shedding or mortality induced by the tagging process is confounded with the loss of tags that occurs when recaptured tags go unreported by the fishers or processors (Hoenig et al., 1998). These factors all contribute to an overall reduction in the number of reported recaptured tags. Unlike the parameters described above for an annual rate of tag shedding, initial loss and reporting rate have the same impact on expected reported recaptures regardless of the time at liberty of the tagging fish. Without auxiliary information to help distinguish between these factors, they were combined into a single parameter, $r = \text{reporting rate} \times \text{initial tag survival}$, which was assumed to apply to all tag types for all years and areas. Thus, no differences in reporting rate between tag type or country of recapture is included.

5.2.5 Observation and statistical models

General framework

Much of the observation and statistical models were derived from elements of the far more complex Stock Synthesis 2 modeling framework (SS2) developed by Methot (2006). The treatment of indices of abundance and age and length compositions are

very similar to that used by SS2, with the incorporation of tagging data the only significant addition to the elements derived from SS2.

The observation model computes predicted values from the population dynamics model that are comparable to the observations made of the true dogfish population. The statistical model measures the fit of these predicted and observed values. A Bayesian statistical framework is used, so prior distributions are included in the statistical model for all the estimated parameters.

The objective function to be minimized, $\mathcal{L}^{\text{total}}$, is the negative log of the posterior density. The posterior density is the product of the prior parameter densities and components representing the fit of the expected to observed values for (a) the indices of abundance, (b) age and length compositions, (c) tag recaptures. The objective function is therefore the sum of the logs of these components. Each of these contributions is described below.

Indices of abundance

Indices of abundance were assumed to be lognormally distributed with the catchability parameter for index i which was integrated across a log-uniform prior following Walters and Ludwig (1994) as

$$q_i = \exp \left(\frac{\sum_i \ln(I_{iy}/\hat{B}_{iy}^{\text{selected}})/\sigma_{iy}^2}{\sum_i 1/\sigma_{iy}^2} \right) \quad (5.11)$$

where I_{iy} is the observed value of abundance index i in year y , and \hat{B}_{iy} is the corresponding expected biomass selected by the fishery or survey for that area and year, and σ_{iy} is the standard error of the I_{iy} . The contribution to the objective function for abundance index i is

$$\mathcal{L}_i^{\text{index}} = 0.5 \sum_y \left(\frac{\ln(I_{iy}) - \ln(q_i \hat{B}_{iy})}{\sigma_{iy}} \right)^2. \quad (5.12)$$

Age and length compositions

The observed and expected age and length compositions were compared using a multinomial likelihood. The lengths are binned into 5 cm bins from 20 cm to 120+ cm, and ages were binned into 2 year bins from age 0 to age 60+. To compute the expected length compositions, the proportion of each age in each length bin is assumed normally distributed and computed using the methodology used in SS2 (Methot, 2006). The observed proportions in each age or length bin were re-normalized after adding the constant 0.001 to avoid 0 values. The contribution to the objective function for the j th age or length composition data is

$$\mathcal{L}_j^{\text{comp}} = -n_j \sum_x p_{jx} \ln(\hat{p}_{jx}/p_{jx}), \quad (5.13)$$

where x is the index of age or length, p_{jx} is the observed proportion in that age or length bin after renormalization, and \hat{p}_{jx} is the corresponding expected proportion (Methot, 2006).

Ageing error is included in the computation of the expected age compositions as in SS2 (Methot, 2006), with a CV of the age estimates assumed to be 0.19 for all ages (Rice, 2007).

Tag recaptures

The contribution of the tagging data to the objective function was divided into two parts: a multinomial distribution for the proportions of annual recaptures by area, and a negative-binomial distribution for the total annual recaptures across areas. This approach is built on the method of Punt et al. (2000) which combined multinomial and Poisson distributions. Punt et al. (2000) chose this method to allow the incorporation of data where the area of recapture was unknown. In this model, the two-part distribution was chosen to allow a shift in the influence of tagging data on the estimation of the movement rates relative to the estimation of initial abundance. The proportions

of annual returns by area that go into the multinomial distribution are independent of reporting rate as long as the reporting rates are assumed to remain constant across all areas, while the total number of recaptures depends on the unknown reporting rate. The overdispersion parameter of the negative binomial (Hampton and Fournier, 2001), allows a reduction in the influence of the assumptions about reporting rate on the estimation of movement parameters.

The multinomial contribution to the objective function of the observed number of recaptures for a given tag release group and year of recapture (Punt et al., 2000) was

$$\mathcal{L}_g^{\text{tags1}} = - \sum_y R_{yg} \sum_{a=1}^{N_a} p_{yga} \log (\hat{p}_{yga}/p_{yga}) \quad (5.14)$$

where R_{yg} is the total number of recaptures in year y from tag group g , N_a is the number of areas in the model, p_{yga} , and \hat{p}_{yga} are the observed and expected proportion of the R_{yg} recaptures from tag group g and year y that took place in area a . The negative binomial contribution to the objective function (Hampton and Fournier, 2001) was

$$\begin{aligned} \mathcal{L}_g^{\text{tags2}} = & \sum_y \left\{ \log \left(\Gamma \left(R_{yg} + \frac{\hat{R}_{yg}}{(\tau - 1)} \right) \right) - \log (\Gamma (R_{yg} + 1)) \right. \\ & \left. - \log \left(\Gamma \left(\frac{\hat{R}_{yg}}{(\tau - 1)} \right) \right) - \frac{\tau R_{yg}}{(\tau - 1)} \log(\tau) + R_{yg} \log(\tau - 1) \right\} \end{aligned} \quad (5.15)$$

where R_{yg} and \hat{R}_{yg} are the observed and expected numbers of tags from tag group g recaptured in year y , Γ is the standard gamma function, and τ is the parameter controlling the degree of overdispersion, given as the ratio of the variance to the mean: $\tau = \frac{\text{var}(R_{yg})}{\text{E}(R_{yg})} = \frac{\text{var}(R_{yg})}{\hat{R}_{yg}}$. This function is undefined at $\tau = 1$. However, setting $\tau = 1.00001$ was found to produce results identical to replacing the negative-binomial with the Poisson distribution. Results described as associated with $\tau = 1$ were calculated in this way.

5.2.6 Prior distributions

Bayesian prior distributions were applied to all estimated parameters (Table 5.6). r and $p_{i \leftrightarrow j}$ are constrained by definition between 0 and 1, and uniform priors were used covering this interval. Large upper limits of 60 years for age at 50% selectivity and 30 years for difference in age at 50% and 95% selectivity were chosen for the uniform priors on the selectivity parameters as sufficient to encompass all likely values of these parameters. The range 4.6–16.1 for the uniform prior on the $\log(B_{0i})$ parameters corresponds to a broad B_{0i} range of 100 mt to 10,000,000 mt for each area. This too was chosen as being sufficient to cover all likely values. Uncertainty in fixed parameters was explored through sensitivity analysis.

5.3 Results

The results show a high degree of uncertainty in estimated initial biomass in the U.S. Coast (USC), Puget Sound (PS), and West Coast of Vancouver Island (WCVI) areas and less uncertainty in the Strait of Georgia (SG) and Northern British Columbia (NBC) areas. The uncertainty appears to be derived in part from the declining trend over the last two decades in the trawl survey USC area. This trend could not be easily explained from the history of fishing in this area, which had been declining in recent years, and generally low compared to the 1940s. As a result, the model tended to fit this index of abundance with either a low initial biomass (B_0) for the USC area which has been declining steadily since the 1940s and is now below 5% of B_0 in 2006 (Case A), or a high USC B_0 parameter which resulted in a smaller decline the in the 1940s and rebuilding since that time to 95% of B_0 in 2006 (Case B).

To illustrate the differences and similarities between these cases, many of the results are shown for both Case A and Case B. The inputs differ only in the fixed parameter chosen for the overdispersion parameter τ of the negative binomial distribution used to fit the observed and expected total number of tags recaptured annually

for each tag group, equation (5.15), with $\tau = 2$ for Case A and $\tau = 1$ for Case B. The parameter τ represents the ratio of the variance to the mean of the recaptured tags and changes the influence of the tagging data relative to other data sources. When τ is estimated freely, it goes to a high level and the tagging data provides very little information about abundance. Cases A and B both have 31 estimated parameters (Table 5.6).

The median estimate for the initial biomass of the 5 areas combined is 392,000 mt for Case A, and 549,000 mt for Case B (Figures 5.5 and 5.6; Tables 5.7). The combined population in 2006 is at 26% of the initial biomass in Case A and 92% in Case B. (Figures 5.7 and 5.8; Tables 5.8). The large difference in depletion between the two cases is largely due to the estimates for the USC, which has the largest B_0 estimate in both cases. USC has a median B_0 estimate of 96,000 mt for Case A and 316,000 mt for Case B.

Although sources and sinks were not allowed in the initial equilibrium, the smaller estimate of USC area in Case A causes it to act as a sink after the 1940s fishery depleted the population. In Case A, the USC area is estimated to decline to 3% of B_0 in 2006 and a net immigration to USC contributes to declines in all other areas, which would remain at a higher level in the absence of movement. Under Case B, the USC area is more than three times larger than in Case A and acts as a source population. As the populations depart from the equilibrium, USC declines only slightly due to the 1940s fishery and then returns to 95% of the B_0 in 2006, causing the other areas to remain at a higher level than would occur in the absence of movement.

Movement patterns were similar in the two cases. Movement rates between the coastal areas, USC, WCVI, and NBC, were higher in both cases than those related to the inside areas, PS and SG (Figures 5.5 and 5.6; Tables 5.7 and 5.8). In Case A, the highest median movement rate estimates, as defined by equations (5.7)–(5.9), were between NBC and WCVI at 0.14 (both northward and southward). Movement between USC and WCVI, the other pair of coastal areas, was 0.04 (northward) and

0.05 (southward). Movement between SG and WCVI was the highest of any related to the inside waters, at 0.03 into SG and 0.04 out of SG. Median estimates for all other movement rates in Case A were below 0.015 (Table 5.8; Figures 5.5). Under Case B, the higher estimate of USC biomass and lower estimates of WCVI and PS biomass compared to Case A meant that the initial equilibrium assumption required a large fraction of the smaller areas to be exchanged with a small fraction of the larger area to achieve equilibrium. Thus, the median estimate for movement was 0.59 from WCVI to USC and 0.19 from PS to USC while movement away from USC to WCVI and PS was estimated at 0.03 and 0.01, respectively.

The uncertainty represented by the Bayesian posterior distributions was generally small compared to the difference between the two cases presented. The CV for all estimated parameters was below 10% in both cases (with the exception of B_0 for WCVI in Case B with a CV of 13%). The difference in estimates between Case A and Case B was typically greater, resulting in 95% posterior probability intervals for the biomass and movement parameters that rarely overlapped between cases (Tables 5.7 and 5.8). Parameter density plots are only presented for Case A (Figures 5.9 and 5.10), but the uncertainty shown by these distributions is similar to that for Case B.

The model did not have trouble fitting the many indices of abundance which were relatively flat and thus uninformative, including the IPHC longline survey in WCVI, the DFO trawl survey in NBC and the three indices for SG (Figure 5.11). The model was also able to fit well the observed 1940s decline in the NBC area described by Barraclough (1948). The declines in PS indices during the 1990s were not fit well by the model in either case presented. As noted above, the decline in USC in the 1990s (Figure 5.12) was fit either by having the population experience a steady decline throughout the time series (Case A) or with a relatively flat trajectory through the middle of the data points (Case B).

The fit of the model to the tag recapture data was mixed (Figures 5.13 and 5.14). The 1980s tagging experiment which had releases in SG, WCVI and NBC had the

highest sample sizes and therefore the greatest influence on the model results and the best fit. Case A, which had the negative binomial overdispersion parameter (representing the ratio of the variance to the mean of the total recaptures) at $\tau = 2$ allowed the expected recaptures to differ more from the observed values than Case B where $\tau = 1$. In particular, the recaptures from the 1940s releases in PS were fit better in Case B (Figure 5.14) than Case A (Figure 5.13). Dogfish landings peaked in the 1940s, but the values used in the model were approximations based on liver oil so uncertainty in the total catch and the fraction of dogfish examined for tags may have contributed to the lack of fit for this time period.

The total number of recaptures for the first few years of the 1970s tagging experiment were not fit well in either case. The years 1969–73 had so few directed dogfish landings (Figure 5.2, Table C.1), and estimates of examined bycatch for these years were so uncertain, that the pattern of expected recaptures predicted by the model did not match the observations under any of the sensitivities considered. Therefore, the negative binomial fit for these 5 years were excluded from the objective function.

In general, the proportions of tags recaptured by area were estimated reasonably well by the model. In Case A, where movement was low between USC and WCVI to allow a greater difference in biomass trends between these areas, the releases in USC show higher than expected recaptures in WCVI and vice versa (Figure 5.13). In Case B, where the biomass trends were more synchronized and the estimated movement rates between USC and WCVI were higher, the fit to these proportions is better (Figure 5.14).

When rates of annual tag retention S^{tags} were estimated freely in the model, the retention of the Petersen disk tags used in the 1940s was estimated to be higher than the elongated disk tag used in the 1980s. This contradicts the observations that the 1940s tags corroded and caused wounding (Holland, 1957; McFarlane and Beamish, 1986) while the 1980s tags held with titanium pins had 100% retention over 3 years in captivity (McFarlane and Beamish, 1986). Under the assumption that the high

retention estimates for the 1940s were incorrect, tag retention for the 1940s and 1970s were fixed at $S_{1940s}^{\text{tags}} = 0.70$ and $S_{1970s}^{\text{tags}} = 0.80$, respectively, which were arbitrary values representing greater tag loss than that which was estimated for the 1980s, which had a median estimates of $S_{1980s}^{\text{tags}} = 0.90$ and $S_{1980s}^{\text{tags}} = 0.89$ for Cases A and B, respectively. The 95% posterior probability intervals for r , the parameter which combined reporting rate, survival of the tagging process, and retention of the tags, were 0.10–0.13 for Case A and 0.23–0.28 for Case B (Table 5.7). The low values in both cases imply either a high rate of initial mortality or tag loss at the time of tagging, or a low reporting rate at the time of recapture.

The model did not capture much of the variability in the observed length compositions (Figure 5.15). However, some of the larger patterns were approximated, and the use of separate selectivity functions for trawl and non-trawl fleets resulted in improvements over earlier models that assumed a single selectivity for all gear types. Some of the variability may be due to non-representative sampling caused by the schooling behavior of spiny dogfish and their segregation by size and sex (Ketchen, 1986). The objective contribution from the length composition data had a strong influence on the estimate of r (Figure 5.21). If more flexible functions were used, allowing features such as dome-shaped selectivity, the length compositions might have been fit more accurately and the influence of this data might have been more focused on the selectivity parameters about which it should be the most informative. The median estimate for age at 50% selectivity for the logistic trawl selectivity function is 13.1 years in Case A and 14.4 in Case B. For non-trawl gear the estimates are 27.9 and 26.5 for Cases A and B, respectively.

5.3.1 *Sensitivities*

A test of the influence of the indices of abundance on the model was conducted by examining the objective function contribution from only the indices under the assumption of no movement allowed between areas (Figure 5.16). Selectivity was

fixed at the values used in the base model.

The minimum objective function values (best fit) were achieved for all 5 areas at either the lowest possible values of B_0 (USC and PS) or the highest values of B_0 (SG, WCVI, and NBC). This pattern is due in part to indices in the two southern areas (USC and PS) which showed declines in the 1990s. At very high B_0 , the population is estimated to be unaffected by fishing and the trajectory is flat. At very low B_0 , the population was never able to recover from the impacts of fishing in the 1940s and has continued to decline ever since. The objective function was dome-shaped in between the high and low B_0 values, indicating that the intermediate B_0 values had the poorest fit. These poor fits at intermediate B_0 are associated with abundance trends that were depleted in the 1940s, but increasing during the period of declining indices of abundance. The fit of such increasing trends is worse than that of the declining trends that comes from low B_0 or the stable trends that comes from high B_0 .

Sensitivity analyses were conducted to estimate the influence of assumptions about model structure, inclusion of data sources, and fixed parameter values on the model results (Table 5.9, Figures 5.17–5.20). A variety of changes, sometimes relatively minor, resulted in a switching of the model from the depleted and declining state similar to Case A to a large, stable total population similar to Case B. Conditions that resulted in the highest 2006 biomass relative to the initial values in Case A were: increasing the sample size for the composition data, increasing the reporting rate parameter r , reducing the overdispersion parameter τ , and increasing the degree of density dependence survival. Setting all movement parameters to 0 resulted in B_0 estimates at the upper limit, resulting in a population rising steadily from B_0 as a result of the density dependent changes in growth and fecundity.

Separate sensitivity analysis was conducted to focus on the estimated parameter r , which represented the confounded variables reporting rate and initial tag survival (Figure 5.21), and the overdispersion parameter τ (Figure 5.22). In both analyses the

parameter estimates went through a rapid switch between states that were similar to Case A and Case B.

The estimates of initial biomass and overall depletion were sensitive to changes in r , resulting in a range of values for the 2006 depletion from 20% to 120% of the initial biomass for all areas combined. At $r > 0.2$, the parameter estimates resembled Case B, with a high USC B_0 estimate. Lower r values resulted in patterns that resembled Case A. If the posterior median for Case A, $r = 0.115$, is close to the true value, then either almost 90% of the recaptured tags go unreported, or the number of tags lost due to shedding or mortality immediately after release is very high. Captive dogfish showed no initial tag loss or mortality and 100% annual retention over 3 years for the elongated disk tags with titanium pins used in the 1980s study (McFarlane and Beamish, 1986). This suggests that if r is truly so low, then it must be attributed to a low reporting rate. The likelihood components that had the biggest influence over the reporting rate value were the length composition data (Figure 5.21), which fit better as r decreased, and the total tag recaptures, which fit better as r increased.

Changing the value of r caused large changes in the catchability coefficient, q , for the NMFS trawl survey in USC (Figures 5.11 and 5.21). This q is the average ratio of observed to expected dogfish biomass selected by the survey (the other surveys had neither the same comprehensive coverage within their area nor an available swept area estimate of absolute abundance). The value of q when r is set to minimize the objective function, $q = 19.3 \text{ or } \log(q) = 3.0$, would indicate that the model is predicting only about 5% of the biomass indicated by the swept area estimates from the survey. q is inversely related to r and if r is increased to 1, q falls to 0.157, a value associated with model predictions of biomass that are 6 times greater than the swept area estimates.

The sensitivity analysis for the overdispersion parameter τ (Figure 5.22), revealed a rapid switch between the two cases described above as τ is changed. When τ is close to 1, resulting in greater influence of the data on the total number of tags recaptured

for each tag group, the parameter estimates are similar to Case B, with USC biomass estimated above 300,000 mt and little estimated depletion in 2006. Between $\tau = 1.3$ and $\tau = 1.4$, the model estimates switch to a pattern like Case A with USC below 120,000 and a depleted 2006 biomass.

5.3.2 MCMC diagnostics

Bayesian posterior density estimates were computed using 2000 values that were sampled from an MCMC chain of length 400,000. Trace plots showed stability and the Raftery and Lewis convergence diagnostic (Raftery and S., 1995) indicates that the chain length was adequate.

In Case A the most positively or negatively correlated parameters in the MCMC samples were the B_0 values for NBC and WCVI, with a correlation coefficient of $\rho = -0.86$. These areas had the highest rate of movement between them in the base model so impacts of removals will be quickly equalized between them, making it difficult to distinguish between many equally likely combinations of initial abundance for the pair. The next most correlated parameters were the pairs of selectivity parameters for each of the two gear types: $a_{50,f}$ and δ_f . Correlation between the trawl selectivity parameters was $\rho = 0.76$. For the non-trawl parameters, $\rho = 0.79$. After this, the next most correlated parameters were the estimated tag retention parameter, S_{1980s}^{tags} , and the reporting rate parameter, r . All other parameters in Case A had $|\rho| < 0.60$.

In Case B the most positively or negatively correlated parameters in the MCMC samples were the two movement parameters associated with the two pairs of coastal areas, at $\rho = -0.92$. The second and third most correlated pairs in Case B were the selectivity parameters as in Case A, at $\rho = 0.82$ for trawl and $\rho = 0.81$ non-trawl. The B_0 for PS and the parameter controlling the movement rate between USC and PS had a correlation of $\rho = -0.65$, indicating that lower movement rates between these areas would require a larger intitial biomass in PS. All other parameters in Case B had $|\rho| < 0.60$.

5.4 Discussion

Prior to the current analysis, (Wood et al., 1979) was the only population dynamics model for spiny dogfish in the NE Pacific. This model was pioneering for its time, but used estimates of growth and maturity now known to be incorrect (Chapter 3; McFarlane et al., 1987). In addition, the model depended on estimates of initial biomass from Ketchen (1969) who himself described them as unsatisfactory. The Wood et al. (1979) model estimated that the 1940s fishery depleted the population to between 40% and 70% from an initial biomass of 300,000–500,000 mt. Wood et al. (1979) estimated that this decline was followed by a period of rebuilding to between 80% and 110% of the initial biomass by the final year of their model, 1977, where the extent of rebuilding depended on the form and strength of the density dependence included in the model.

The metapopulation model developed here is fit to 12 indices of abundance, 9 sources of age or length compositions, and 3 tagging studies spanning 60 years. Very few of these data were available at the time of the previous population dynamics model (Wood et al., 1979). Estimates of length and maturity at age derived from recently aged samples from the 1940s (Chapter 3) and recent sampling programs (Tribuzio, 2004), along with values from published literature (Saunders and McFarlane, 1993) also contributed to making this model as accurate a description of the population dynamics of spiny dogfish in the NE Pacific as possible. The median total initial biomass estimates from Cases A and B presented above, 392,000 mt and 549,000 mt (Table 5.8), are notably similar to the 300,000–500,000 mt range estimated by Ketchen (1969). Cases A and B differ only in the tag data overdispersion parameter τ , but they span a broad range of estimated current depletion (Figures 5.7 and 5.8; Tables 5.8), with Case A more pessimistic and the total population around 26% of B_0 and Case B more optimistic with the total population around 92% of B_0 . However, both cases differ from previous analyses in the estimated overall productivity of the

population. Whereas Wood et al. (1979) estimated that the impact of the 1940s fishery were large but the population had recovered to near the virgin level, within 20–30 years, the current analysis suggests that if the population showed a 50% decline in the 1940s, then it would not have rebuilt to near the virgin level even after 50 years. In the current analysis, the sensitivities which showed the population to be close the virgin level in 2006 were those in which the initial biomass was high and the 1940s fishery had a relatively small impact on the total population. This change in the estimated productivity is not surprising given that the revision in ageing methodology (McFarlane et al., 1987) which occurred after the Wood et al. (1979) model showed dogfish to be longer lived, slower growing, and later maturing than previously believed.

The model developed here is the first analysis of dogfish movement rates within the context of a population dynamics model. Previous analyses of movement (Holland, 1957; Fujioka and DiDonato, 1974; McFarlane and King, 2003) provided valuable insight into movement patterns, especially within an area where fishing effort is likely to be more uniform (McFarlane and King, 2008a). However, the estimates of abundance from a population dynamics model such as the one presented here allow the computation of the number of expected tag recaptures taking into account potential differences in fishing mortality between areas. These estimated movement rates have strong implications for the management of the species. The high estimates of movement between the coastal areas (Figures 5.5, 5.6, and 5.10; Table 5.8) is consistent with qualitative descriptions of the tagging data and the seasonal movement described Chapter 3 and the previous reports on movement rates. The higher degree of population connectivity between the coastal areas indicates that coordinated management of dogfish by the U.S. and Canada is needed to ensure the sustainability of dogfish fisheries in coastal waters. The lower estimates of movement between the outside and inside waters indicates that the sustainability of removals in PS and SG cannot depend on immigration from outside coastal waters.

The results presented here rest upon certain assumptions. The population was

assumed to begin in 1935 at an equilibrium which had no areas that were sources or sinks. In fact, dogfish were being fished commercially since the late 1800s for purposes like lamp oil and greasing skid roads for log transport (Ketchen, 1986). Thus, some reductions in biomass may have occurred prior to the first year of this model. The notion of a stationary population at equilibrium is also questionable given the possibility of large scale climate and ecosystem variability (Chapter 4; Mantua et al., 1997). Time varying growth, fecundity and maturity were included as fixed values, but a more complex model could include a dynamic density dependent response in the fecundity and maturity. The assumptions of time-invariant survival and movement applying equally to all ages in the population simplified the modeling, but the true dynamics are more complex. However, the complexity of the model and the number of estimated parameters needs to be balanced with the amount of data available to get meaningful results. The inclusion of spatial structure allowed the incorporation of more data and more complexity in this analysis than could have been included in a simpler, single-area model. A simpler model would have required fewer assumptions, but likely given a less accurate picture of dogfish population dynamics. Indeed, Frisk et al. (2008) found evidence that immigration of dogfish to Georges Bank from other areas in the NW Atlantic provided a better explanation for changes in catch rates than local dynamics alone.

Sensitivity analyses indicate that the results are highly dependent on the inclusion of different data sources or adjustment of fixed or estimated parameters (Table 5.9, Figures 5.17–5.22). Two parameters which had a strong influence on the results were τ , the overdispersion parameter which gives the ratio of the variance to the mean of the number of annual tag recaptures, and r , which combines the confounded quantities of reporting rate, initial tag mortality and initial tag loss. Changing either τ (Figure 5.22) or r (Figure 5.21) led to dramatic changes in estimates of the initial biomass. The 95% Bayesian posterior probability intervals for Cases A and B did not overlap for any of the B_0 parameters, in spite of these results differing only in

the value of τ . This indicates that the statistical uncertainty incorporated into the model through the Bayesian framework is not capturing the full uncertainty that exists with regard to the population status. This may imply that observation error is small compared to the error associated with the choice of model structure and the extent to which the model accurately describes those processes which generated the observed data.

The model fit many of the data sources well, especially considering the range of simplifying assumptions that were made. The declines in the 1990s in the NMFS triennial groundfish trawl survey in the USC area and the WDFW surveys in the PS area (Figures 5.11 and 5.12) were one area where the fit was less good. The NMFS survey shows dogfish abundance increasing four-fold from 1980 to 1986 and then quickly declining to a level below the 1980 value by 2001. Case A fit this by estimating a steady decline in the USC from the beginning of the 1940s fishery onward, ending in 2006 at less than 5% of the 1935 biomass. Two indications that the USC area is unlikely to be so depleted and Case A unrealistic in this regard, are the associated estimates of r and q . Although reporting rates are difficult to estimate from the data available in this study, expert opinion used in other tagging models for sharks (Aires-da-Silva, 2008) suggests that 0.115, the median estimate for r in Case A, is too low. A doubling of r essentially results in a doubling in the 2006 biomass relative to the initial state (Figure 5.21). The second factor indicating that the USC area is not as depleted as indicated by Case A is the estimate of q for the NMFS survey. The NMFS triennial survey in the USC area has been extrapolated to provide an estimate of the total biomass for this area under the assumption that the gear catches exactly the dogfish biomass that is found in the area swept by the net. The posterior median $q = 18.8$ (Figure 5.12) is an order of magnitude above 1.0, the value which would be true if the swept-area estimate and the model estimate matched perfectly. The high estimate of q from Case A could only be accurate if the trawl gear was herding 18 dogfish into the net for every one that was already in the path of

the gear. This scenario seems unrealistic, suggesting that Case A is underestimating the biomass in the USC area. Case B has a median estimate of $q = 0.296$ for the USC survey. This value below 1.0 would be associated with the majority of dogfish avoiding the gear in spite of being within the area swept by the net. Both the true q for the NMFS survey and the true B_0 for the USC area are likely to be somewhere between estimates from Case A and Case B.

The fluctuations in the NMFS survey may be the result of changes in distribution or availability resulting from external forces, such as warming ocean temperatures (Hansen et al., 2006) or changes in the food web (Reum, 2006; Gallucci and Langseth, 2008). If a northward shift in distribution since 1986 was caused by rising temperatures, it would be consistent with the decline in the USC survey as well as those in the WDFW surveys in PS. It would also help explain the apparent patterns of increasing abundance of dogfish in Alaskan waters to the north of the areas modeled in this study (Menon, 2004; Rice, 2007; Wallace et al., 2008). Including a temporal shift in distribution in future models would be one way to allow the model to better capture the variability in the USC survey.

In the future, a longer time series from the NMFS NWFSC annual groundfish trawl survey (Keller et al., 2007) will complement the NMFS triennial survey results used in the current analysis and may lead to better understanding of the dynamics in the USC area. An additional step that would reduce the uncertainty about dogfish abundance throughout the NE Pacific would be conducting surveys that apply the same methodology across different areas considered in this model, such as a co-ordinated survey for Puget Sound and the Strait of Georgia. This would anchor the biomass estimates for the different areas relative to each-other and reduce the range of results shown by Case A and Case B.

The sensitivity analyses showed a wide range of possible levels of depletion as a result of small changes in fixed parameters (Figure 5.20). Given the troubled history of spiny dogfish fisheries in the Atlantic (Rago et al., 1998; Fordham et al., 2006), and

the slower growth and later maturity of dogfish in the NE Pacific, this uncertainty suggests that the precautionary catch limits put in place in the USC area by NMFS to avoid the possibility of an expanded fishery (NMFS, 2006) are a wise measure until more precise estimates of the current status are available. Additional precautionary catch limits should be considered for the other areas described in this analysis. If the more optimistic scenarios, such as Case B, are accurate, then appropriate limits on landings and bycatch will ensure that dogfish in the NE Pacific may avoid the fate of so many unproductive shark populations (Musick et al., 2000b; Myers and Worm, 2003) in spite of growing slower, maturing later, and living longer than any other shark population for which estimates are available. If the more pessimistic scenarios, such as Case A, are accurate, then it is better to begin the process of rebuilding the population soon, as the situation in the Atlantic has shown the problems associated with delaying such efforts (Fordham et al., 2006).

The age-, sex-, and spatially-structured metapopulation model presented here is a valuable addition to the knowledge of spiny dogfish population dynamics in the NE Pacific. The spatial structure considered in this analysis allowed the integration of tagging data with disparate indices of abundance in a way that would not be possible in a single-area model, and the results therefore expand the understanding of dogfish dynamics in the NE Pacific beyond anything which has come before. Nevertheless, more data collection is needed and much remains to be understood about this species. Nothing is known about how the population might be impacted by changes in prey availability or predator abundance. The impacts of warming ocean temperatures and fishing pressure on dogfish are already confounded (Chapter 4), and as climate change continues, these impacts will surely change in ways that are difficult to predict. Finally, mysteries remain even within the context of the movement patterns which were the focus of this model, such as why the demersal dogfish has been observed crossing the Pacific from the U.S. and Canadian coasts to Japan.

5.5 Tables

Table 5.1: Indices of abundance used in fitting the model. * indicates CV values were unavailable and assumed to be 0.40 (surveys) or 0.60 (fishery CPUE) for all years. n is number of years in each index. A map of areas is provided in Figure 5.1. U.S. Coast values were computed from data provided by NMFS. Puget Sound values were from Palsson (2008), who reported survey values covering different sub-areas within U.S. inside waters in different years. The values for each sub-area were treated as a separate index, but assumed to be proportional to selected biomass throughout the PS area in this model. Strait of Georgia, W. Coast Van. Is. and Northern B.C. values are from King and McFarlane (2008) with the exception of Northern B.C. gillnet CPUE, which is from Barraclough (1948).

| Area | Gear | Abundance index | Mean | CV | n | Range |
|-------------------|-----------|-----------------------------|-------|----|-----|-----------|
| U.S. coast | trawl | NMFS triennial trawl survey | 0.31 | | 9 | 1980–2004 |
| Puget Sound | trawl | WDFW trawl survey (North) | 0.35 | | 6 | 1989–2004 |
| Puget Sound | trawl | WDFW trawl survey (Middle) | 0.29 | | 4 | 1989–2004 |
| Puget Sound | trawl | WDFW trawl survey (South) | 0.25 | | 5 | 1989–2004 |
| Puget Sound | trawl | Commercial trawl CPUE | 0.60* | | 33 | 1970–2001 |
| Strait of Georgia | non-trawl | Commercial longline CPUE | 0.60* | | 7 | 1981–2001 |
| Strait of Georgia | trawl | Commercial trawl CPUE | 0.60* | | 7 | 1980–2000 |
| Strait of Georgia | trawl | DFO trawl survey | 0.40* | | 3 | 1986–2005 |
| W. Coast Van. Is. | trawl | NMFS triennial trawl survey | 0.30 | | 7 | 1980–2001 |
| Northern B.C. | non-trawl | Commercial gillnet CPUE | 0.60* | | 5 | 1943–1947 |
| Northern B.C. | trawl | DFO trawl survey | 0.40* | | 9 | 1984–2000 |
| Northern B.C. | non-trawl | IPHC longline survey | 0.11 | | 10 | 1997–2006 |

Table 5.2: Age and length compositions used in fitting the model. Some composition data corresponded to 2 or 3 years, in which case the median year was used. Map of areas is provided in Figure 5.1. Sample sizes are provided in the plot of the fit to these data, Figure 5.15.

| Type | Year | Gear | Area | Reference |
|--------|------|-----------|------------------|--|
| Age | 1943 | trawl | Puget Sound | Sampling (Chapter 4; Bonham et al., 1949) |
| Age | 1943 | non-trawl | Puget Sound | Sampling (Chapter 4; Bonham et al., 1949) |
| Age | 1980 | trawl | Str. Georgia | Sampling (Saunders and McFarlane, 1993) |
| Age | 2002 | non-trawl | Puget Sound | Sampling (Tribuzio, 2004; Vega, 2006) |
| Length | 1943 | trawl | Puget Sound | Tagging studies (Holland, 1957) |
| Length | 1943 | non-trawl | Puget Sound | Tagging studies (Holland, 1957) |
| Length | 1969 | trawl | Puget Sound | Tagging studies (Fujioka and DiDonato, 1974) |
| Length | 1970 | trawl | Puget Sound | Tagging studies (Fujioka and DiDonato, 1974) |
| Length | 1970 | trawl | W. Coast Van. I. | Tagging studies (Fujioka and DiDonato, 1974) |
| Length | 1971 | trawl | Puget Sound | Tagging studies (Fujioka and DiDonato, 1974) |
| Length | 1972 | trawl | Puget Sound | Tagging studies (Fujioka and DiDonato, 1974) |
| Length | 1977 | non-trawl | Str. Georgia | Commercial (King and McFarlane, 2008) |
| Length | 1983 | non-trawl | Str. Georgia | Commercial (King and McFarlane, 2008) |
| Length | 1986 | non-trawl | Str. Georgia | DFO survey (King and McFarlane, 2008) |
| Length | 1989 | non-trawl | Str. Georgia | DFO survey (King and McFarlane, 2008) |
| Length | 1998 | trawl | U.S. Coast | NMFS survey |
| Length | 2001 | trawl | U.S. Coast | NMFS survey |
| Length | 2002 | non-trawl | Str. Georgia | Commercial (King and McFarlane, 2008) |
| Length | 2003 | trawl | U.S. Coast | NMFS survey |
| Length | 2005 | non-trawl | Str. Georgia | DFO survey (King and McFarlane, 2008) |

Table 5.3: Tag groups used in the five area model. Areas: USC, United States Coast; PS, Puget Sound; WCVI, W. Coast Vancouver I., SG, Strait of Georgia; NBC, Northern British Columbia (map of areas in Figure 5.1). Types: SD, standard Peterson disk; PD, plastic dart; ED, elongated disk. Bold numbers indicate recovery in area of release.

| Release area | Release years | Tag type | Number released | Number recovered | Fraction recovered by area | | | | |
|--------------|---------------|----------|-----------------|------------------|----------------------------|--------------|--------------|--------------|--------------|
| | | | | | USC | PS | SG | WCVI | NBC |
| USC | 1942–46 | SD | 1308 | 49 | 55.1% | 6.1% | 6.1% | 28.6% | 4.1% |
| PS | 1940–46 | SD | 7674 | 608 | 1.2% | 66.9% | 29.8% | 2.0% | 0.2% |
| WCVI | 1940–46 | SD | 778 | 33 | 36.4% | 18.2% | 15.2% | 24.2% | 6.1% |
| PS | 1969–72 | PD | 17430 | 1082 | 2.2% | 94.2% | 2.8% | 0.8% | 0.0% |
| WCVI | 1970–70 | PD | 6759 | 109 | 11.9% | 37.6% | 20.2% | 26.6% | 3.7% |
| SG | 1978–88 | ED | 51063 | 2371 | 0.5% | 1.6% | 94.3% | 3.1% | 0.5% |
| WCVI | 1984–87 | ED | 10087 | 259 | 18.9% | 6.9% | 18.5% | 52.5% | 3.1% |
| NBC | 1980–87 | ED | 9620 | 167 | 9% | 1.8% | 16.2% | 34.7% | 38.3% |

Table 5.4: von Bertalanffy growth parameters used in the model. Female growth parameters were assumed to change linearly over time between these estimates and to be constant before and after. Values were taken from (Chapter 4), and published literature (Saunders and McFarlane, 1993). Length at age was normally distributed with a CV of 0.13.

| gender | Year | L_∞ (cm) | k (yrs $^{-1}$) | t_0 (yrs) | W_∞ (kg) |
|---------|------|-----------------|--------------------|-------------|-----------------|
| females | 1943 | 140.2 | 0.023 | -5.04 | 7.15 |
| females | 1955 | 114.9 | 0.040 | -3.56 | 7.15 |
| females | 2002 | 109.3 | 0.048 | -2.04 | 7.15 |
| males | all | 91.9 | 0.067 | -1.57 | 3.36 |

Table 5.5: Maturity and fecundity estimates used in the model. a_{50} is the age at 50% maturity, δ -age is the difference between the age at 95% maturity and the age at 50% maturity, $pups_y^{100}$ is the number of pups per maturity female of length 100 cm, and $pups_y^{slope}$ is the change in the average number of pups per litter associated with a 1 cm increase in maternal length, as described in equation (5.2). Maturity and fecundity parameters were assumed to change linearly over time between these estimates and to be constant before and after. Values were taken from (Chapter 4), and published literature (Ketchen, 1972; Saunders and McFarlane, 1993).

| Maturity estimates: | | |
|---------------------|----------|---------------|
| Year | a_{50} | δ -age |
| 1943 | 44.8 | 16.0 |
| 1955 | 35.5 | 17.0 |
| 2002 | 33.5 | 24.3 |

| Fecundity estimates: | | |
|----------------------|----------------|------------------|
| Year | $pups_y^{100}$ | $pups_y^{slope}$ |
| 1943 | 5.90 | 0.214 |
| 1955 | 6.76 | 0.200 |
| 2002 | 6.70 | 0.214 |

Table 5.6: Summary of estimated parameters and their prior distributions. Catchability parameters (q) were integrated analytically using equation (5.11) following Walters and Ludwig (1994).

| Parameter | Description | Prior | Count |
|---------------------------|--|---|-------|
| B_{0i} | equilibrium biomass (in mt) in each area | log-uniform: $\log(B_{0i}) \sim U(4.6, 16.1)$ | 5 |
| $p_{i \leftrightarrow j}$ | movement rate for each pair of adjacent areas | uniform: $U(0, 1)$ | 8 |
| $a_{50,s}$ | age at 50% selectivity for selectivity ogive s | uniform: $U(0, 60)$ | 2 |
| δ_s | difference between ages at 95% and 50% selectivity for selectivity ogive s | uniform: $U(0, 30)$ | 2 |
| S_{1980s}^{tags} | tag loss for elongated disk tags used in 1980s tagging | uniform: $U(0, 1)$ | 1 |
| r | reporting rate \times initial tag survival | uniform: $U(0, 1)$ | 1 |
| q | catchability parameter for indices of abundance | log-uniform: $\log(q_f) \sim U(-\infty, \infty)$ | 12 |
| Total: | | | 31 |

Table 5.7: Parameter posterior median and 95% probability intervals for the two cases. The τ parameter which differs between cases is the overdispersion for the negative-binomial fit of the tagging data. Catchability is only reported for the NMFS triennial survey in the USC area because this is the only survey which has an estimate of total biomass based on extrapolation from area swept by the trawl gear.

| Parameter | Case A ($\tau = 2$) | | Case B ($\tau = 1$) | |
|---|---------------------------------------|-------------------|---------------------------------------|-------------------|
| | Med. | (95% int.) | Med. | (95% int.) |
| Initial biomass parameters ($\times 1000$ mt) | | | | |
| B_0 U.S. Coast (USC) | 96 | (92, 100) | 316 | (287, 354) |
| B_0 Puget Sound (PS) | 70 | (64, 76) | 20 | (19, 22) |
| B_0 Strait of Georgia (SG) | 70 | (66, 73) | 86 | (78, 92) |
| B_0 W. Coast Vancouver I. (WCVI) | 77 | (65, 89) | 16 | (14, 23) |
| B_0 N. British Columbia (NBC) | 79 | (70, 90) | 110 | (96, 130) |
| Sum of initial biomass parameters | 392 | (387, 397) | 549 | (517, 587) |
| Movement parameters (mean annual fraction) | | | | |
| USC \leftrightarrow PS | 0.002 | (0.001, 0.004) | 0.102 | (0.091, 0.114) |
| PS \leftrightarrow SG | 0.014 | (0.012, 0.016) | 0.015 | (0.013, 0.017) |
| SG \leftrightarrow WCVI | 0.034 | (0.027, 0.042) | 0.037 | (0.030, 0.045) |
| USC \leftrightarrow WCVI | 0.046 | (0.036, 0.060) | 0.309 | (0.245, 0.351) |
| WCVI \leftrightarrow NBC | 0.140 | (0.102, 0.196) | 0.139 | (0.099, 0.211) |
| USC \leftrightarrow SG | 0.006 | (0.002, 0.012) | 0.002 | (0.000, 0.005) |
| PS \leftrightarrow WCVI | 0.006 | (0.004, 0.008) | 0.003 | (0.001, 0.007) |
| SG \leftrightarrow NBC | 0.006 | (0.002, 0.011) | 0.015 | (0.010, 0.021) |
| Selectivity parameters (years) | | | | |
| trawl age at 50% selectivity (a_{50}) | 13.1 | (12.6, 13.6) | 14.4 | (13.7, 15.1) |
| trawl selectivity slope (δ -age) | 6.5 | (5.9, 7.2) | 7.9 | (7.1, 8.7) |
| non-trawl age at 50% selectivity (a_{50}) | 27.9 | (26.9, 28.9) | 26.5 | (25.6, 27.3) |
| non-trawl selectivity slope (δ -age) | 10.5 | (9.9, 11.2) | 10.4 | (9.8, 11.0) |
| Parameters for tagging and survival | | | | |
| Reporting rate \times initial tag surv. (r) | 0.115 | (0.102, 0.129) | 0.251 | (0.229, 0.278) |
| Annual tag retention 1940s (S^{tags}) | 0.7 | fixed | 0.7 | fixed |
| Annual tag retention 1970s (S^{tags}) | 0.8 | fixed | 0.8 | fixed |
| Annual tag retention 1980s (S^{tags}) | 0.903 | (0.882, 0.924) | 0.894 | (0.905, 0.882) |
| Overdispersion of tag recaps. (τ) | 2.0 | fixed | 1.0 | fixed |
| Density dependent surv. frac. (S^{frac}) | 0.5 | fixed | 0.5 | fixed |
| Other | | | | |
| Catchability q for USC survey | 18.8 | (16.2, 21.7) | 0.296 | (0.252, 0.343) |

Table 5.8: Derived quantity posterior median and 95% probability intervals for the two cases. The τ parameter which differs between cases is the overdispersion for the negative-binomial fit of the tagging data. Depletion calculations include males and females of all ages. Movement quantities are calculated from estimated parameters using equation (5.9).

| Quantity | Case A ($\tau = 2$) | | Case B ($\tau = 1$) | |
|--|---------------------------------------|-------------------|---------------------------------------|-------------------|
| | Med. | (95% int.) | Med. | (95% int.) |
| Depletion (B_{2006}/B_0) | | | | |
| U.S. Coast (USC) | 0.034 | (0.029, 0.042) | 0.953 | (0.897, 1.007) |
| Puget Sound (PS) | 0.496 | (0.407, 0.578) | 0.941 | (0.890, 0.990) |
| Strait of Georgia (SG) | 0.318 | (0.261, 0.378) | 0.827 | (0.780, 0.873) |
| West Coast Vancouver Island (WCVI) | 0.202 | (0.162, 0.262) | 0.711 | (0.649, 0.803) |
| Northern British Columbia (NBC) | 0.346 | (0.288, 0.412) | 0.937 | (0.890, 0.987) |
| Total depletion (all areas) | 0.263 | (0.222, 0.310) | 0.923 | (0.870, 0.972) |
| Movement (annual fraction) | | | | |
| PS → USC | 0.002 | (0.001, 0.004) | 0.193 | (0.170, 0.215) |
| USC → PS | 0.002 | (0.001, 0.003) | 0.012 | (0.011, 0.014) |
| SG → PS | 0.014 | (0.012, 0.017) | 0.006 | (0.005, 0.006) |
| PS → SG | 0.014 | (0.012, 0.016) | 0.024 | (0.021, 0.028) |
| WCVI → SG | 0.032 | (0.026, 0.041) | 0.062 | (0.050, 0.077) |
| SG → WCVI | 0.036 | (0.028, 0.045) | 0.012 | (0.009, 0.017) |
| WCVI → USC | 0.051 | (0.040, 0.067) | 0.588 | (0.466, 0.664) |
| USC → WCVI | 0.041 | (0.032, 0.054) | 0.029 | (0.022, 0.045) |
| NBC → WCVI | 0.139 | (0.105, 0.183) | 0.036 | (0.026, 0.051) |
| WCVI → NBC | 0.141 | (0.095, 0.221) | 0.243 | (0.168, 0.375) |
| SG → USC | 0.007 | (0.003, 0.014) | 0.003 | (0.000, 0.007) |
| USC → SG | 0.005 | (0.002, 0.010) | 0.001 | (0.000, 0.002) |
| WCVI → PS | 0.005 | (0.004, 0.008) | 0.004 | (0.001, 0.008) |
| PS → WCVI | 0.006 | (0.004, 0.009) | 0.003 | (0.001, 0.007) |
| NBC → SG | 0.006 | (0.002, 0.010) | 0.013 | (0.010, 0.017) |
| SG → NBC | 0.006 | (0.002, 0.012) | 0.017 | (0.011, 0.024) |
| Other | | | | |
| Equilibrium survival (S^{eq}) | 0.931 | fixed | 0.931 | fixed |

Table 5.9: Description of sensitivity analyses conducted to examine influence of adjusting model assumptions. Sensitivities are relative to Case A. Results of these sensitivities are shown in Figures 5.17–5.20.

| Name | Description |
|----------------|--|
| Case A | Base model |
| RRhigh | Reporting rate fixed at 0.50 instead of freely estimated near 0.1 |
| Case B (ODlow) | Tag recaptures overdispersion parameter τ decreased from 2.0 to 1.0. |
| ODhigh | Tag recaptures overdispersion parameter τ increased from 2.0 to 3.0. |
| NoTags | No tagging data was used in the model. |
| No1940sTags | Tagging data from the 1940s experiment was excluded from the model. |
| No1970sTags | Tagging data from the 1970s experiment was excluded from the model. |
| No1980sTags | Tagging data from the 1980s experiment was excluded from the model. |
| TLlow | Annual retention of tags for 1940s and 1970s fixed at $S^{tags} = 0.85 \& 0.90$. |
| TLhigh | Annual retention of tags for 1940s and 1970s fixed at $S^{tags} = 0.5$. |
| NoMovement | All movement parameters fixed at 0. |
| NoIndices | No indices of abundance were used in the model. |
| DDlow | Density dependent increase in survival (S^{frac}) was decreased from 0.5 to 0. |
| DDhigh | Density dependent increase in survival (S^{frac}) was increased from 0.5 to 1. |
| 1940sDemog | Maturity, fecundity and growth were fixed at the estimate for 1942. |
| 2000sDemog | Maturity, fecundity and growth were fixed at the estimate for 2002. |
| CompNlow | Divide observed sample size for age and length comps by 100 instead of 10. |
| CompNhigh | Use full observed sample size for age and length comps. |

5.6 Figures

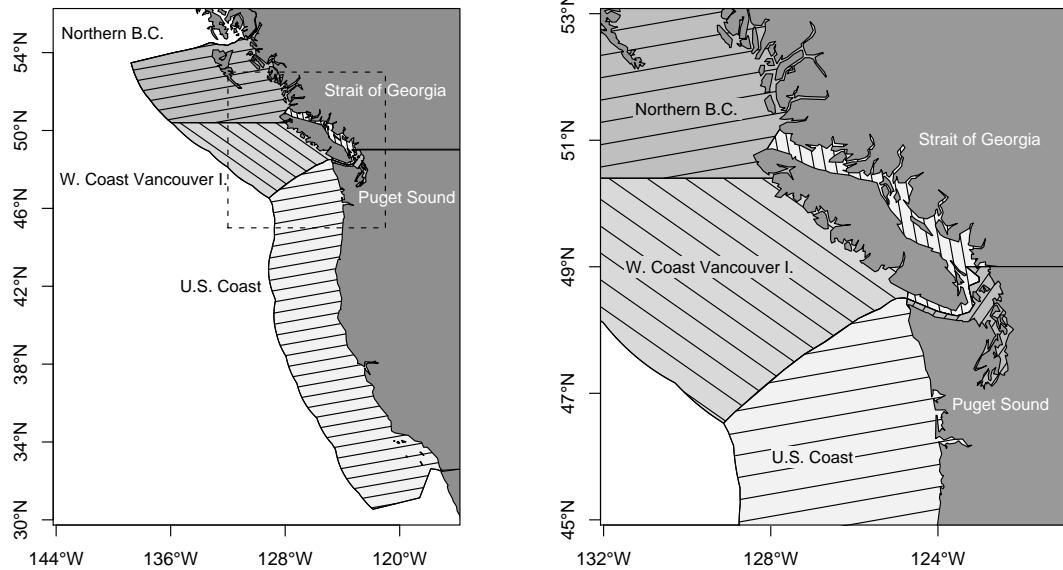


Figure 5.1: The 5 areas considered in the model.

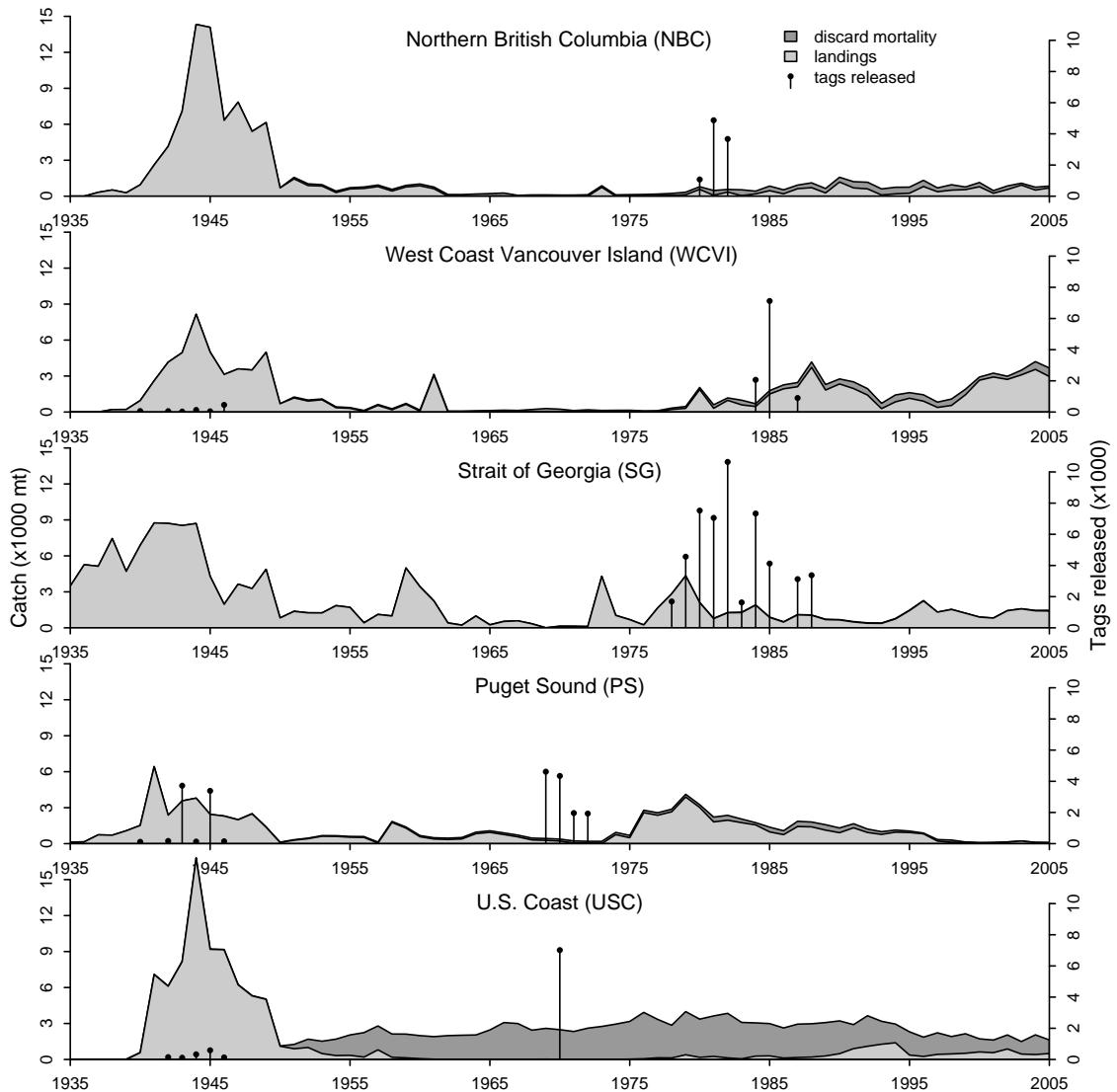


Figure 5.2: Estimated catch history of spiny dogfish in the NE Pacific by area with tag releases. Landed catch (including estimated biomass from which livers were landed) is in light grey and estimated discarded bycatch is in dark grey. Trawl and non-trawl gear are combined.

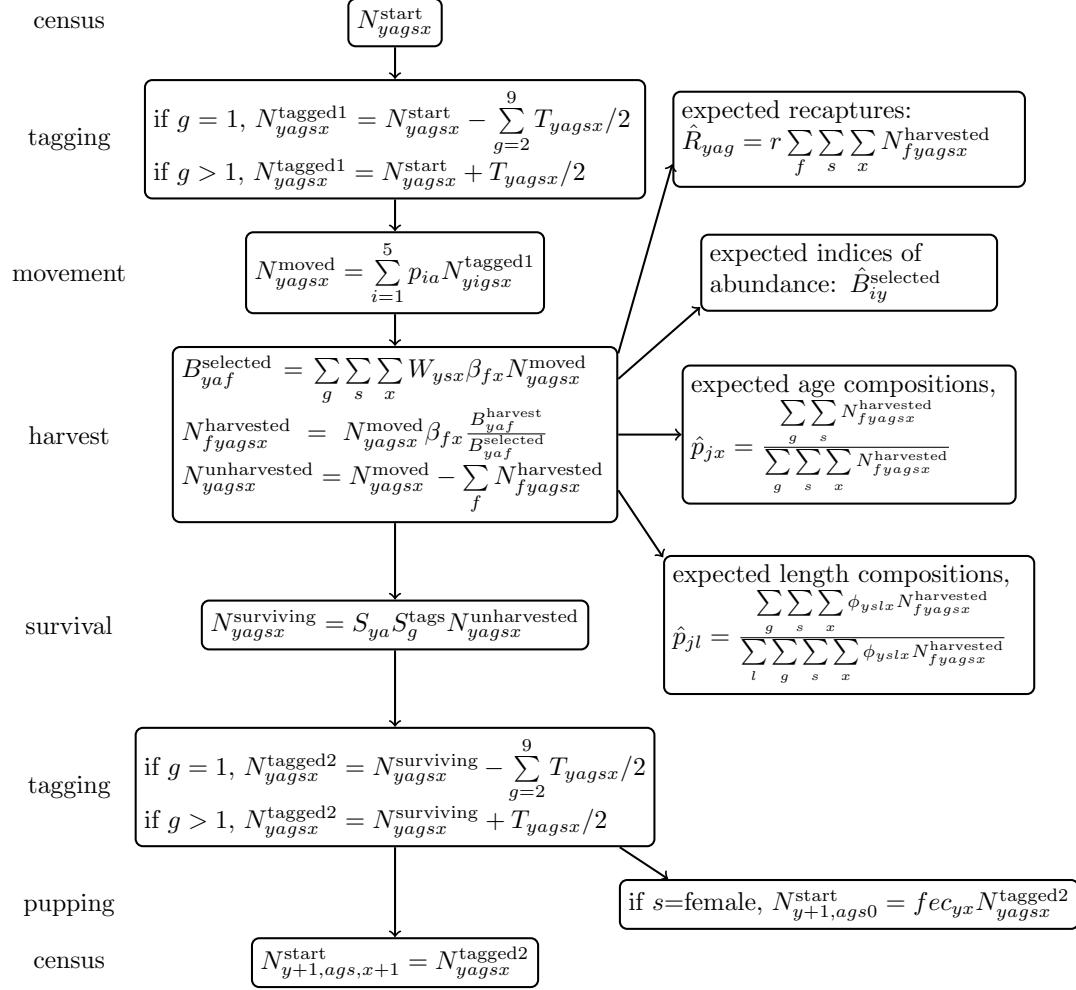


Figure 5.3: Diagram illustrating population dynamics. Subscripts are: y , year; a , area; g , tag group ($g = 1$ is group for untagged fish); s , sex; x , age; l , length bin; f , fishery; i , index of abundance; j , age or length composition. Values are: N , numbers; T , tags; B , biomass; W , weight; p , movement rate; β , selectivity; ϕ , proportion of age at length; S , survival; S^{tags} , tag retention; r reporting rate \times initial tag survival; and fec , fecundity. B_{yaf}^{harvest} is the annual removal input to the model. Changes in length, weight and fecundity are assumed to take place just prior to the census, when remaining numbers at age x are assigned to age $x + 1$. Expected indices and compositions are computed for the combination of fishery, year, and area which corresponds to the observed index i or composition j .

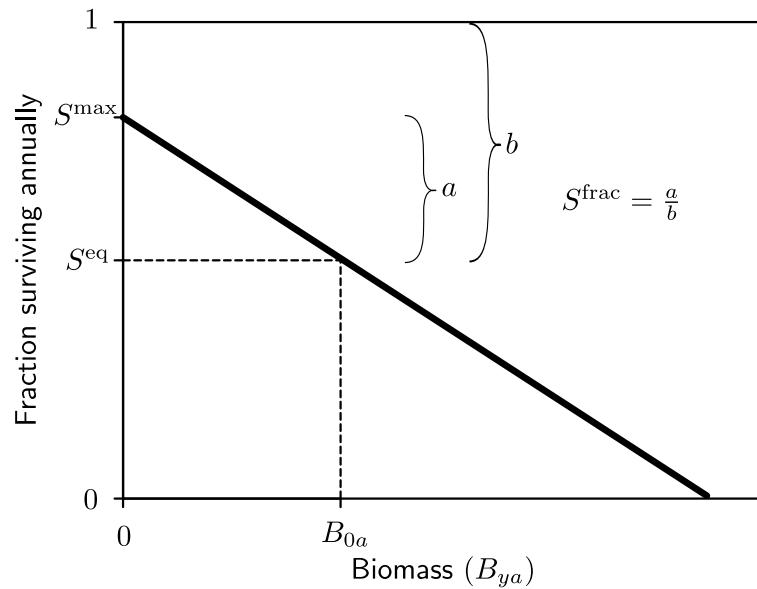


Figure 5.4: Density dependent survival as a function of the initial (B_{0a}) and current (B_{ya}) biomass in each area, as defined by equations 5.4 and 5.5. Survival values were computed assumed constant across all ages for a given year and area.

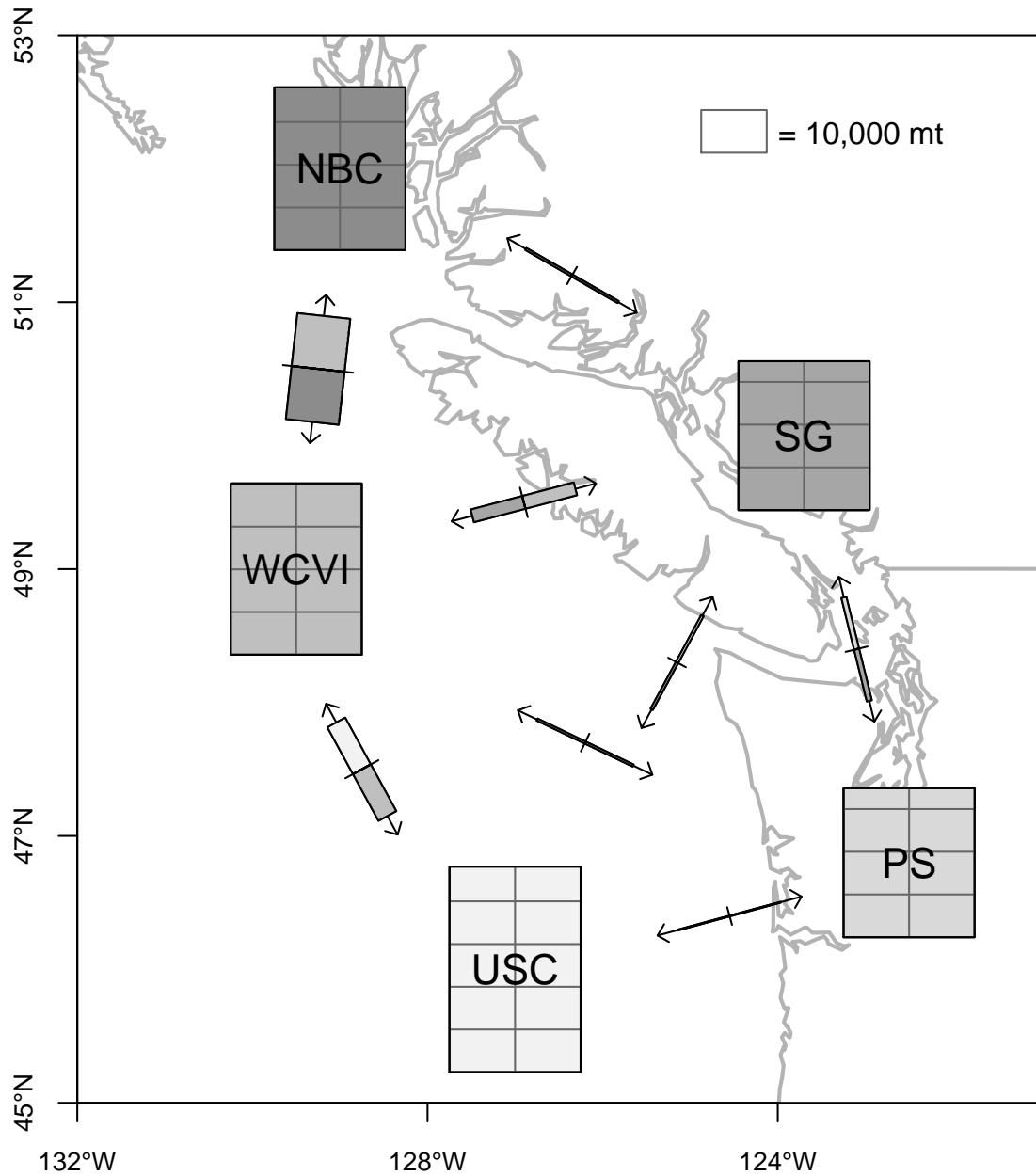


Figure 5.5: Graphical depiction of relative size of each area and movement between areas at initial equilibrium for Case A ($\tau = 2$). Shaded boxes represent proportional size of total initial biomass in each area (B_{0i}) and total biomass moving between areas at equilibrium ($p_{ij} B_{0i}$). Shaded arrows correspond to similarly shaded area from which arrow is pointing. Values are maximum posterior density estimates. Delineation of areas is shown in Figure 5.1.

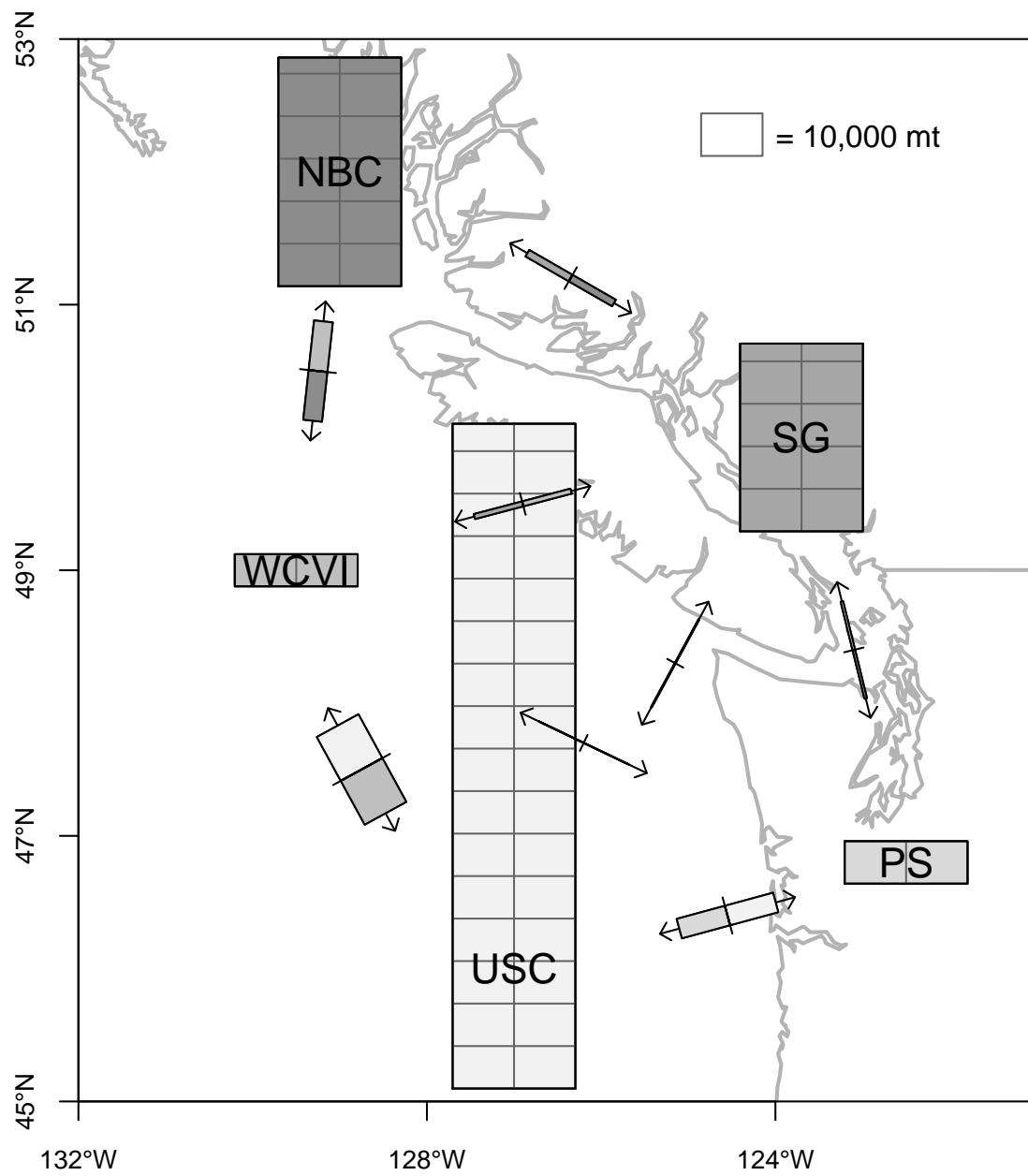


Figure 5.6: Repeat of Figure 5.5 showing size of each area and movement between areas at initial equilibrium for Case B ($\tau = 1$).

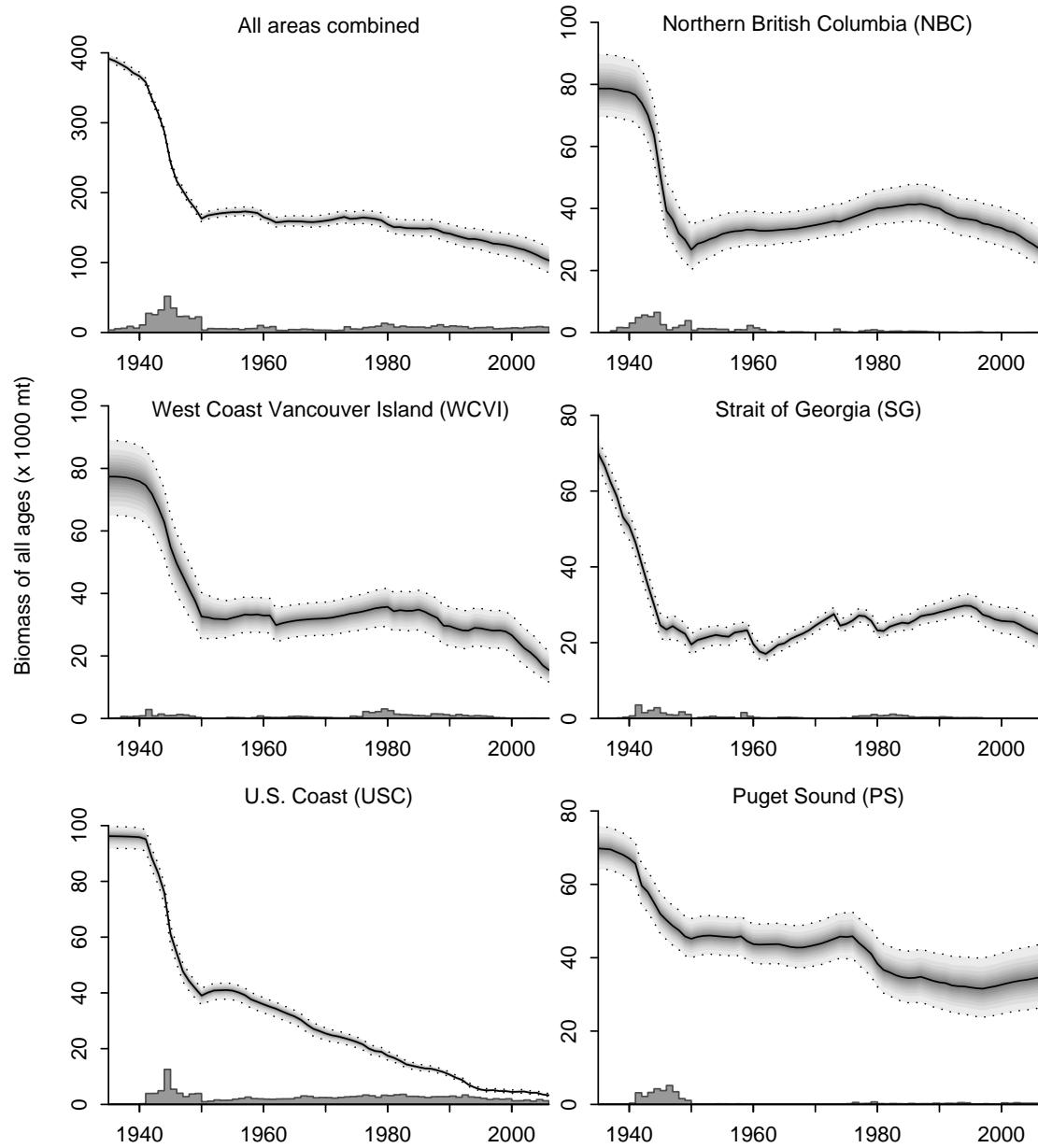


Figure 5.7: Posterior distributions of trajectories of total biomass in each area for Case A ($\tau = 1$). Histogram shows catch history for each area. Solid line shows the median value, dashed line shows the central 95% posterior probability interval, and shades of grey each indicate a 10% change in posterior probability interval from 5% to 95%. The initial year corresponds to the pattern shown in Figure 5.5.

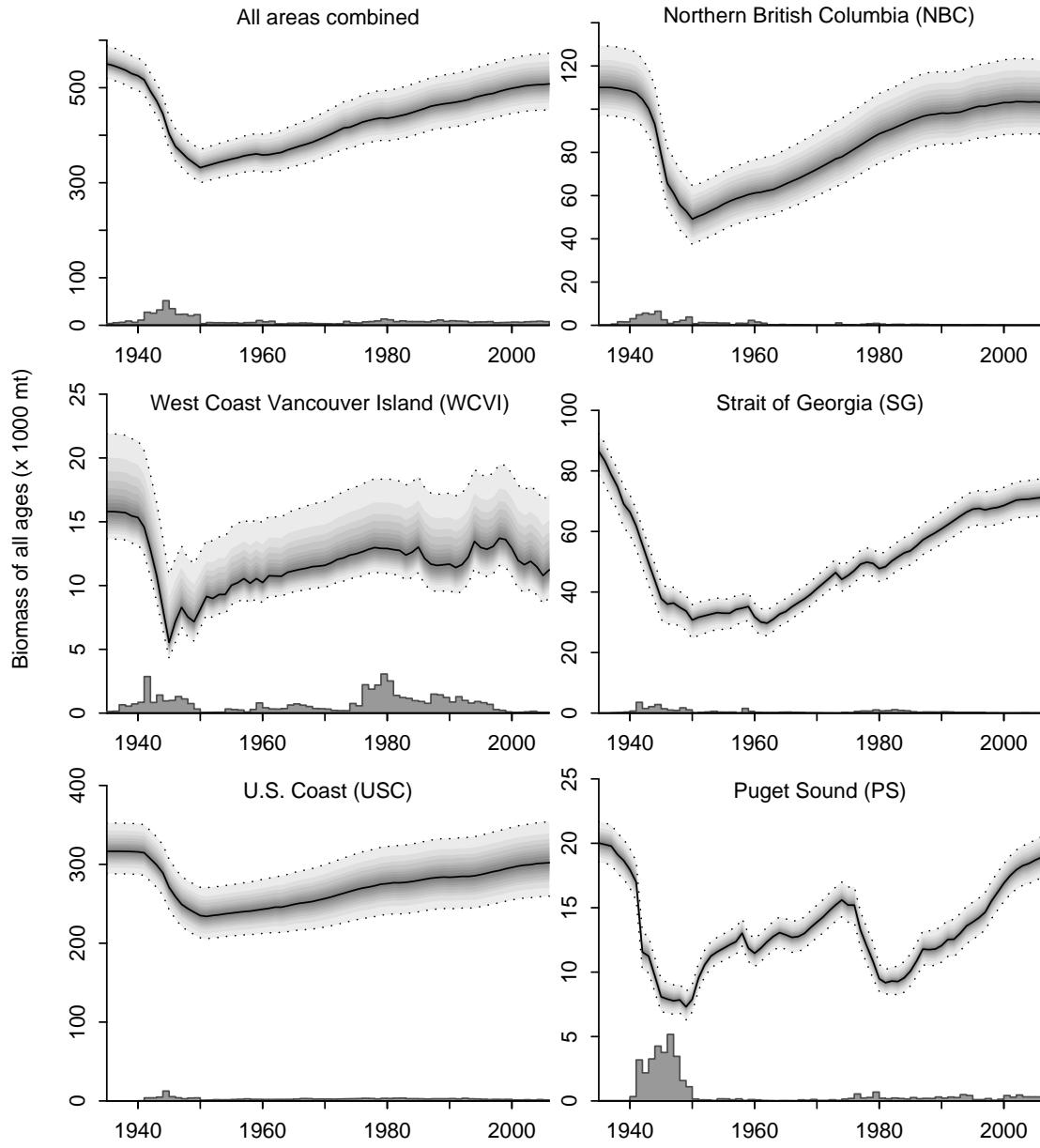


Figure 5.8: Repeat of Figure 5.7 showing posterior distributions of trajectories of total biomass in each area for Case B ($\tau = 1$). The initial year corresponds to the pattern shown in Figure 5.6.

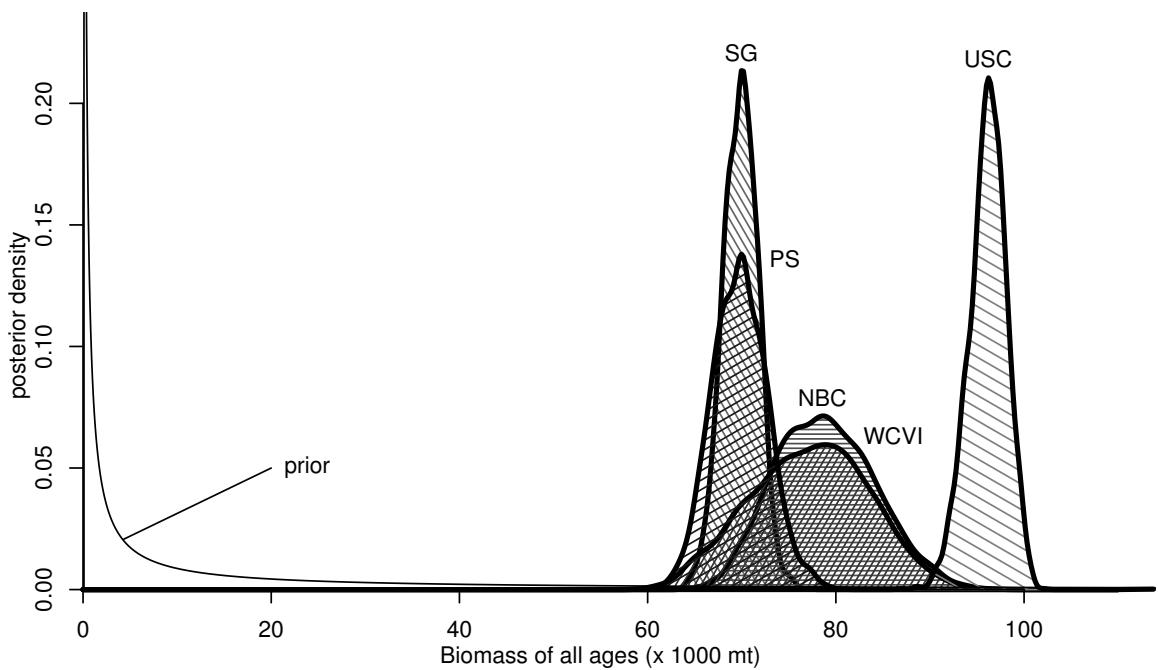


Figure 5.9: Posterior distributions for initial biomass (B_0) in each of the 5 areas for Case A.

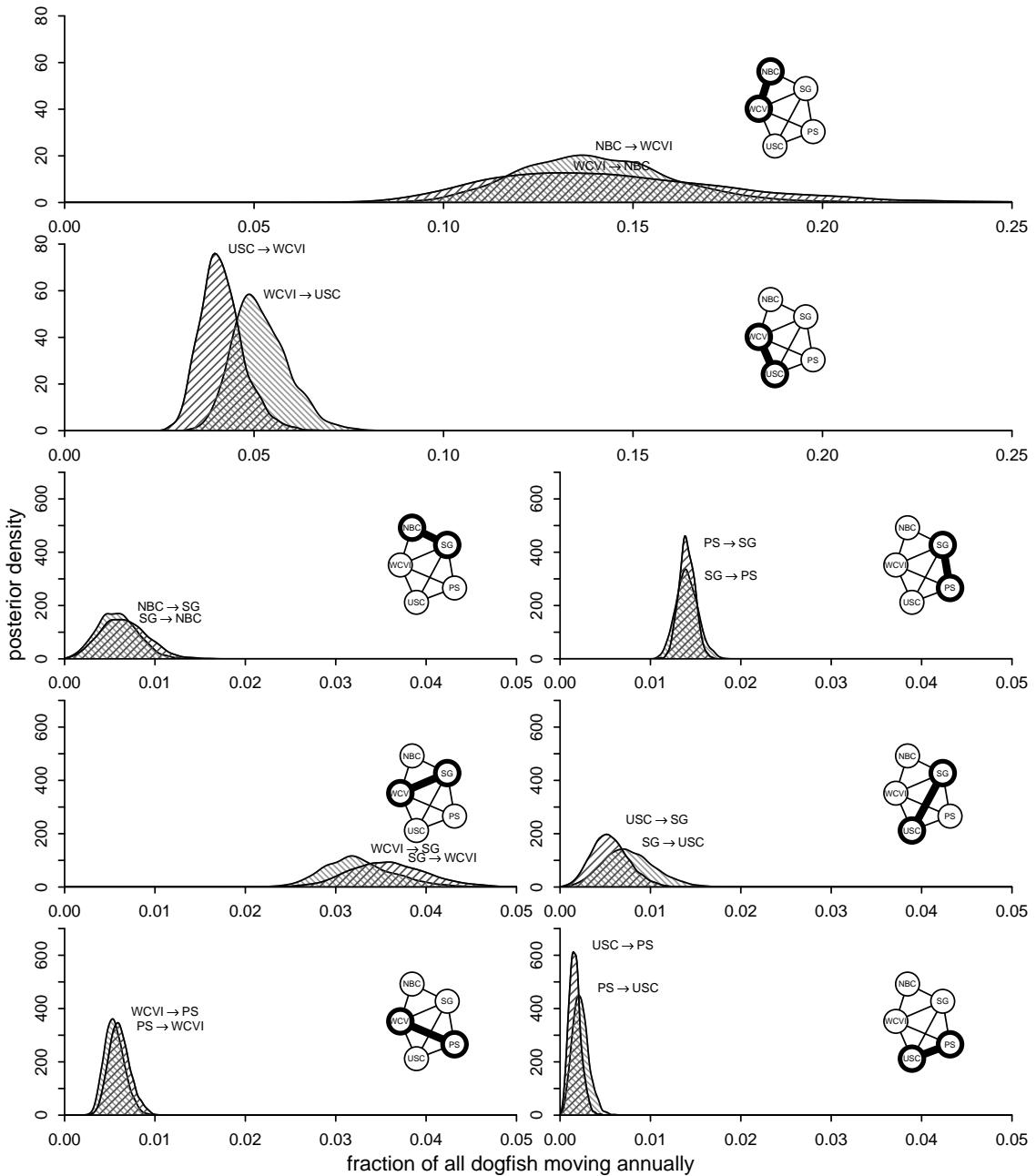


Figure 5.10: Posterior distributions for the 16 movement rates derived from equation (5.9) for Case A. Top two plots for movement between coastal areas are shown on a different scale from remaining plots. Bold circles in diagram indicate which pair of areas are included in each plot and text labels distinguish between the two movement rates.

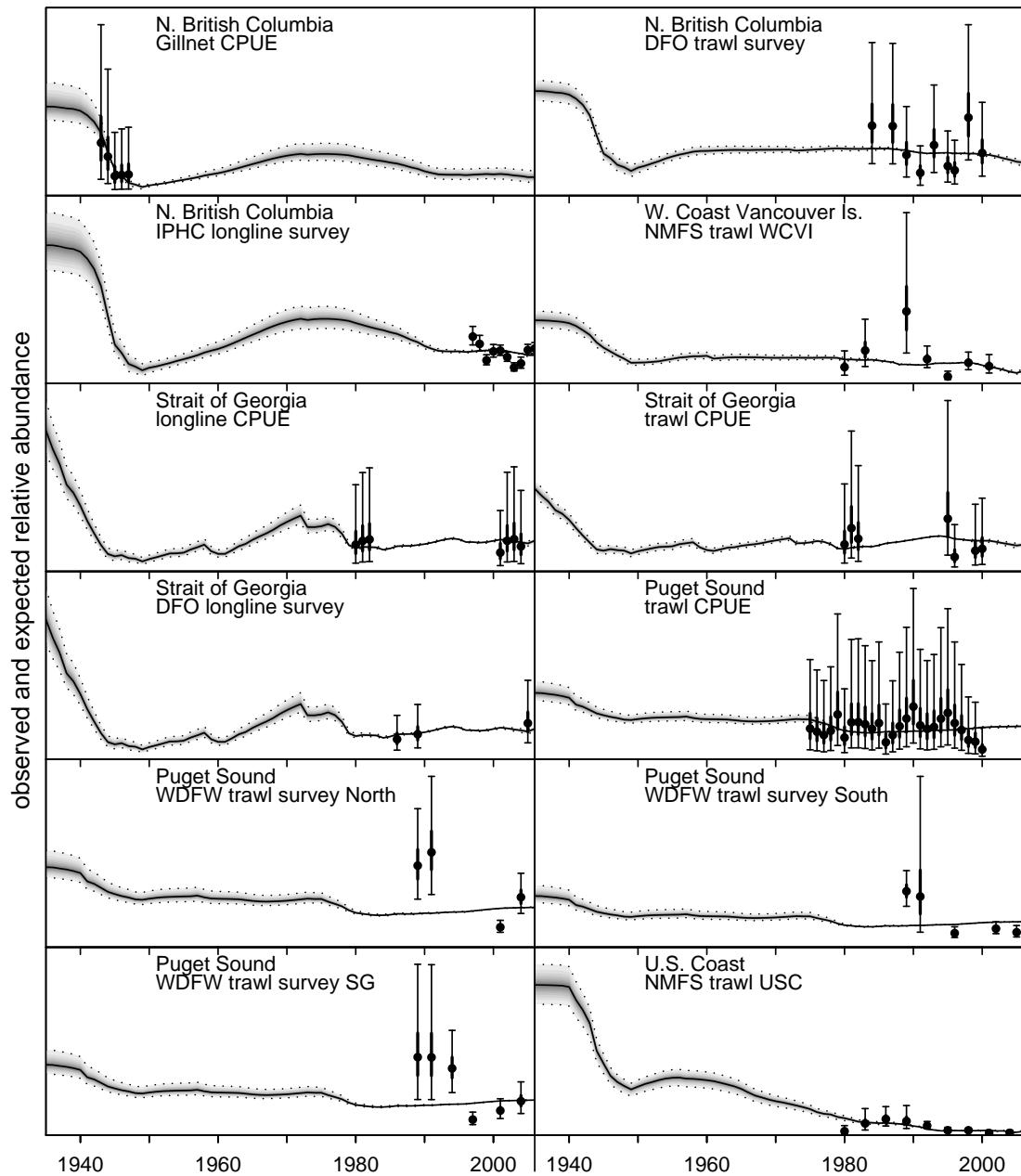


Figure 5.11: Posterior distributions of fit of selected population to indices of abundance for Case A. For index values, thick vertical lines show inter-quartile range, and thin lines show 95% interval, under assumption of lognormal error. For trajectories of selected population, solid line shows the median value, dashed line shows the central 95% posterior probability interval, and shades of grey each indicate a 10% change in posterior probability interval from 5% to 95%.

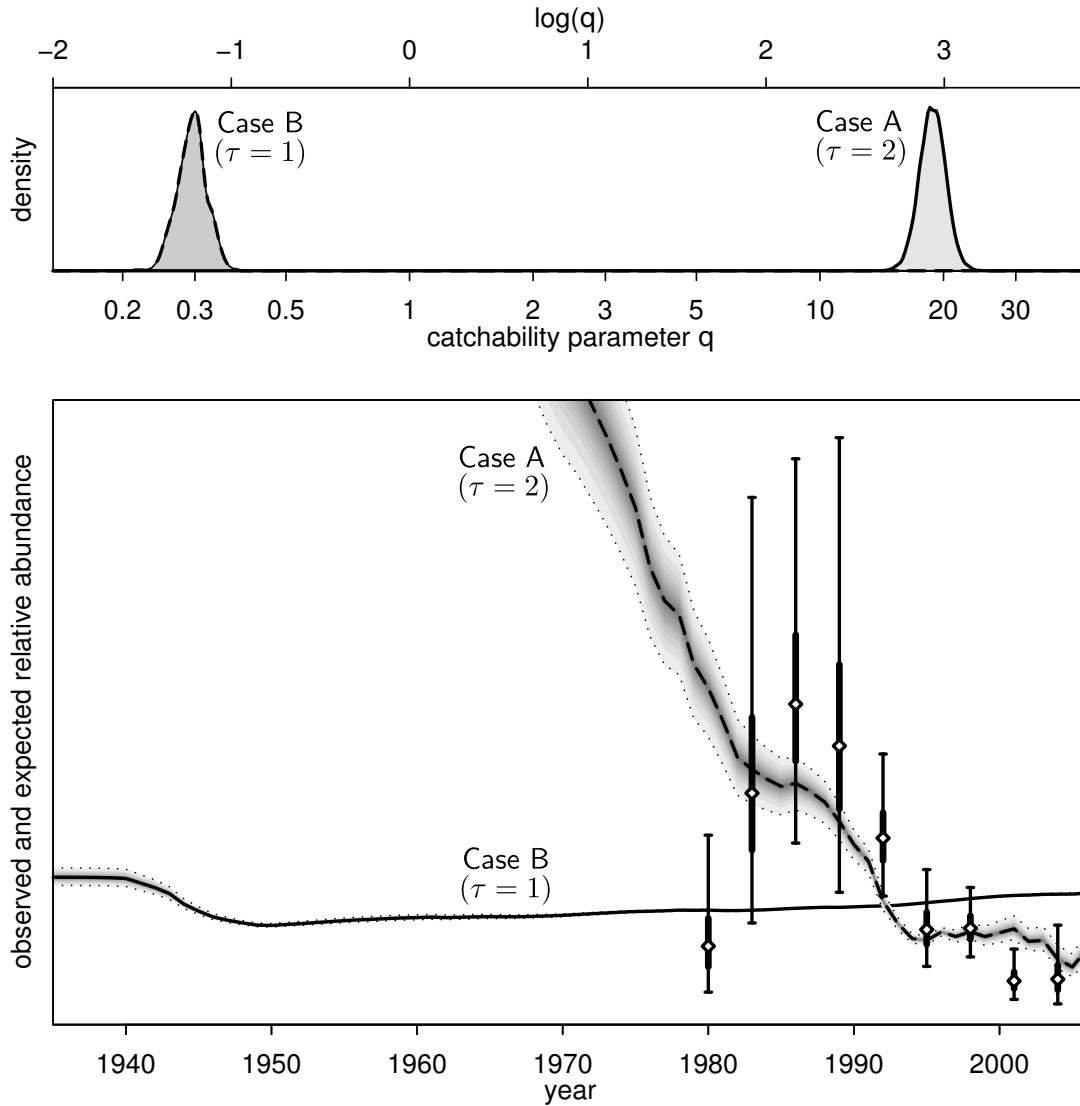


Figure 5.12: Focus on bottom-right panel of Figure 5.11 showing posterior distributions of fit of the selected population for both Case A ($\tau = 2$) and Case B ($\tau = 1$) to the NMFS triennial trawl survey in the USC area (lower panel) and posterior distribution of catchability parameter q for each case (upper panel).

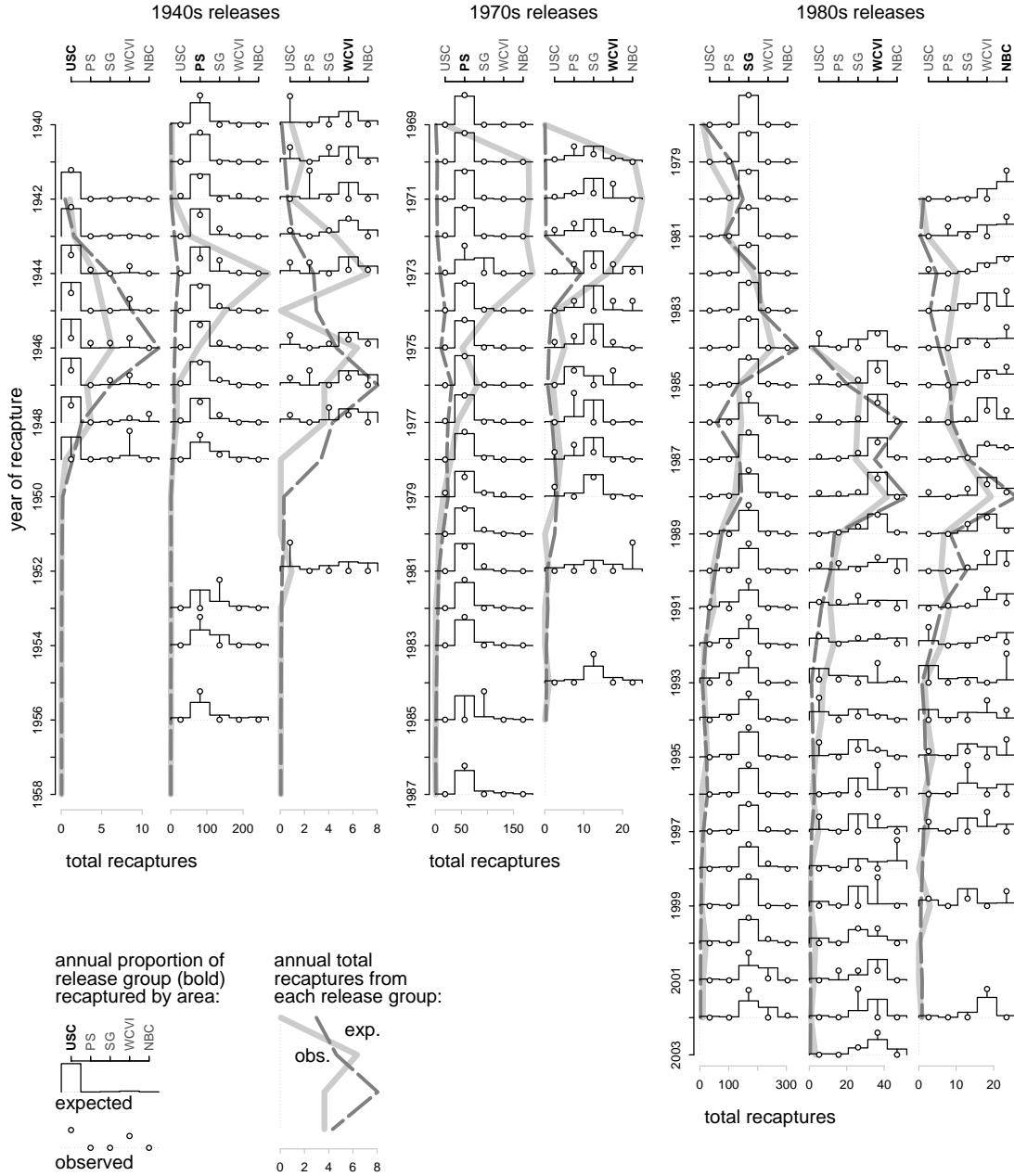


Figure 5.13: Fit of model to tag recapture data (maximum posterior density estimate) for Case A ($\tau = 2$). Histograms show expected (lines) and observed (points) proportions of recaptures from each release group (name in bold) recaptured in each area. Thick grey lines show total expected (dashed) and observed (solid) recaptures from each group summed across areas. The proportions and totals contribute separately to the objective function according to equations (5.14) and (5.15).

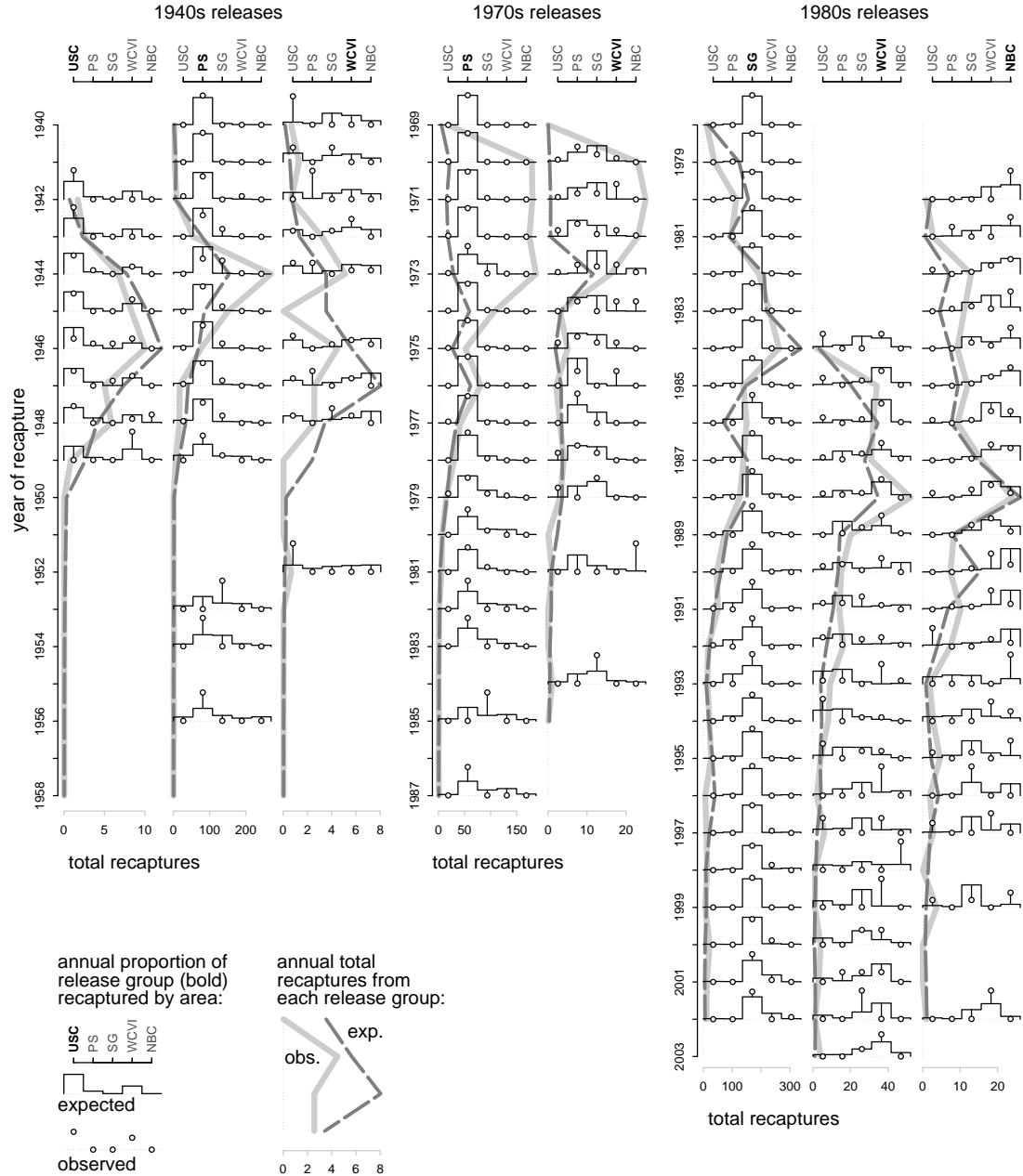


Figure 5.14: Repeat of Figure 5.13 showing fit of model to tag recapture data for Case B ($\tau = 1$). Histograms show expected (lines) and observed (points) proportions of recaptures from each release group (name in bold) recaptured in each area. Thick grey lines show total expected (dashed) and observed (solid) recaptures from each group summed across areas. The proportions and totals contribute separately to the objective function (Equations 5.14 and 5.15).

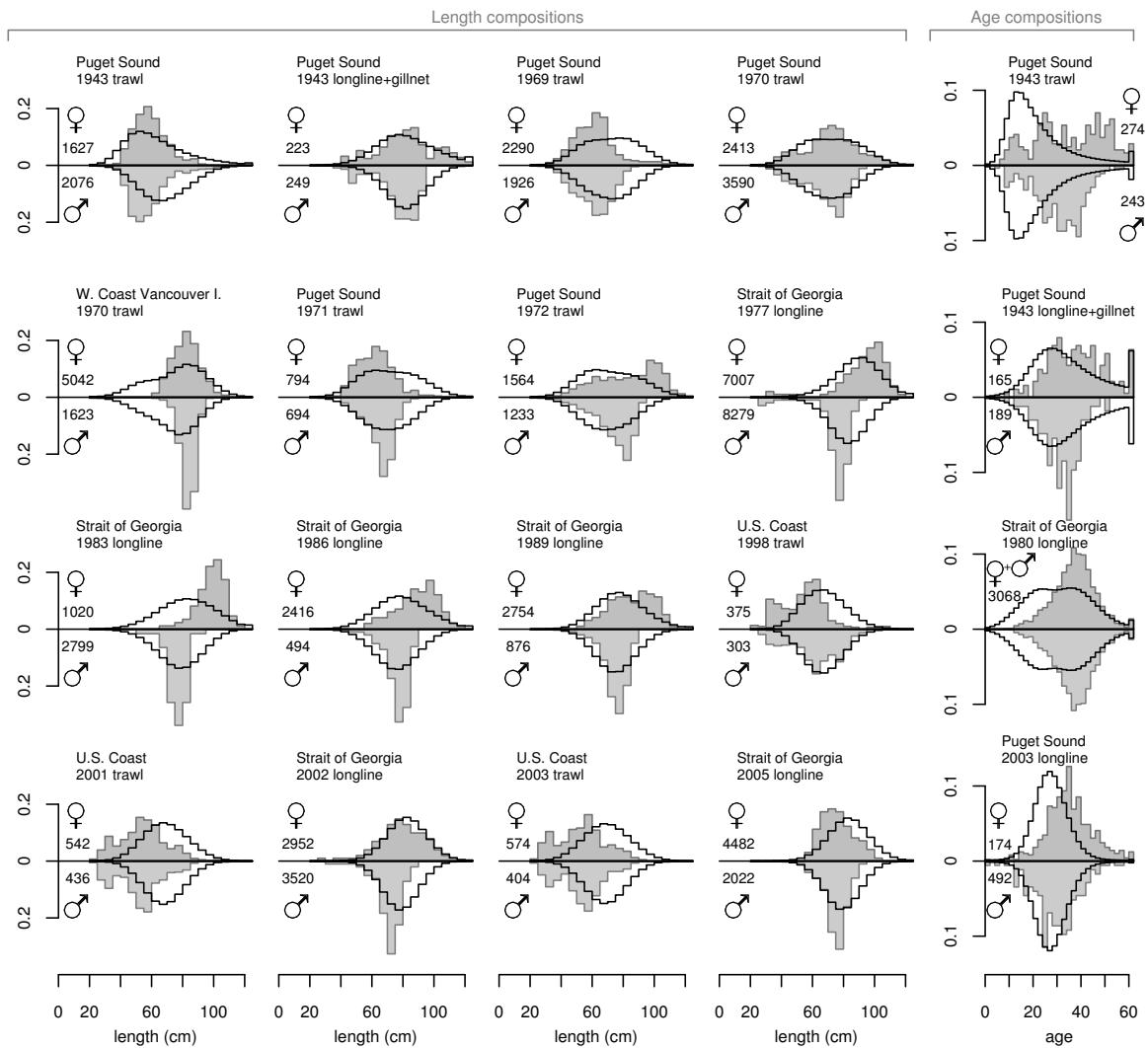


Figure 5.15: Fit of expected (open) to observed (filled) length and age compositions at the maximum posterior density estimate for Case A. True sample sizes are provided above (females) and below (males) the center line of each plot. Sample size used in model was 1/10 the total number of measurements taken. Only the larger mode in the bimodal data for the Strait of Georgia 1983 longline was used as the smaller mode was primarily associated with a single trip (King and McFarlane, 2008).

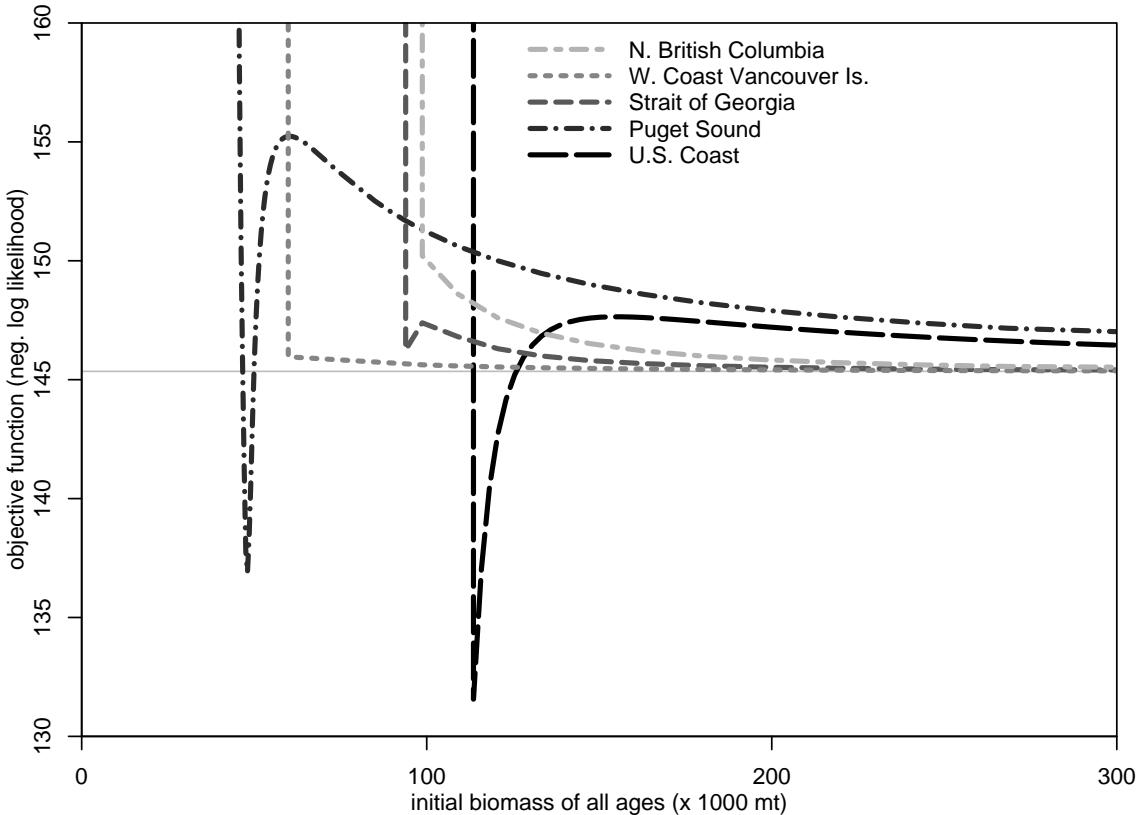


Figure 5.16: Profile over initial biomass B_0 of fit to indices of abundance, with lower values indicating better fit. The objective function includes only the contribution from fit to indices, equation (5.12). Movement rates are all fixed at 0 and B_0 values are each adjusted over a range from 0 to 300,000 mt. All B_0 with the exception of the adjusted value are fixed at 10,000,000 mt, an arbitrarily high value at which the impact of fishing is negligible. The vertical lines at the left end of each curve represent the minimum possible B_0 for each area, defined as the point where the removals from that area would result in a negative abundance at lower B_0 . No parameters are estimated, and selectivity is fixed at the maximum posterior density estimate for Case A. The dome shapes for the U.S. Coast and Puget Sound areas show that the best fits to these areas come from B_0 values which are either very high or close to their minimum.

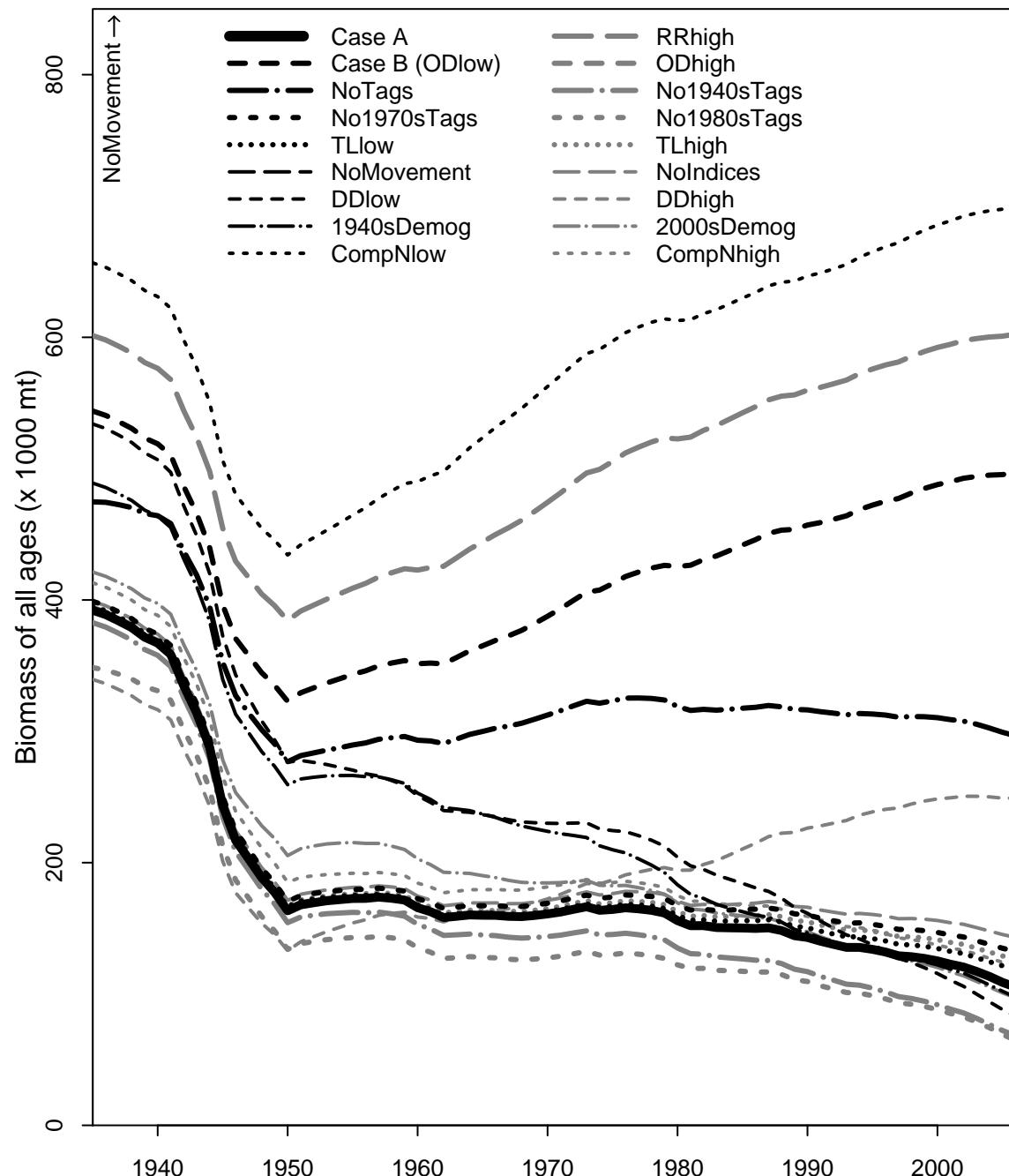


Figure 5.17: Trajectories of total biomass of all ages in all areas combined under different sensitivities relative to Case A. Sensitivities and their codes are described in Table 5.9.

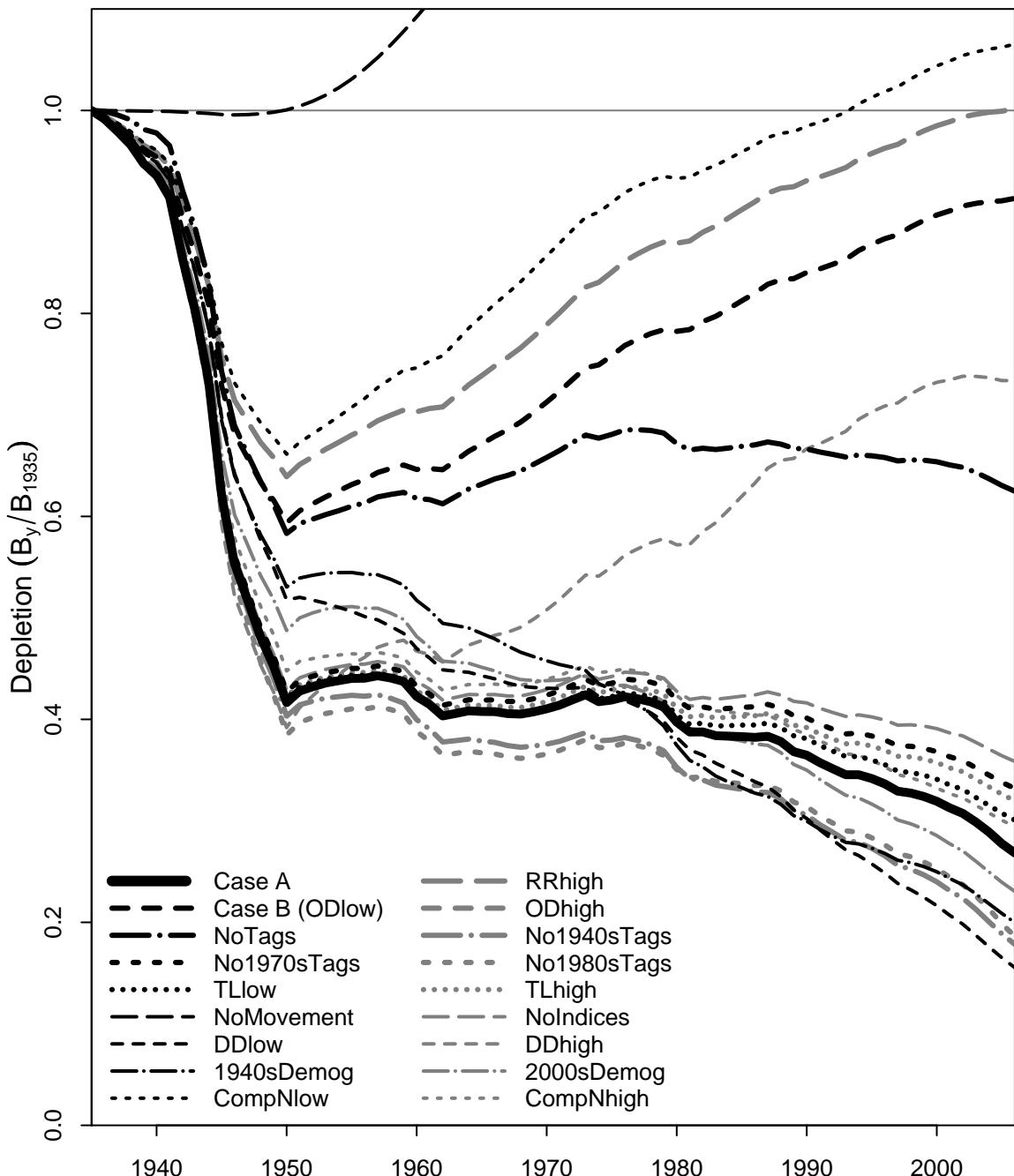


Figure 5.18: Trajectories of total depletion for all ages in all areas combined under different sensitivities relative to Case A. Sensitivities and their codes are described in Table 5.9.

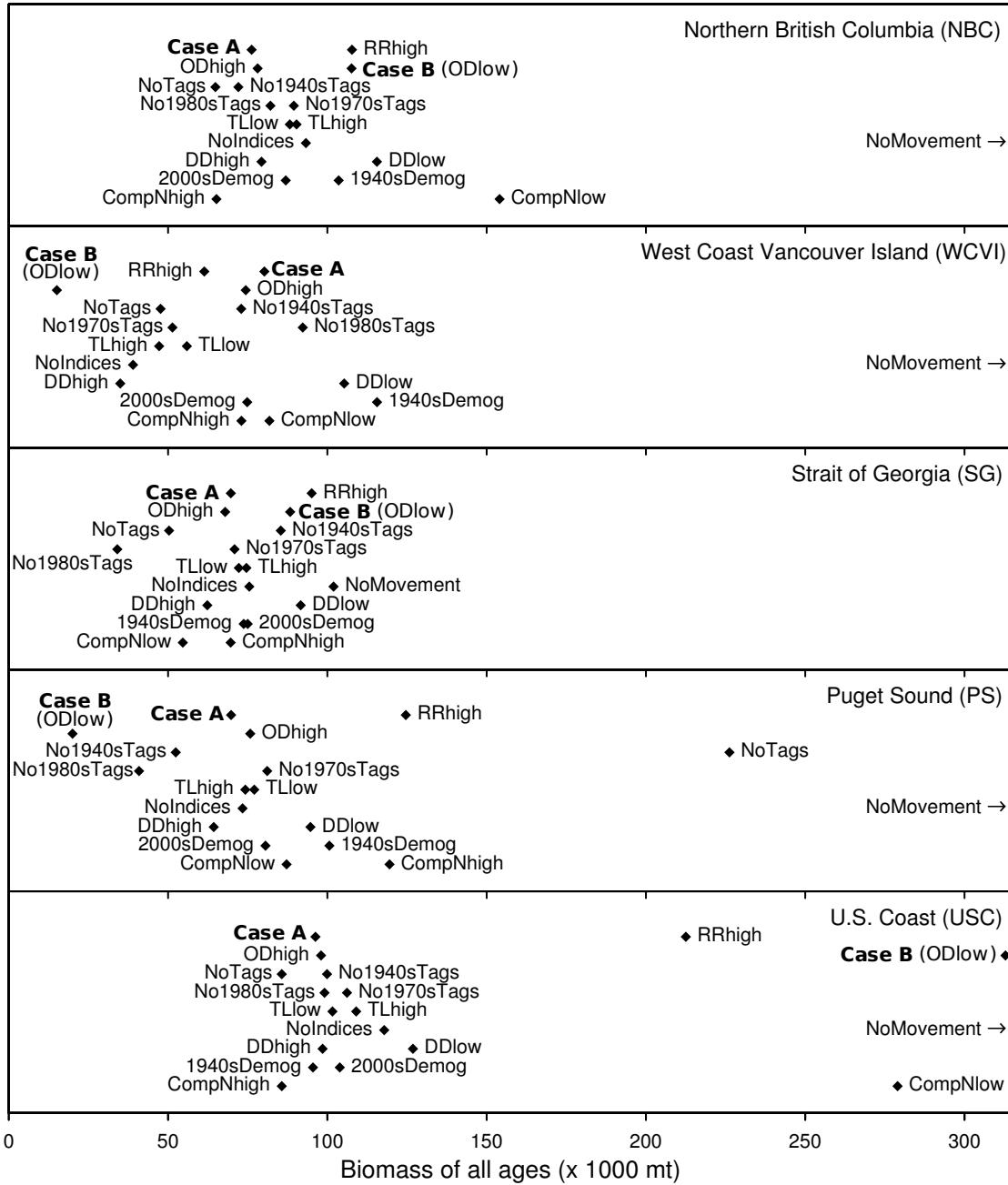


Figure 5.19: Maximum posterior density estimates of initial biomass (B_0) for each area under different sensitivity tests. Vertical positioning of each point is for clarity only. Sensitivities and their codes are described in Table 5.9.

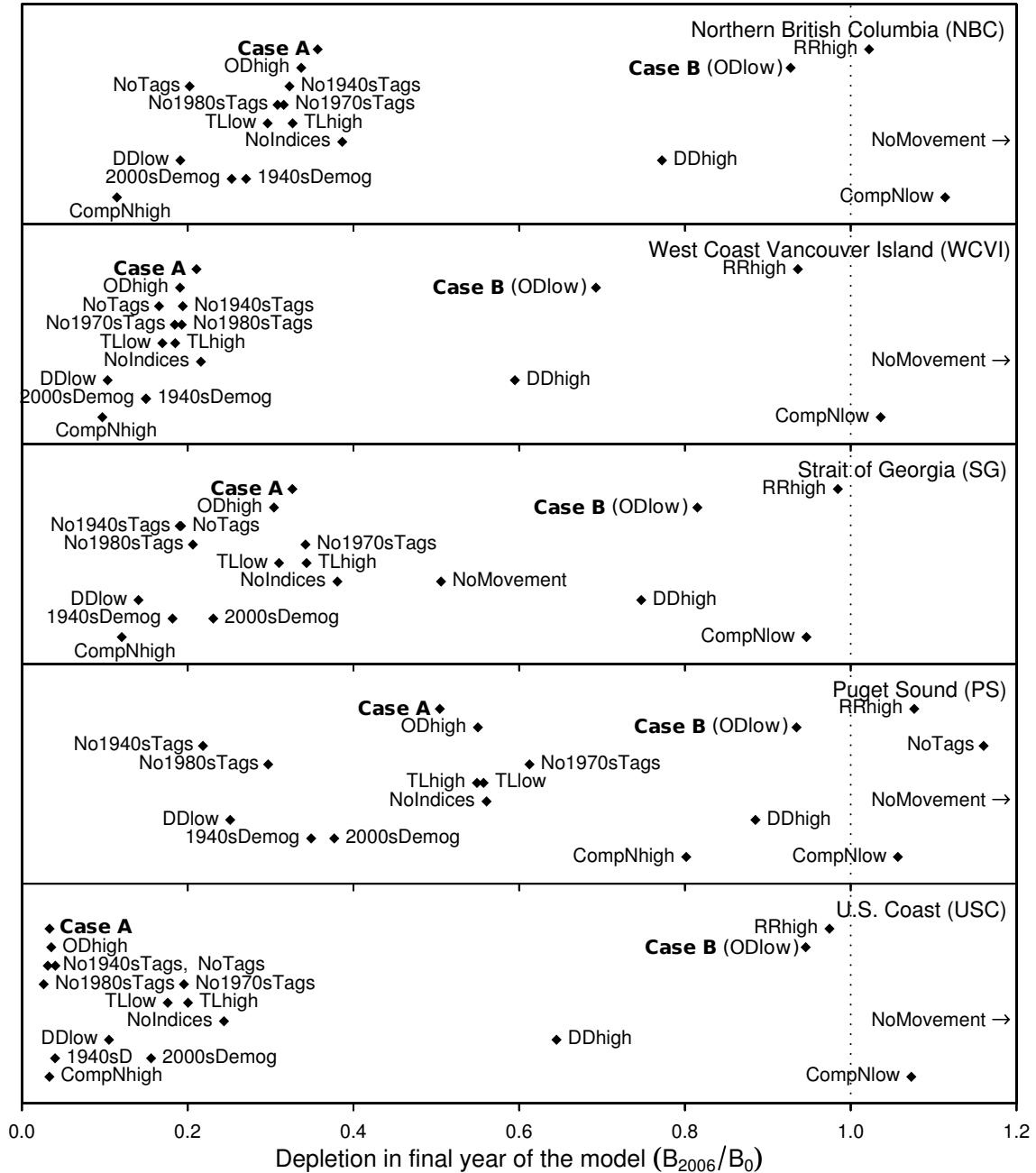


Figure 5.20: Maximum posterior density estimates of final depletion level (B_{2006}/B_0) in each area under different sensitivity tests. Vertical positioning of each point is for clarity only. Sensitivities and their codes are described in Table 5.9.

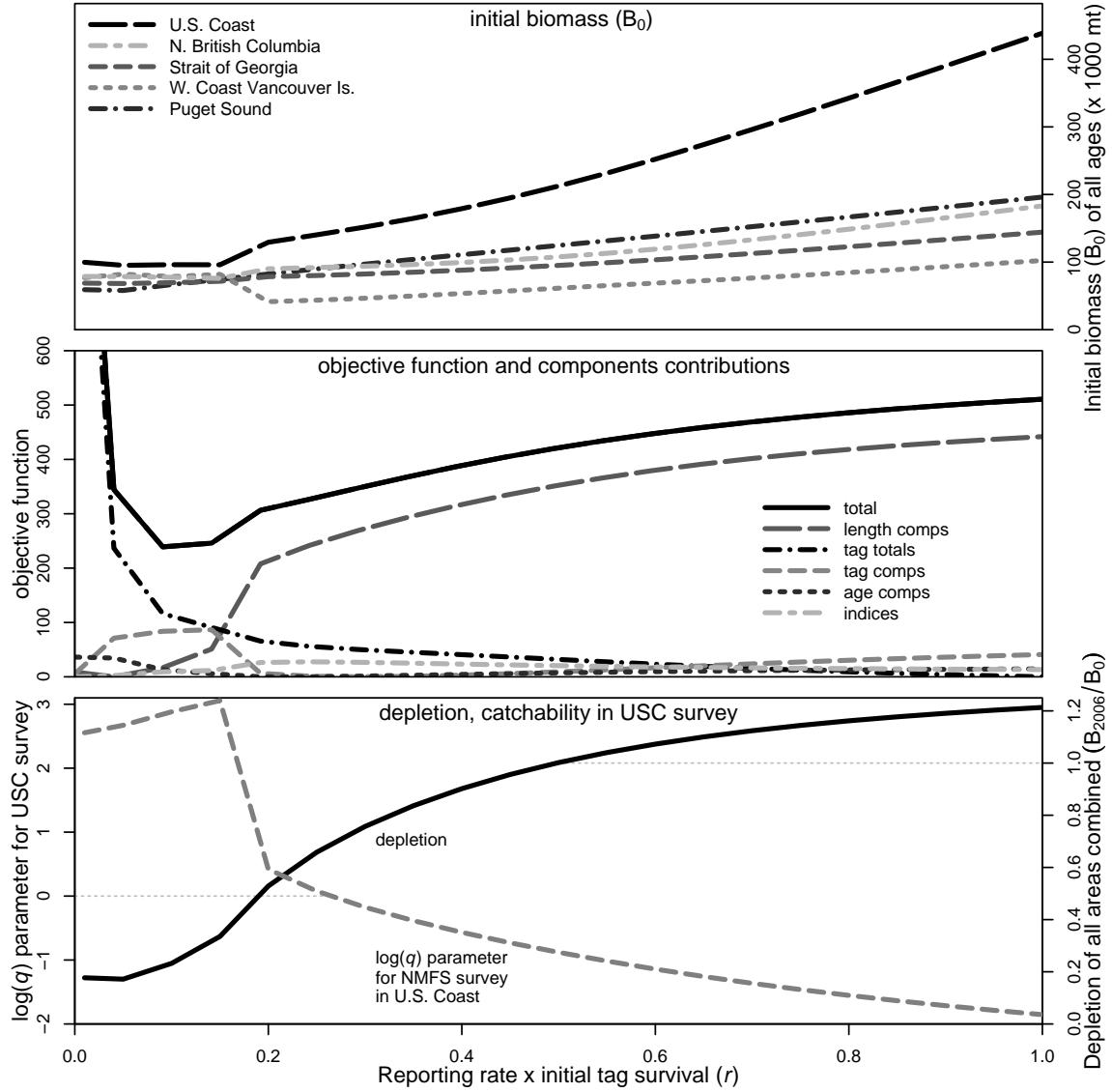


Figure 5.21: Sensitivity to changes in reporting rate \times initial tag survival (r) with τ fixed at 2 as in Case A. The top panel shows changes in estimates of B_0 for each area. The middle panel shows the change in objective function components from their minimum within the range of r considered here. The total objective function shown here is the sum of these rescaled components for illustrative purposes, not the true total. The lower panel shows changes in overall depletion across all areas: $\sum B_{2006,a} / \sum B_{0,a}$ and the log of the catchability parameter $\log(q)$ for the NMFS survey in the U.S. Coast area. A value of $\log(q) = 0$ would indicate that the survey was an absolute index of abundance.

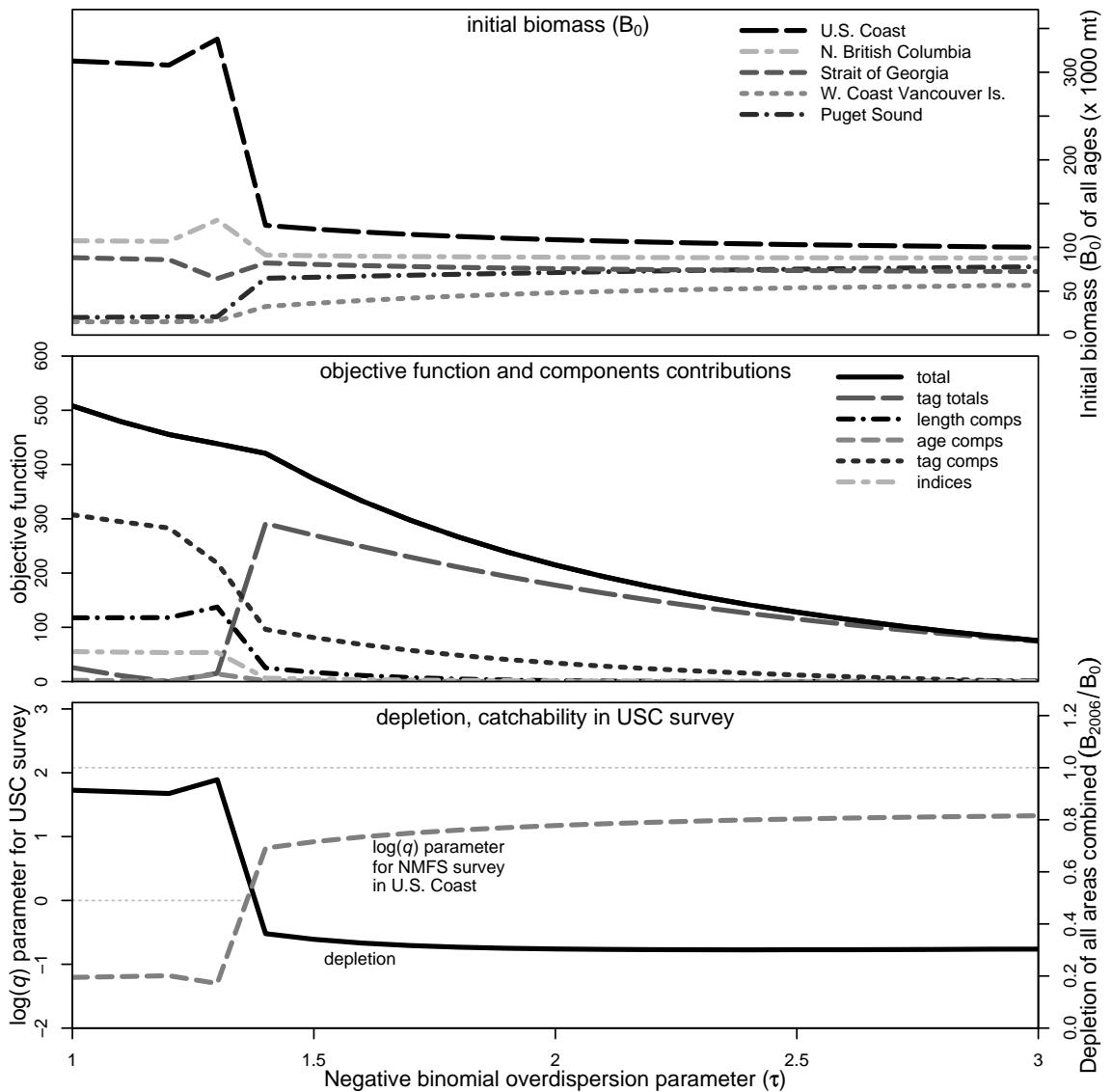


Figure 5.22: Sensitivity to changes in overdispersion parameter τ . The top panel shows changes in estimates of B_0 for each area. The middle panel shows the change in objective function components from their minimum within the range of r considered here. The total objective function shown here is the sum of these rescaled components for illustrative purposes, not the true total. The lower panel shows changes in overall depletion across all areas: $\sum B_{2006,a} / \sum B_{0,a}$ and the log of the catchability parameter $\log(q)$ for the NMFS survey in the U.S. Coast area. A value of $\log(q) = 0$ would indicate that the survey was an absolute index of abundance.

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Appendix A

PARAMETERIZATION OF THE LOGISTIC FUNCTION

Starting from the linear equation using in logistic regression,

$$\log \left(\frac{p(x)}{1 - p(x)} \right) = \alpha + \beta x, \quad (\text{A.1})$$

and solving for p gives,

$$p(x) = \frac{e^{\alpha+\beta x}}{1 + e^{\alpha+\beta x}}, \quad (\text{A.2})$$

which can be simplified to the form,

$$p(x) = \left(1 + e^{-(\alpha+\beta x)} \right)^{-1}. \quad (\text{A.3})$$

However, α and β are hard to interpret. They represent the value the logit of the proportions, $\log(p/(1 - p))$, at $x = 0$, and the change of the logit associated with a unit increase in x , respectively. More meaningful, especially when the logistic equation is used to describe maturity at length or age, are x_{50} and x_{95} , the values of x corresponding to $p = 0.5$ (the point of inflection) and $p = 0.95$. By definition of x_{50} and x_{95} ,

$$0.5 = \left(1 + e^{-(\alpha+\beta x_{50})} \right)^{-1}, \quad (\text{A.4})$$

$$0.95 = \left(1 + e^{-(\alpha+\beta x_{95})} \right)^{-1}, \quad (\text{A.5})$$

which can be solved to get,

$$x_{50} = \frac{-\alpha}{\beta}, \quad (\text{A.6})$$

$$x_{95} = \frac{\log(19) - \alpha}{\beta}. \quad (\text{A.7})$$

The difference, $\delta = x_{95} - x_{50}$ can be solved for using (A.4) and (A.5),

$$\delta = \frac{\log(19)}{\beta}. \quad (\text{A.8})$$

Solving for α and β using (A.6), (A.7), and (A.8), gives

$$\beta = \frac{\log(19)}{x_{95} - x_{50}} = \frac{\log(19)}{\delta}. \quad (\text{A.9})$$

and,

$$\alpha = \frac{-\log(19)x_{50}}{x_{95} - x_{50}} = \frac{-\log(19)x_{50}}{\delta}, \quad (\text{A.10})$$

Substituting α and β from (A.9), and (A.10) into (A.3), gives,

$$p(x) = \left(1 + e^{-\log(19)\left(\frac{x-x_{50}}{x_{95}-x_{50}}\right)}\right)^{-1} = \left(1 + e^{-\log(19)\left(\frac{x-x_{50}}{\delta}\right)}\right)^{-1} \quad (\text{A.11})$$

The delta method (Seber, 1973) can be used to get CVs for x_{50} and x_{95} based on the variances of α and β , and their covariance. From the general form of the delta method,

$$\text{var}(f(\alpha, \beta)) \approx \text{var}(\alpha) \left(\frac{\partial f}{\partial \alpha}\right)^2 + \text{var}(\beta) \left(\frac{\partial f}{\partial \beta}\right)^2 + \text{cov}(\alpha, \beta) \left(\frac{\partial f}{\partial \alpha}\right) \left(\frac{\partial f}{\partial \beta}\right), \quad (\text{A.12})$$

the solutions for x_{50} and x_{95} are,

$$\text{var}(x_{50}) = \text{var}\left(\frac{-\alpha}{\beta}\right) \approx \frac{\alpha^2}{\beta^2} \left(\frac{\text{var}(\alpha)}{\alpha^2} + \frac{\text{var}(\beta)}{\beta^2} - \frac{2\text{cov}(\alpha, \beta)}{\alpha\beta}\right), \quad (\text{A.13})$$

and,

$$\text{var}(\delta) = \text{var}\left(\frac{\log(19)}{\beta}\right) \approx \frac{\log(19)\text{var}(\beta)}{\beta^4}. \quad (\text{A.14})$$

Appendix B

EXTRAPLATION FOR WORN SPINES AND CONVERSION OF LENGTHS

Extrapolation for worn annuli was conducted using the formula of Ketchen (1975), $Y = aX^b$, where X is the spine base diameter in millimeters and Y is the estimated age in years from conception. The parameters for the extrapolation were estimated from the subset of the spines that were declared by the reader to show no evidence of worn annuli and had a readability index of 1, 2, or 3, out of 5. It was assumed that no banding occurred during gestation so for the unworn spines, Y corresponds to the observed number of annuli plus 2 years.

All length values used in this analysis were total length (TL) with the tail extended. Lengths for dogfish that had been measured with the tail in the natural position were converted using allometric relationship, $TL_{extended} = 1.0216TL_{natural}$ ($n = 47$, $R^2 = 0.9999$), estimated from dogfish collected in Puget Sound in the 2000s for which both measurements were taken.

The estimated extrapolation function for worn spines, parametrized from the unworn 1940s spines was, $Y = 1.703X^{1.815}$, where X is the base diameter and Y is the estimated number of annuli formed since conception (Fig. B.1). The annuli counts ranged from 1 to 48 with a median of 18. The estimated number of missing annuli for the 871 worn spines from Puget Sound and coastal waters varied from 0 to 56.5 with a median of 8.7.

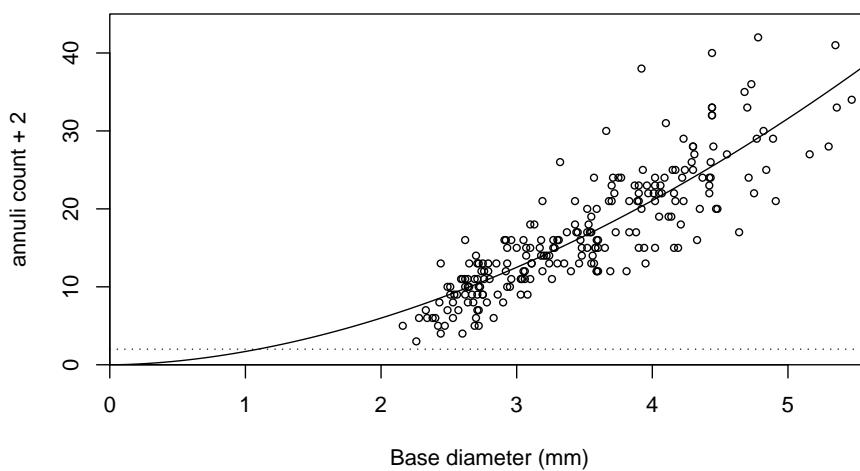


Figure B.1: Function for extrapolating annuli on worn spines fit to annuli counts from the 1940s dogfish. The dashed horizontal line corresponds to a count of 0 annuli.

Appendix C

COMPUTATION OF HISTORIC CATCH AND BYCATCH

C.1 Directed Catch

C.1.1 Total landings

Directed catch (Table C.1) for the years 1876–1980 was taken from Ketchen (1986). Catches reported by Ketchen (1986) for the areas, “Queen Charlotte Islands,” “Queen Charlotte Sound,” and “Hecate Strait,” shown as statistical areas 5A to 5E in Fig. 2 of Ketchen (1986) were combined for this analysis into the single “Northern British Columbia (NBC)” area. Catches associated with “Washington,” “Oregon,” “California,” statistical areas 1C to 3B, were combined to form the single “United States Coast (USC)” area. The “West Coast of Vancouver Island (WCVI)” area comprised catches from statistical areas 3C and 3D. The “Strait of Georgia (SG)” area was equated to statistical area 4B, and the “Puget Sound (PS)” area was equated to statistical area 4A.

Ketchen (1986) estimated landings for much of the time period by extrapolating from landings of dogfish livers, and reports low and high estimates. The average of the low and high estimates was used in this analysis. Ketchen (1986) also reported uncertainty in the allocation of the spatial distribution of the catch in Canadian waters during the period 1938–1953. For simplicity, the unallocated portion of the total catch, described in Appendix 6 of Ketchen (1986), was divided equally between the three Canadian areas used in this analysis, SG, WCVI, and NBC. Likewise, DFO landings records of indeterminate area for the period 1996–2005 were divided equally between the three Canadian areas.

Total landings for the the USC area in the years 1981 onward was taken from

the on-line PacFIN (Pacific coast Fisheries Information Network) database summary reports (Sampson and Crone, 1997). Landings for PS from 1970 onward was taken from Palsson (2008). Catch from WCVI, SG, and NBC for 1978 onward was obtained from DFO records (G.A. McFarlane, pers. comm.).

C.1.2 Gear types

Data on the proportion of the directed catch associated with different gear types is sparse prior to the commencement of the food fish fishery for dogfish in the late 1970s. However, differences in selectivity between trawl and longline fisheries appeared to be large enough that an attempt was made to separate the catch for the full time series of landings into gear types using the information available. To facilitate this process, all non-trawl gear types (including longlines, pots, and gillnets) were assumed to have the same selectivity. Ketchen (1986) suggests 1937 as the first year of significant use of trawl vessels for targeting dogfish, so for simplicity the trawl fishery was assumed to be 0 until that time.

The first available data on the relative proportion of trawl to non-trawl landings is for the years 1941 and 1944 in Holland (1945), during which time the fraction of liver landings in US waters taken by trawl vessels rose from 45% to 75%. Ketchen (1986) reports landings by gear type data for Canadian waters beginning in 1943, but these data are only reasonably complete from 1946–59 and 1976–82. From 1981 onward for USC and 1978 onward for the other 4 areas, data are available on landings by gear type and the ratio of trawl to non-trawl fishing is calculated for each area separately. Prior to those years, incomplete data on landings by gear type were dealt with by using the known trawl catch from all areas combined taken as a fraction of the total catch of known gear type from all areas combined. For years with particularly incomplete data on landings by gear type (1937–40, 1945, and 1960–75), the trawl fishery was assumed to constitute a fraction of the landings that was a linear interpolation between the estimated values in the years immediately preceding and following the set of unknown

years. The landings of known gear type were not assumed to constitute all landings, so the ratio of trawl to non-trawl landings was calculated independently from landings of known gear type and applied to the total landings for each area.

C.2 Bycatch

C.2.1 Bottom-trawl groundfish fisheries

In the USC area, landings of dogfish have often been relatively small compared to the amount of discarded bycatch in other fisheries. Therefore, it is likely that the level of bycatch is more dependent on the fishing effort of the groundfish fishery as a whole than on the effort of fishers targeting dogfish. Relatively few boats target dogfish compared to the size of the total west coast groundfish fleet. Therefore, the bycatch of dogfish was modeled as a proportion of the directed catch of all groundfish (which was assumed to be a proxy for fishing effort), rather than as a proportion of directed dogfish catch. As more observer data is collected in the future, estimates of bycatch in these fisheries may be improved.

Data on bycatch of dogfish in the USC area was available from a study conducted in 1985–87 (Pikitch et al., 1998), which observed 51.3 mt of discarded dogfish for 789.5 of utilized groundfish catch in 1279 observed hauls, for a ratio of 0.065. Hastie and Bellman (2006) estimated a total of 1067 mt of discarded dogfish for the Non-hake trawl fishery in 2005, which was 0.048 of the total landings for all trawl fisheries for the year, excluding hake, as reported by PacFIN. Dogfish discards rates were assumed to be 0.065 up to 1985 and decrease linearly to 0.048 in 2005. These rates were applied to total landings from all groundfish trawl fisheries in the USC area, which were available from the PMFC Groundfish Data Series (PMFC, 1984) for the years 1956–1980 and from PacFIN for the years 1981–2005. Discarded dogfish bycatch in the USC area was assumed to have increased linearly from 0 in 1950, prior to which the commercial value of dogfish would have resulted in low discards rates, to the estimated value in

1956.

Data on bycatch of dogfish in groundfish trawl fisheries in the three Canadian areas was available for the years 1996–2005 (G.A. McFarlane, pers. comm.). The ratio of dogfish bycatch in each area in 1996 to total groundfish landings in B.C. in 1996, combined with the time series of total groundfish landings in B.C. (Ainsworth, 2006) was used to extrapolate estimated bycatch for each area for the years 1951–1995.

C.2.2 Mid-water trawl hake fisheries

Bycatch data were available for the years 1991–2005 from the At-Sea Hake Observer Program, which was collected by observers on US vessels participating in the at-sea fishery for hake (*Merluccius productus*) within the USC area (V. Tuttle, pers. comm.). This data included estimated biomass of dogfish and estimated biomass of hake caught in each observed tow. A simple ratio of total observed dogfish bycatch per year as a fraction of the total observed hake catch per year was computed for the years 1991–2005. The ratio ranged from a low of 0.0007 in 1994 to a high of 0.0084 in 2004. The ratio for each year was applied to the total landings of Hake in US waters for those years (Helser and Martell, 2007), to get an estimate of bycatch of dogfish in the hake fishery, under the assumption that the shoreside and tribal components of the hake fishery had the same rate of bycatch as the observed at-sea hake fishery. For the years 1966–1990, in which hake fisheries were operating, but bycatch data were not available, the mean dogfish bycatch ratio across the observed years, 0.0048, was applied to the total landings from US waters.

The rate of bycatch in the hake fishery in Canadian waters, which has averaged about 1/3 the volume of landings of the hake fisheries US waters (Helser and Martell, 2007), was assumed to have the same mean rate of dogfish bycatch, 0.0048. For simplicity, this bycatch was assumed to take place exclusively in the WCVI area.

The dogfish bycatch in the hake fisheries was assumed to have the same selectivity as the groundfish trawl fisheries. The dogfish caught in the mid-water trawls of the

hake fishery may be younger and smaller than those caught in groundfish fisheries, based on the belief that juvenile dogfish are more pelagic than adults (Ketchen, 1986). However, the magnitude of the hake bycatch is small compared to that from the groundfish trawl fisheries, and lengths compositions for dogfish bycatch in the hake fishery were not available, so no additional selectivity function for the hake fishery was estimated.

C.2.3 Non-trawl commercial fisheries

In the USC area, Hastie and Bellman (2006) estimated 150 mt of discarded dogfish bycatch in fixed-gear groundfish fisheries in 2005 (excluding the Pacific Halibut Fishery). Dogfish made up the largest component of the discards of these fisheries, in which the primary target species (73% of landings) is sablefish (*Anoplopoma fimbria*). Sablefish landings were therefore chosen as a proxy for changes in effort in the non-trawl commercial fisheries. The ratio of discarded dogfish bycatch to retained sablefish in 2005, 0.0475, was applied to the time-series of sablefish catch as reported by Schirripa and Colbert (2005) to get an estimate of dogfish bycatch from non-trawl fisheries for the USC area. A similar extrapolation process using logbook data reported in Haist et al. (2005) gave estimates of the total dogfish bycatch for the three Canadian areas which never totalled more than 10 mt, and therefore were not included in the model.

C.2.4 Recreational fisheries

Data on recreational fisheries in the PS and USC areas was available from the RecFIN database for the years 1980–1989 and 1996–2002. The average weights of examined catch across all years (1.8 kg for PS and 2.4 kg for USC) were used to convert the estimated angler-reported quantity of dead catch in each year to an estimate of biomass removed. For the PS area, recreational dead catch was assumed to be 0 in 1945, an arbitrary start year associated with the end of WWII, and increase linearly to the estimated value of 230 mt in 1980. A linear interpolation was likewise used for the

period 1990–1995, and recreational dead catch was assumed to remain constant after 2002. For the USC area the estimates of recreational dead catch were highly variable, but amounted to less than 1% of the bycatch in trawl fisheries in all but two years, and therefore was not included. No data were available from recreational fisheries in Canadian waters, but should be sought for future analyses.

C.2.5 Bycatch mortality

All discarded dogfish bycatch in commercial fisheries was assumed to have a mortality rate of 50%, as was used in the most recent NW Atlantic stock assessment (NEFSC, 2006) for trawl bycatch. Mortality of bycaught dogfish in trawl and gillnet fisheries has been the subject of recent research (Mandelman and Farrington, 2007a,b; Rulifson, 2007), which found bycatch mortality to be lower than values previously used in dogfish stock assessments. However, Mandelman and Farrington (2007a) found tow-weight to be a significant predictor of mortality over the 100-350 kg observed range of tow-weights. The tow-weights of commercial trawl fisheries in the NE Pacific are substantially higher than this range, so the 50% value from NEFSC (2006), which took into account the results of Mandelman and Farrington (2007a) and Rulifson (2007), was used here. The same 50% value was used for all non-trawl bycatch in the absence of studies on bycatch mortality for dogfish in longline fisheries. Recreational catch described in the RecFIN database reported by anglers to be “alive” and “dead” were assumed to have 0% and 100% mortality, respectively.

Table C.1: Estimated catch and bycatch by area and gear type. Types are: T, trawl directed catch; NT, non-trawl directed catch; BTG, bycatch in bottom-trawl groundfish fisheries; BTH, bycatch in mid-water trawl hake fisheries; BNT, bycatch in non-trawl commercial fisheries; R, recreational dead catch. Mortality is assumed to be 50% for BTG, BTH, and BNT catch and 100% otherwise.

| Year | U.S. Coast | | | | | | Puget Sound | | | | | | Strait of Georgia | | | | | | W. Coast Vancouver I. | | | | | | Northern B.C. | | | | | | | | |
|------|------------|------|------|-----|----|------|-------------|------|------|------|------|------|-------------------|------|------|---|---|---|-----------------------|---|---|------|-------|------|---------------|---|---|----|---|---|-----|---|--|
| | T | | | NT | | | BTG | | | BTH | | | BNT | | | T | | | NT | | | BTG | | | T | | | NT | | | BTG | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1935 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 126 | 0 | 0 | 3484 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1936 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 150 | 0 | 0 | 5268 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1937 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 82 | 653 | 0 | 570 | 4565 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 36 | 288 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1938 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 156 | 548 | 0 | 1653 | 5794 | 0 | 45 | 159 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 115 | 403 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1939 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 356 | 717 | 0 | 1563 | 3146 | 0 | 70 | 141 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 95 | 192 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1940 | 250 | 314 | 0 | 0 | 0 | 0 | 25 | 672 | 845 | 0 | 3050 | 3835 | 0 | 422 | 531 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 422 | 531 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1941 | 3923 | 3159 | 0 | 0 | 0 | 0 | 25 | 3561 | 2867 | 0 | 4846 | 3901 | 0 | 1445 | 1164 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1445 | 1164 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1942 | 3950 | 2155 | 0 | 0 | 0 | 0 | 25 | 1535 | 837 | 0 | 5637 | 3075 | 0 | 2690 | 1468 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2690 | 1468 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1943 | 4917 | 3238 | 0 | 0 | 0 | 0 | 25 | 2151 | 1416 | 0 | 5145 | 3387 | 0 | 2985 | 1965 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4273 | 2813 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1944 | 12562 | 4232 | 0 | 0 | 0 | 0 | 25 | 2839 | 957 | 0 | 6508 | 2193 | 0 | 6100 | 2055 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10719 | 3611 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1945 | 5447 | 3739 | 0 | 0 | 0 | 0 | 25 | 1448 | 994 | 0 | 2546 | 1748 | 0 | 2963 | 2033 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8351 | 5732 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1946 | 4008 | 5142 | 0 | 0 | 0 | 0 | 25 | 1007 | 1292 | 7 | 858 | 1101 | 0 | 1372 | 1761 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2770 | 3554 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1947 | 2788 | 3436 | 0 | 0 | 0 | 0 | 25 | 891 | 1098 | 13 | 1633 | 2013 | 0 | 1612 | 1986 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3515 | 4331 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1948 | 3743 | 1558 | 0 | 0 | 0 | 0 | 25 | 1754 | 730 | 20 | 2311 | 963 | 0 | 2475 | 1030 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3812 | 1587 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1949 | 3934 | 1077 | 0 | 0 | 0 | 0 | 25 | 1076 | 295 | 26 | 3832 | 1049 | 0 | 3914 | 1072 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4821 | 1321 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1950 | 981 | 122 | 0 | 0 | 0 | 0 | 25 | 81 | 10 | 33 | 736 | 92 | 0 | 615 | 77 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 616 | 77 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1951 | 832 | 61 | 336 | 0 | 25 | 268 | 20 | 39 | 1282 | 93 | 8 | 1097 | 80 | 74 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1349 | 98 | 126 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1952 | 938 | 59 | 671 | 0 | 25 | 390 | 24 | 46 | 1176 | 74 | 9 | 860 | 54 | 84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 836 | 52 | 142 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1953 | 475 | 15 | 1007 | 0 | 25 | 599 | 19 | 52 | 1208 | 37 | 7 | 991 | 31 | 67 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 823 | 25 | 113 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1954 | 184 | 142 | 1343 | 0 | 25 | 341 | 264 | 59 | 1040 | 807 | 8 | 203 | 157 | 71 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 172 | 134 | 120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1955 | 207 | 135 | 1679 | 0 | 25 | 324 | 212 | 66 | 1032 | 673 | 7 | 187 | 122 | 61 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 367 | 240 | 103 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1956 | 133 | 65 | 2014 | 0 | 27 | 348 | 170 | 72 | 280 | 136 | 8 | 41 | 20 | 71 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 435 | 212 | 120 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1957 | 691 | 113 | 1942 | 0 | 49 | 44 | 7 | 79 | 959 | 156 | 8 | 476 | 78 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 691 | 113 | 127 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1958 | 160 | 21 | 1923 | 0 | 20 | 1565 | 203 | 85 | 873 | 114 | 9 | 166 | 22 | 81 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 381 | 50 | 137 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1959 | 62 | 74 | 1946 | 0 | 33 | 588 | 708 | 92 | 2265 | 2725 | 9 | 291 | 350 | 78 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 350 | 421 | 132 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1960 | 30 | 38 | 1873 | 0 | 47 | 254 | 323 | 98 | 1510 | 1922 | 10 | 32 | 40 | 89 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 381 | 485 | 151 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1961 | 10 | 13 | 1854 | 0 | 27 | 164 | 222 | 105 | 952 | 1282 | 9 | 1308 | 1763 | 82 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 266 | 358 | 139 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1962 | 2 | 3 | 1957 | 0 | 26 | 143 | 203 | 111 | 167 | 239 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 151 | 2 | 3 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1963 | 0 | 0 | 1997 | 0 | 22 | 156 | 237 | 118 | 88 | 134 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1964 | 0 | 0 | 2008 | 0 | 34 | 320 | 513 | 125 | 377 | 605 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1965 | 1 | 3 | 2429 | 0 | 28 | 349 | 592 | 131 | 92 | 156 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1966 | 0 | 0 | 2726 | 328 | 24 | 271 | 487 | 138 | 190 | 341 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1967 | 0 | 0 | 2446 | 425 | 85 | 195 | 374 | 144 | 200 | 384 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1968 | 6 | 11 | 2231 | 146 | 46 | 102 | 209 | 151 | 111 | 225 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |

Continued on next page

Table C.1 (continued)

VITA

Ian Taylor grew up in Seattle and Bellingham, Washington. He earned a Bachelor of Arts in Mathematics from Carleton College after which he taught mathematics at Vuti Secondary School in rural Zimbabwe for the U.S. Peace Corps. Ian returned to Seattle to enroll in the interdisciplinary graduate program in Quantitative Ecology and Resource Management at the University of Washington. During his graduate studies he was a research assistant in the U.W. School of Aquatic and Fishery Sciences. In 2008, Ian graduated from the University of Washington with a Ph.D. in Quantitative Ecology and Resource Management.