

**ASSESSING THE ABUNDANCE OF BASKING SHARKS (*CETORHINUS
MAXIMUS*) IN ATLANTIC CANADIAN WATERS**

By

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Dalhousie University is located in Mi'kma'ki, the ancestral and unceded territory of the
Mi'kmaq. We are all Treaty people.

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ABSTRACT

The Atlantic Canadian population of basking sharks (*Cetorhinus maximus*) is designated Special Concern by COSEWIC. Little is known about their population size or life history, though they are considered to have long life histories and be inherently unproductive. Estimating population size from aerial surveys gave mean abundances ranging from 3,600 to 7,146 in 2007 and from 13,544 to 27,682 in 2016, depending on assumptions. The estimated median intrinsic rate of population increase was 0.0197, and potential population growth became negative if historical bycatch was accounted for. These population growth rates cannot account for the increase in abundance predicted from aerial survey data. Substantial migration into Canadian waters and/or a much more productive life history would be needed in conjunction. These results highlight the need for continued monitoring, potential improvement in methods to estimate abundance, and the development of non-lethal sampling for determining life history parameters.

LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
BoF	Bay of Fundy
CDS	Conventional Distance Sampling
CI	Confidence or Credible Interval
CITIES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CMS	Convention on Migratory Species
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CPUE	Catch Per Unit Effort
DFO	Fisheries and Oceans Canada
DSM	Density Surface Model
DUs	Designatable Units
DVM	Diel Vertical Migration Pattern
EEZ	Exclusive Economic Zone
Eq	Equation
ESS	Effective Sample Size
GAM	Generalized Additive Modeling
GLM	Generalized linear Modeling
GoM	Gulf of Maine
GoSL	Gulf of St. Lawrence
HMC	Hamiltonian Monte Carlo
ICES	International Council for the Exploration of the Sea
ID	Identification
IUCN	International Union for the Conservation of Nature
MC	Monte Carlo
MCDS	Multiple Covariate Distance Sampling
MCMC	Markov Chain Monte Carlo
MLE	Maximum Likelihood Estimation
MPMM	Multinomial-Poisson Mixture Model
MRDS	Mark-Recapture Distance Sampling
NAISS	North Atlantic International Sighting Survey
NARWC	North Atlantic right Whale Consortium
NL	Newfoundland and Labrador
NMFS	National Marine Fisheries Service
NOAA	National Ocean and Atmospheric Administration
POSE	Precocial-Opportunistic-Survivor-Episodic [framework]
PSAT	Pop-Up Satellite Archival Tags
SARA	Species at Risk Act (Canada)
SD	Standard Deviation
SDM	Species Distribution Model
SNESSA	Southern New England to Scotian Shelf Abundance [survey]
SPUE	Sightings Per Unit Effort
SS	Scotian Shelf
TNASS	Trans North Atlantic Sightings Survey
WAIC	Watanabe-Akaike Information Criterion

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CHAPTER 1: INTRODUCTION

1.1. OVERVIEW

An estimated one-third of the world's sharks and rays (i.e., elasmobranchs) are threatened with extinction (Dulvy et al. 2021) and as such, efficient and effective management is crucial to their conservation (Davidson and Dulvy 2017, Birkmanis et al. 2020). Many elasmobranchs have a late age at maturity and low fecundity leading to low lifetime reproductive output (Cortés 2000, Pardo et al. 2016). This makes them particularly vulnerable to over-exploitation, as they cannot compensate for fishing mortality as easily as commercially exploited teleost species with higher rates of reproduction (Myers et al. 1999, Simpfendorfer and Kyne 2009). However, there are many challenges to effective shark conservation, which include, but are not limited to, the over-simplification of the threats and possible management solutions, the under-management of fishing mortality and the fact that many species traverse multiple national jurisdictions (Dulvy et al. 2017). The first step in effective management and understanding the effectiveness of conservation actions is to assess population status and abundance (Dulvy et al. 2017, Birkmanis et al. 2020).

Basking sharks (*Cetorhinus maximus*, Gunnerus 1765) are zooplanktivorous, charismatic “gentle giants” that remain poorly studied. They are large, slow moving, filter-feeding sharks that typically spend a large percentage of their time “basking” at the surface (Sims 2008). They are one of the largest fish in the ocean, second only to the whale shark (*Rhincodon typus*, Smith 1828), reaching lengths of up to 12m and weights of approximately 4 tonnes (Sims 2008). The life history characteristics of basking sharks are uncertain, but they are considered slow growing, late to mature, and long lived, making them particularly vulnerable to overexploitation (Dulvy et al. 2014). While this information about their basic biology and ecology is known, little is known about their population size or structure.

The aim of this thesis is to estimate the abundance of basking sharks in Atlantic Canada in 2007 and 2016 and evaluate the feasibility of these estimates within what is known about the life history of basking sharks. This chapter will introduce the study by first discussing the background to life history and abundance estimations – by explaining fundamental concepts, introducing methods within each topic, and covering some applications – followed by a brief

overview of the biology, ecology and status of basking sharks, with a specific focus on Canadian context, and then detailing the research problem, aims and objectives of this thesis.

1.2. LIFE HISTORY

1.2.1. FUNDAMENTAL CONCEPTS

Life history describes the pattern of events in an organism's life that relates to its growth, development, reproduction and survival (Hutchings 2021). Life histories reflect the expressions of traits (i.e., *life history parameters*) that are closely related to fitness, such as the age at maturity, size at maturity, fecundity (the number of offspring produced in a single breeding season), offspring size and longevity (i.e., lifespan) (Hutchings 2021). The *life history strategy* of a species is the overall pattern in the timing and nature of life history events averaged over all of the individuals in a species (Allen and Pizer 2008). The life history of a species is a product of evolutionary adaptation to the environment in which the species lives, and is shaped by trade-offs (i.e., resource allocation) to growth, reproduction, and survival. The study of these trade-offs and the evolutionary pressures that shape them falls under the umbrella of *life history theory* (Roff 2002, Hutchings 2021). Quantitative analyses of life history traits can be used in *life table analysis* with *age-specific* information on reproduction and survival to estimate quantities like the rate of population growth, r , or extinction risk (e.g., Myers et al. 1999, Hutchings et al. 2012).

1.2.2. CLASSIFICATION OF LIFE HISTORY STRATEGIES

One of the most famous methods of classifying life history strategies comes from Robert MacArthur and Edward O. Wilson in 1967. MacArthur and Wilson (1967) coined the terms r -selection and k -selection to describe two ends of a continuum of reproductive strategies. Species that are considered r -selected generally experience high population growth rates, as r represents the intrinsic rate of increase of a population (MacArthur and Wilson 1967). Organisms that are at the r -selected end of the spectrum tend to grow fast, mature early, have many offspring and have short life spans (MacArthur and Wilson 1967). Examples of this include most insects, small vertebrates such as mice and rabbits, and weedy plant species such as dandelions and grasses (Allen and Pizer 2008). On the other hand, species that are k -selected experience lower rates of increase in populations that are at, or near, the population carrying capacity, K

(MacArthur and Wilson 1967). Organisms that follow this strategy tend to grow slow, mature later, have few offspring and live long (MacArthur and Wilson 1967). Examples of *k*-selected organisms are large mammals such as elephants and whales, reptiles like tortoises and crocodiles, and long-lived plant species like oak and maple trees (MacArthur and Wilson 1967).

The *r*- and *k*- selection classification scheme is less commonly used now due to the limitation pointed out by Pianka (1978) and others that many species do not fall along this continuum (e.g., salmonid fish, Hutchings and Morris 1985). Other classifications have been proposed; for example, the use of the terms *fast* and *slow* life histories (Gaillard et al. 1989, Dobson and Oli 2008), the “life history cube” of Charnov (2002) or the POSE framework of Kindsvater et al. (2016). The POSE (precoial-opportunistic-survivor-episodic) framework categorizes species into a continuum of four general strategies, then uses them to understand which species can withstand various types of mortality and which are at greatest risk of extinction (Kindsvater et al. 2016). The four general strategies are based on the variation between fast and slow life histories (adult mortality) and density-dependant compensatory capacity (juvenile mortality) (Kindsvater et al. 2016). Species that would have typically been characterized as *k*-selected by MacArthur and Wilson (1967), with long lifespans, large body sizes, low reproductive output and late age-at-maturity are classified as survivors under the Kindsvater et al. (2016) POSE framework. Popular examples of this strategy would be humpback whales (*Megaptera novaeangliae* Borowoski 1781), Asian Elephant (*Elephas maximus* Linnaeus 1758), and Galapagos Tortoises (*Chelonoidis niger* complex Fitzinger 1835). Species that have long lives, large body sizes, slow growth, and late maturity in addition to *highly variable* recruitment such as Atlantic cod (*Gadus morhua*, Linnaeus 1758) are classified as episodic (Kindsvater et al. 2016). This framework expands on the original framework of MacArthur and Wilson (1967) to account for the limitation pointed out by Pianka (1978) and explicitly links characteristic life history strategies to the understanding of compensatory capacity (i.e., ability to tolerate increased mortality) (Kindsvater et al. 2016).

1.2.3. APPLICATIONS OF LIFE HISTORY THEORY

The study of life history parameters can have many useful applications for biologists. Life history provides the basis for understanding and predicting the effect of environmental changes on the fitness of an organism and populations as a whole. There is a wealth of research on the impact of fisheries on life history traits (summarized in Wootton and Smith 2015). Work by Hutchings et al. (2010, 2012) correlates life history traits to extinction risk and recovery potential. Higher extinction risk has been linked to large body size (Bennet and Owens 1997, Denney et al. 2002, Dulvy et al. 2014), long lifespan (Smith et al. 1998, Stevens et al. 2000), delayed age-at-maturity (Reynolds et al. 2005, Hutchings et al. 2012) and low fecundity (Musick et al. 2000).

Life table analysis, as previously mentioned, can be used to estimate r , the intrinsic rate of per capita population growth. In its simplest form, the rate of population growth, r , depends on per capita birth rate b and death rate d with $r = b - d$ (Simpfendorfer 2005, Kindsvater et al. 2016). Life tables describe *age-specific* schedules of survivorship (l_x , the probability of surviving until age x) and reproduction (m_x , fecundity at age x) for a cohort (Pearl and Reed 1920, Cortés 2002). Using these, population growth rates can be estimated from age-specific survival and age-specific reproduction through one of three methods: (i) generation time method, (ii) Leslie projection matrix (Leslie 1945) or (iii) the Euler-Lotka method (Lotka 1907 based on Euler 1760) (Allen and Pizer 2008, Simpfendorfer 2005). The generation time method is the simplest, but least accurate of the methods (McAllister et al. 2001). The Leslie projection matrix generalizes the approach of the Euler-Lotka method using matrix algebra (Cortés 2016). The Euler-Lotka method obtains an estimate of r by summing the product of age-specific survivorship and age-specific reproduction across the entire lifespan of the animal. This measure of per capita population growth can then be applied to density-dependant or density-independent models of population growth to project and predict changes in population size over time. Cortés (1998) suggests that life table analysis is well suited for sharks due to their high rates of survival and well-defined reproductive cycle, and it has been used by Campana et al. (2008) for basking sharks, as well as Bowlby and Gibson (2020) for white sharks (*Carcharodon carcharias*, Linnaeus 1758), among others.

1.3. ESTIMATING THE ABUNDANCE OF A POPULATION

1.3.1. FUNDAMENTAL CONCEPTS

The definitions of *population* can vary depending on the source, or the aim of the research (Hammond et al. 2021). Here, a *population* can be defined as is a group of individuals of the same species that live within a defined area and interbreed (Hammond et al. 2021). Population *abundance* (i.e., size) is then the number of individuals in the population, and population *density* is the number of individuals per unit area (Thompson et al. 1998). Additionally, biological populations are subject to the processes of birth, death, immigration and emigration, so one needs to define if the population is *closed* or *open*. A population is considered *geographically closed* when there is no movement of animals across the boundary of the study area (i.e., no immigration or emigration) (Seber 1982). Conversely, an *open* population is one that is not fixed in number and composition during a specified time period (Thompson et al. 1998). Assessing abundance requires either a *census* or a *survey*, which are not interchangeable terms. A census is a complete count within a particular area and time period, whereas a survey is a partial count of animals in that same area and time period. Census' are rarely possible in studies of animal populations (Thompson et al. 1998, Seber 1982), particularly for marine populations where species are often wide-ranging, at various depths, and highly mobile (Hammond et al. 2021). Consider, for example, attempting to census the Bay of Fundy. It constitutes a relatively small part of Atlantic Canadian waters and yet it is approximately 21,145 km². It is not logistically feasible to count all the animals in that area due to the massive effort required, even if they were all visible from the surface and available for detection.

1.3.2. METHODS OF ESTIMATING ABSOLUTE ABUNDANCE

Most estimates of absolute abundance and density come from survey data, which only sample a proportion of the population. This sample then must be extrapolated to estimate the total number of animals in the population. There are two general techniques that are most commonly used for sampling: (i) capture-recapture methods or (ii) area-based counts (Seber 1982, Krebs 2001).

Capture-recapture methods involve capturing animals, marking them, releasing them and then recapturing them (either once or multiple times). The idea is that the proportion of marked animals in the recaptured sample is representative of the proportion marked in the entire

population (Krebs 2001). This allows the abundance of the entire population to be estimated from the size of the original marked population divided by the proportion of the population marked on recapture (Seber 1982). This is known as the *Peterson method* (1898). The more general model of Jolly and Seber (1965) called the J-S model can account for open populations and is more commonly used now. Marks can either be added to the animal, such as a small external tag on a fish or a bird, or marks may inherently exist on animals such as the humpback whale (*Megaptera novaeangliae*, Borowski 1781) that have recognizable patterns on their tail flukes (Kacev et al. 2017). Inherent marks can be recognized non-invasively with photo-identification (photo-ID) methods. Capture-recapture methods are generally the preferred method for estimating marine animal abundance, with many examples from the fish literature using tags (e.g., Conner et al. 2015, Osmundson and White 2015, Budy et al. 2017, etc.) or in the marine mammal literature using photo-identification (e.g., Ramp et al. 2014, Pace et al. 2017, Kuit et al. 2021, Hammond et al. 2021, etc.). Photo-ID mark-recapture for basking sharks has been attempted by Gore et al. (2016) in the eastern North Atlantic, and by Hoogenboom et al. (2015) in the Bay of Fundy but there is not enough similar data to do so across Atlantic Canadian waters.

On the other hand, area-based counts do not require recapture/resighting and can include the use of quadrats and transects, or swept-area biomass estimators. In the swept-area method, it is assumed that the area swept up by a trawl or net is representative of the entire area over which the species is distributed. For example, Wallace et al. (2009) used this method for spiny dogfish (*Squalus acanthias* Linnaeus 1758). Conversely, the use of quadrats (i.e., a sampling area of any shape) or transects involves counting all the individuals on several, randomly sampled, quadrats or transects of known size and then extrapolating the average count to the whole area (Seber 1982, Krebs 2001). Quadrats are used extensively in plant ecology, as well as for invertebrates, whereas transects and point counts are commonly used for birds, though less commonly in the marine environment (Krebs 2001). When all animals in the sampled quadrats are not able to be directly counted, either due to an inability to detect animals when they are available for detection (i.e., *perception bias*) or because they are not available for detection (i.e., *availability bias*), additional methods to estimating the true abundance in the quadrat or transect must be used (Buckland et al. 2015). A common solution to mitigate perception bias is to incorporate *distance*

sampling methods, which utilises a model of detection probability with respect to distance to estimate the true abundance in the sampled area (Buckland et al. 1993). This encompasses plot sampling and line transect methods (Borchers et al. 2006). In the marine environment in particular, line transects are often used to collect data from aerial- and boat-based surveys (Buckland et al. 2015).

1.3.3. METHODS OF ESTIMATING RELATIVE ABUNDANCE

If absolute abundance cannot be estimated, it may also be sufficient to estimate the *relative* abundance of a population. Indices of relative density depend on the idea that the collection of samples represents some constant but unknown relationship to the total population size. For example, between two areas of equal size, area x has twice as many of this species than area y . There are many indices of relative abundance (or density) including, but not limited to: percent cover of an area, roadside counts, dung counts, traps, vocalization frequencies, catch per unit fishing effort (CPUE) and pelt records (Krebs 2001). These cannot be used to determine absolute abundance, but they may be useful in monitoring trends in population size over time.

1.4. BASKING SHARKS

1.4.1. SPECIES DESCRIPTION

The basking shark is the sole member of the family Cetorhinidae in the order Lamniformes (mackerel sharks). Other common names include sun shark, bone shark and elephant shark (UK CITES 2002). In Atlantic Canada, they can also be called “ground shark”, although this name is also used for the Greenland shark (*Somniosus geoenlandicus*, Bloch and Schneider 1801).

The basking shark is a large-bodied fish with a fusiform body shape. Maximum total lengths have been estimated at between 12.2 m and 15.2 m, though most specimens do not exceed 9.8 m (Compagno 1984). They appear grey-brown to black and can have lighter dappled patterns (Sims 2008). They have a conical snout and huge sub-terminal mouth with very small (~5mm) hooked teeth arranged in 3-7 rows (Matthews and Parker 1950). They are typified by the 5 gill slits that encircle the head (Matthews and Parker 1950). When the mouth is open, the gill rakers (comb like structures on the distal portion of each gill arch) are used to filter zooplankton prey from the flow of seawater produced by swimming (“*ram-filter feeding*”) (Sims 2008). Some

studies suggest that basking sharks shed their gill rakers in the late autumn/early winter (Matthews 1962, Parker and Boseman 1954) but others have found basking sharks in winter with gill rakers present and food in their stomachs (Sims 1999).

1.4.2. DISTRIBUTION

Basking sharks are a circumglobal species, known to inhabit temperate waters of continental shelves and coastal regions (Compagno 2001). The basking shark has been recorded in the western Atlantic from Newfoundland to Florida, and from Southern Brazil to Argentina (Compagno 2001). Tracking studies from Massachusetts show that they go as far south as the Dominican Republic, mainly by remaining in deeper, cooler waters (Skomal et al. 2009). Sharks tagged around Cape Cod in the Gulf of Maine travelled as far south as Brazil (Bruan et al. 2018). In the Eastern Atlantic, they are present from Iceland and the Russian White Sea to the Mediterranean Sea (Compagno 2001). They have also been found in the north and south Pacific Ocean, the Sea of Japan, off southern Australia and around New Zealand. In Atlantic and Pacific Canadian waters, records show that they occupy all coastal temperate waters where temperatures exceed 6 or 7 °C.

Analyses show that basking sharks are strongly associated with tidal fronts, areas dominated by transitional waters between mixed and stratified water columns (Sims et al. 2006). These tidal fronts are often sites of enhanced zooplankton abundance. The preferred prey of basking sharks are Calanoid copepods (Sims and Quayle 1998, Cotton et al. 2005), specifically *Calanus finmarchius* (Gunnerus 1770). A study in the eastern North Atlantic demonstrated that basking sharks near frontal zones spent 60% of their time near the surface during the day, whereas when in well-stratified waters, they spent <1% of their time near the surface (Sims et al. 2005). Findings by Sims et al. (2005) suggest that sharks in shallow, inner shelf areas near thermal fronts undergo a strong *reverse* diel vertical migration (DVM) pattern with dusk descents and dawn ascents, whereas sharks in deep waters or on shelf-edges exhibit normal DVM (i.e., dusk ascent-dawn descent) that characterises the traditional movement of zooplankton and their associated predatory species. Satellite tagging in the southern Gulf of Maine by Curtis et al. (2014) found that basking shark movement in summer and fall is restricted primarily to continental shelf waters (<200 m depth) with 66.4% of time spent in the upper 25 m of the water column, and that primary productivity and depth were the strongest predictors of

movement. While they are primarily recorded in coastal areas near the surface, this may not represent their entire habitat range as they have been hypothesized to also inhabit the epipelagic zone (0-200 m depth) of ocean basins (Southall et al. 2005) and may sometimes enter deeper waters (>200 m). While basking sharks tend to show strong inter-annual seasonal residency (Doherty et al. 2019, Lieber et al. 2020) an 8 m long female basking shark was tracked to a maximum dive depth of 1264 m in an area west of the Mid-Atlantic ridge by Gore et al. (2008). The high squalene content (11.8% to 38%, Kunzlik 1988) in the livers of basking sharks is characteristic of species that explores deep-water habitats (Karnovski et al. 1948). Additionally, new tracking studies (e.g. Braun et al. 2018, Doherty et al. 2019) suggest that basking sharks may spend winter and early spring moving southward and in deep water (>500 m) with periods of occupancy at depths greater than 1000 m.

Many shark species have a tendency to segregate by sex and body size (Sims 2005, Wearmouth and Sims 2008), however there is no current evidence to indicate differential distribution between the sexes for basking shark. Both sexes have been observed in the same areas during summer (Matthews and Parker 1950, Sims et al. 2000) and large aggregations in excess of 1300 individuals have been observed with a mix of mature and immature individuals (Kenney et al. 1985, Skomal et al. 2004, Crowe et al. 2018). The causes of episodic aggregation behaviour are unknown, but speculated to be related to either foraging, with observed feeding in high-density zooplankton patches (Crowe et al. 2018), and/or mating (Harvey-Clarke et al. 1999).

1.4.3. REPRODUCTION AND LIFE HISTORY

It is believed that males mature at a length of 5-7 m, at ages between 12-16 years (Compagno 2001). Rapid clasper growth occurred in males between 6.0 and 7.5 m body length (Francis and Duffy 2002). Females are estimated to mature at 8.1-9.8 m, at ages of approximately 16-20 years (Matthews 1950, Matthews and Parker 1950). The individual growth rate of basking sharks is not known with certainty but is estimated at 0.4 m per year by Pauly (2002) or at 0.86 m per year by Parker and Stott (1965). Attempts to age basking sharks have proved difficult as findings show that there is not a consistent number of vertebral rings along body length which means that basking sharks cannot be aged by conventional methods of band-

pair counts (Natanson et al. 2008). Despite this, longevity was estimated by Pauly (2002) at 40-50 years.

1.4.4. POPULATION STRUCTURE

Historically, it was suggested that basking sharks form local populations (Parker and Stott 1965). New studies using genetic techniques and satellite tracking refute this idea (Sims 2008). Work by Sims et al. (2003b) found that tracked sharks remain in particular regions for several months, but also moved rapidly between regions over a period of a few weeks. These movements were primarily driven by foraging for high densities of zooplankton (Sims et al. 2006, Doherty et al. 2017). Additionally, sharks tracked by Sims et al. (2003b) freely mixed around the UK, suggesting that population differentiation at local scales was unlikely. In the western North Atlantic, studies using pop-up satellite archival tags (PSAT) show that basking sharks can make extensive north-south migrations (Skomal et al. 2004, 2009, Skomal 2005, Braun et al. 2018). Campana et al. (2008) suggests that it is likely that Atlantic Canadian basking sharks are part of the same population as basking sharks in the U.S.

Early genetic work by Hoelzel et al. (2006) suggested that basking sharks lack a global population structure and display low worldwide genetic variability. New studies provide evidence of transatlantic mixing (Gore et al. 2008, Johnston et al. 2019), and while this mixing behaviour is far from common, it is enough to ensure that genetic population diversity is maintained (Hoelzel et al. 2006). However, recent genetic studies by Noble et al. (2006) and Lieber et al. (2020) found evidence of limited gene flow across oceanic regions which suggests some level of population structuring in the eastern North Atlantic.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has designated the Canadian Atlantic and Pacific populations of basking sharks as separate Designatable Units (DUs) as a result of their biogeographic separation and a lack of evidence for trans-oceanic mixing (COSEWIC 2007, 2009).

1.4.5. STATUS AND THREATS

As of 2019, the International Union for the Conservation of Nature (IUCN) has upgraded the species listing to Endangered (EN) globally, on the basis of a decreasing trend in the global population (Rigby et al. 2019). The trade of fins to Asian countries continues to be of

international concern (COSEWIC 2007). Basking shark fins have been valued at ~USD 30,000/t (Fairfax 1998, COSEWIC 2007). Basking sharks were listed under Appendix II of the Convention on International trade in Endangered Species of Wild Fauna and Flora (CITES) in 2002, and Appendices I and II of the Convention on Migratory Species (CMS) in 2005, in response to this. At present there is a zero quota in European and Canadian waters (COSEWIC 2007) though fins may continue to be harvested in other regions or in the high seas (i.e., international waters).

In Canada, COSEWIC listed the Pacific population of basking sharks as Endangered in 2007, and the Atlantic population as Special Concern in 2009 (COSEWIC 2007, 2009). Currently, the main threat facing basking sharks in Canada is ongoing mortality from fisheries operations (often as bycatch or entanglement in fishing gear) (COSEWIC 2009). The Canadian Pacific population has declined to the point of “virtually disappearing” (COSEWIC 2007) from targeted killing (commercial and recreational), bycatch and a directed eradication program (1955-1969) by the Department of Fisheries and Oceans. There have only been 6 sightings of basking sharks since 1996 on the Pacific coast of Canada (COSEWIC 2007, Pawson 2020). Conversely, there has never been a directed fishery for basking sharks in Atlantic Canadian waters and sightings are common on an annual basis in certain regions (Campana et al. 2008) A low level of bycatch occurs annually in commercial fisheries on the Atlantic coast, primarily from redfish and groundfish trawl fisheries in Maritimes region (Campana et al. 2008). McInturf et al. (2022) identified the following knowledge gaps for basking shark research: genetic sampling, improved data collection for dynamic predictors, effective strategies for conservation and systematic monitoring effort. In particular, they underscored the need for improved understanding of abundance, distribution and movement patterns that are required for effective conservation (McInturf et al. 2022).

1.5. STUDY AIMS AND CHAPTER OUTLINES

This thesis was carried out in order to present an updated assessment of the status of basking sharks in Atlantic Canada. Updated abundance information is necessary because the Atlantic population of basking sharks is up for re-assessment by COSEWIC as it has been over 10 years since the last one. Based on the gaps in the existing literature and the need for reassessment this thesis focuses on two major goals that relate to accurately assessing the

population of basking sharks in Atlantic Canada: (1) estimating abundance in 2007 and 2016 using fisheries-independent data and (2) using what is currently known about the life history of basking sharks to infer the validity of the trend in abundance from 2007 to 2016. These goals are addressed separately in Chapters 2 and 3. In Chapter 2, estimates of abundance for 2007 and 2016 are presented based on survey data from Fisheries and Oceans Canada, using multiple distance sampling methods. In Chapter 3, population growth is simulated based on life history information and the population is projected forward to 2016 from the estimated abundance in 2007. By exploring several sources of uncertainty related to basking shark life history, the feasibility of the trend from Chapter 2 can be evaluated. The results from the previous two chapters are brought together in Chapter 4 to discuss and speculate on other factors that may account for the trend predicted by Chapter 2 and recommend approaches for future research to address the limitations in this paper.

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CHAPTER 2: ABUNDANCE ESTIMATION OF BASKING SHARKS IN ATLANTIC CANADA

2.1. INTRODUCTION

There is a sizable gap in knowledge of the basic biology of many shark and ray species compared to commercially exploited fish species, with sharks and rays being the most data-deficient of all vertebrate groups (Hoffmann et al. 2010). Economically important species are sampled in commercial fisheries so their life history characteristics can be sampled and catch-per-unit-effort (CPUE) can be calculated with some degree of accuracy (Maunder et al. 2006). CPUE data is often too sparse and variable to use for non-target species, and it can be problematic to use for abundance estimates because many factors can affect measures of effort (Hillborn and Walters 1992, Pennino et al. 2016). The non-commercial species have limited information and aren't sampled sufficiently to understand much about life history or abundance. Collecting information on these species relies instead on non-lethal sampling methods to obtain information (Heupel and Simpfendorfer 2010, Hammershlag and Sulikowski 2011) that are favoured for large, non-commercial species (e.g., whales, seals and turtles in marine environments; Lew 2015). In addition, widely dispersing pelagic sharks are hard to monitor, particularly in offshore environments.

Information about the prevalence and distribution of marine species is derived from two main sources: (1) fisheries-independent data (designed, scientific surveys) and (2) fisheries-dependant data (information collected during commercial fishing operations). While fisheries-dependant data is often more abundant, easier to obtain and can provide a long time series, there are numerous challenges with deriving an unbiased estimate of abundance from these data, especially for non-target species and/or species at risk (Maunder et al. 2006). Fisheries-dependant data can be biased due to management constraints and misreported catches, issues with species identification, and preferential sampling due to repeated visits to specific fishing locations (Pennino et al. 2016). In the case of collecting data on species-at-risk, there are more restrictions due to ethical issues and catches may be under-reported (Robinson et al. 2018). On the other hand, fisheries-independent data is considered higher quality because sampling is standardized and scientifically designed with the target species in mind (Pennino et al. 2016).

However, surveying wide-ranging species can be extremely costly and surveys are often restricted in spatial and temporal coverage. This leads to lack of reliable abundance information for many pelagic and semi-pelagic marine megafauna that are not targeted by commercial fisheries. In rare instances when marine surveys exist, it becomes possible to use these data.

Distance sampling refers to a set of methods used to estimate the density and/or abundance of biological populations from standardized survey data, by taking detection probability into account by using the recorded distances between the species of interest and the observer (Buckland et al. 2001, Buckland et al. 2004, Buckland et al. 2015). The idea is that the further an object is away from the observer, the less likely it is that an observer will see it – allowing a model to be built of the probability of detection given the distance from the observer, known as the detection function (Miller et al. 2019). The detection function can be used to estimate how many objects were missed, and therefore estimate density within a maximum, predetermined detection distance from a transect line (i.e., the transect width) (Miller et al. 2019). Abundance in the total area can be extrapolated from density by multiplying by the proportion of the study area to the total area.

Understanding abundance and trends of marine megafauna is required to meet objectives under the Canadian *Species at Risk Act* (SARA) and is critical to national and international conservation efforts. Basking sharks (*Cetorhinus maximus*, Gunnerus 1765) were listed under Appendix II of the Convention on International trade in Endangered Species of Wild Fauna and Flora (CITES) in 2002, and Appendices I and II of the Convention on Migratory Species (CMS) in 2005. In 2019 the IUCN upgraded the species listing to Endangered (EN) globally, based on a globally decreasing trend (Rigby et al. 2019). In Canada, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated the Pacific population of basking sharks as Endangered in 2007, and the Atlantic population as Special Concern in 2009 (COSEWIC 2009). The designation in Atlantic Canada was based on a highly uncertain estimate in 2008 of 10,125 individuals (no CI reported) from Campana et al. (2008). There is a need to re-assess abundance in order to determine changes in conservation status.

In this Chapter, multiple distance sampling analysis methods are used to update abundance estimates for basking sharks in Atlantic Canada, using fisheries-independent aerial

survey data from 2007 and 2016. Data from 2016 will give the most current abundance estimate. Estimating abundance from the 2007 data using the same approach gives two points in time, to determine if there are any trends in abundance after the COSEWIC designation of the Atlantic population of basking sharks in 2009. The three methods will be compared to determine the effect of analysis assumptions on estimates. Updated abundance information is necessary because the Atlantic population of basking sharks is up for re-assessment by COSEWIC as in 2022, it has been over 10 years since the last assessment (2009). There is an immediate need to quantify the trends in abundance to estimate the effectiveness of any conservation efforts (e.g., Appendix II listing), understand fisheries interaction potential, and population responses to climate change.

2.2. METHODS

2.2.1. SURVEY DATA

Abundance estimates used aerial survey data collected during the Trans North Atlantic Sightings Survey (TNASS) in 2007 and the North Atlantic International Sighting Survey (NAISS) in 2016 (Figure 2.1). Although both surveys were designed for marine mammal assessment, they included any sightings data of basking sharks. Basking sharks are similar to cetaceans in that they are large bodied marine animals that spend a substantial portion of their time ‘basking’ near the surface. However, basking sharks are different in that they do not breathe at the surface, and do not have “blows” that can be used as cues; making them more difficult to spot. They share their primary prey species, calanoid copepods, with many common baleen whales in Atlantic Canada, such as the fin whale *Balaenoptera physalus* (Linnaeus 1758), the north Atlantic right whale *Eubalaena glacialis* (Müller 1776) and humpback whales *Megaptera novaeangliae* (Borowski 1781), and as such, are all often tightly associated with the distribution of the copepods (Sims 2008). While basking sharks can be more difficult to observe than similarly sized whales, this dataset was used because of the similarities in ecology.

Line transect surveys are designed to estimate animal abundance in a survey area and rely on the principles of randomization and replication (Buckland et al. 2015). A well-designed survey will sample randomly with respect to the distribution of the study animal and will contain a sufficient number of lines to ensure that variance in the encounter rate can be estimated

(Strindberg et al. 2004). Flying (or sailing) parallel lines are the standard design for distance sampling and is more appropriate in cases where the width of the study area varies substantially (Buckland et al. 2015). Zig-lines are more useful in a larger study area where there is a significant cost to travelling from one transect to the next (Buckland et al. 2015). Both patterns are intended to ensure equal inclusion probabilities, meaning that areas with specific characteristics are not to be surveyed more than another. The orientation of lines across the study area is also of importance, as often there are changes in species composition along depth gradients (Thomas et al. 2010). Lines are often flown perpendicular to depth gradients so that specific gradients are not over-represented, as they would be if transect lines were flown parallel to equivalent depths. Survey design is essential to minimizing bias in abundance estimation.

Fisheries and Oceans Canada (DFO) conducted the Canadian component of TNASS between July 17 to August 24, 2007 (Table 2.1), using single-platform observers on three aircraft: two Cessna 337s that flew into the Gulf of the St Lawrence (hereafter “GoSL”) and the Scotian Shelf (hereafter “SS”), and a Twin Otter that flew off the coast of Newfoundland and Labrador (hereafter “NL”) (Lawson and Gosselin, 2009). Observations of basking sharks in the Bay of Fundy (hereafter “BoF”) in 2007 come predominantly from the SNESSA (Southern New England to Scotian Shelf Abundance) aerial survey conducted by the National Oceanic and Atmospheric Administration (NOAA) and coordinated by the U.S. National Marine Fisheries Service (NMFS) – Woods Hole. The NL portion of the 2007 survey was conducted in an equal-angle, zigzag pattern (Lawson and Gosselin, 2009) (Figure 2.1 left panel, Table 2.1). Transect lines were oriented across depth gradients in NL and flown at an altitude of 183m, at a speed of 204 km/h. The GoSL and SS portion of the survey had transects arranged in parallel, flown at an altitude of 193m and a speed of 185 km/h (Figure 2.1 left panel). In the St. Lawrence estuary, lines were flown perpendicular to the main axis of the estuary. In all other areas within the GoSL and SS portion, lines were flown perpendicular to depth gradients.

The 2016 NAISS survey (Figure 2.1 right panel) was flown between August 1 to September 27, 2016 (Table 2.2), at an altitude of 183 metres ASL using a deHavilland Twin Otter 300 and two Cessna 337 Skymasters (Lawson and Gosselin 2016). The 2016 survey expanded on TNASS (2007) by extending the coverage of transect lines to at least 20 miles (~32 km) beyond shelf breaks and crossed isobaths (Figure 2.1 right panel) (Lawson and Gosselin

2016). Lines were again flown in a zig zag pattern in NL and in parallel in the other regions (BoF, GoSL, NL). Extending coverage beyond shelf breaks increases the representativeness of the sampling and reduces or eliminates edge effects (Buckland et al. 2015). It ensured that shelf- and non-shelf habitats had equivalent inclusion probabilities and that they weren't over-represented in the study design. The 2016 survey also used dual platform observers, instead of single-platform like in 2007, meaning that two observers searched independently from the same platform (Lawson and Gosselin, 2016).

2.2.2. ANALYSES

2.2.2.1. Design-based Estimation

Design-based estimation, otherwise known as “strip transect sampling” for line transects, is the most straight-forward approach for estimating animal abundance in an area (Thomas et al. 2010). It rests on the simple assumption that all animals on the sampled transects are detected (Buckland et al. 2015). A purely design-based framework assumes that the number of animals in the strip transect multiplied by the proportion of the sampled area to the total area is equal to the abundance of the species in the total area, N . In other words, to estimate abundance:

$$N = DA \quad (1)$$

with true density D and area size A , observations are required of the total number of animals detected across all transects, n and the total size of the plots a . For strip transect sampling with K lines, the total size of the plot, \bar{a} , is:

$$\bar{a} = 2wL \quad (2)$$

where

$$L = \sum_{k=1}^K l_k \quad (3)$$

is the total length of K lines and w is the truncation distance (Buckland et al. 2015). Then, the total abundance would be:

$$\hat{N} = \frac{nA}{2wL} \quad (4)$$

Design-based estimators are vulnerable to under-estimating the true abundance of animals in the study region because of their underlying assumptions about detectability, namely

that all animals in the sampled plots are detected. This assumption may not be appropriate for these data, for two reasons. First, because one cannot guarantee that all individuals are available for detection, a.k.a. the *availability bias*, because they could not be observed. In this case, this would occur because the basking sharks may be under the surface, and unlike whales, they do not need to surface to breathe. Availability bias is accounted for via a multiplier. Secondly, one cannot guarantee that all individuals present are detected, a.k.a. *perception bias*, as there are challenges in surveying animals in a marine habitat from a ship, or in this case, an airplane. This can be due to factors such as water conditions and light, among others. To deal with perception bias, the simple design-based estimator of abundance was extended in the next section by introducing a model-based estimator that modeled detection as a function of the observation distance.

2.2.2.2. Hybrid Design-based and Model-based Estimation

Conventional distance sampling (CDS) estimates density as a function of the location of the observations relative to the observer (Buckland et al. 2001). CDS combines design-based and model-based estimators. A purely design-based framework would be equivalent to using a uniform detection function, where there is no change in observability with increased distance from the observer. This relies in the assumption that all animals on the line are detected (Thomas et al. 2010). CDS relaxes this assumption by introducing a model of detection probability with respect to distance, known as the *detection function*, $g(y)$. The key assumptions in this method are as follows: (i) objects on the line are detected with certainty, (ii) objects do not move, and (iii) measurements are exact. Additionally, DISTANCE assumes that detections are independent events and that animal locations are independent of the position of the lines, which requires a sufficient number of equally spaced lines and randomized locations.

Estimation of abundance in CDS follows Miller et al. (2019) and is formulated in terms of the Horvitz-Thompson (HT) estimator. The classic HT estimator is as follows:

$$\hat{\tau} = \sum_{i=1}^n \frac{x_i}{P_i} \quad (5)$$

with x_i as the value of the response of interest for the i th unit, $\hat{\tau}$ as the estimate of the sum of all the x_i in the population, and P_i , the probability that the i th unit appears in the sample, i.e., the

inclusion probability. The estimator by Horvitz and Thompson (1952) was developed for cases in which the inclusion is known. Distance sampling extends the HT estimator to estimate the unknown true inclusion probabilities (Borchers and Burnham 2004).

This allows for the hybrid approach of combining design-based (extrapolation from the transects) and model-based (within the transects) estimators, including modelling the probability of detection. Total abundance in the entire study area is scaled up from abundance in the sampled area:

$$\widehat{N} = \frac{A}{\bar{a}} \widehat{N}_c \quad (6)$$

where A is the area of the study region and \bar{a} is the sampled area. For line transects, the sampled area is given in Eq. 2, as twice the truncation distance, w , multiplied by the total length of the transects surveyed, L (Buckland et al. 2015). The left truncation distance was determined in relation to the furthest sightings in the database, after excluding clear outliers such as the sighting >3400m away from the observer in 2007 (Figure 2.2).

The equation for the abundance in the sampled area, \widehat{N}_c , is as follows:

$$\widehat{N}_c = \sum_{i=1}^n \frac{1}{\widehat{p}_i} \quad (7)$$

with \widehat{p}_i the estimated inclusion probability for animal i and n is the number of observations. \widehat{p}_i has two components: (i) the probability animal i falls within the sampled plots, p_i and (ii) an estimate of its probability of detection, $g(y)$. The probability animal i falls within the sample plots is simply

$$p_i = \frac{a}{A} \quad (8)$$

where a is the area sampled and A is the area of the study region (Buckland et al. 2015).

The rate at which detectability changes with respect to distance y_i from the observer was modelled by the detection function, $g(y)$. CDS incorporates the assumption that detection at zero distance is certain ($g(0) = 1$) and that $g(y)$ stays at or close to one for animals at small distances

from the transect line, called a *shoulder* (Buckland et al. 2015). This shape for the detection function can be modelled as a half-normal model, given by:

$$g(y_i, z_i) = \exp\left(\frac{-y_i^2}{2\sigma^2(z_i)}\right), 0 \leq y_i \leq w. \quad (9)$$

or a hazard-rate model given by:

$$g(y_i, z_i) = 1 - \exp\left[\left(-\frac{y_i}{\sigma(z_i)}\right)^{-b}\right], 0 \leq y_i \leq w. \quad (10)$$

with the scale parameter, σ , the shape parameter in the hazard-rate model, b , and covariates, z_i . The scale parameter does not change the shape of the detection function but is allowed to vary with covariates, affecting how quickly the detection probability changes with distance from the line. The shape parameter in the hazard-rate model gives it more flexibility than the other models, and a more defined shoulder region.

There are many examples of why the probability of detection may not depend exclusively on distance from the observer. The probability of observing an animal may also depend on factors like habitat type, weather, observer platforms and/or conditions, animal behaviour, or cluster size (discussed in Marques et al. 2007). The multiple-covariate distance sampling (MCDS) extension of CDS allow the detection function to be modelled as a function of covariates (z_i). The design-based portion of the estimator remains the same, while the model-based portion allows the scale parameter to change with covariates, as in Equations 9 and 10 above. The scale parameter with covariates, $\sigma(z_i)$, is modelled as:

$$\sigma(z_i) = \exp\left(\alpha + \sum_{q=1}^Q \beta_q Z_{iq}\right) \quad (11)$$

where $z_i = (z_{i1}, z_{i2}, \dots, z_{iQ})$ are the covariate values recorded for the i^{th} detected animal and $\alpha, \beta_1, \dots, \beta_Q$ are the coefficients to be estimated. Cluster size can easily be added into MCDS as a covariate on the detection function, and the only major difference is the Horvitz-Thompson-like estimator adds one term:

$$\widehat{N}_C = \sum_{i=1}^n \frac{s_i}{\hat{p}_i} \quad (12)$$

where s_i is the size of the i^{th} detected cluster. MCDS uses a conditional likelihood; the likelihood of distances y from the line or point, conditional on the number n of animals detected. With covariates, z , this makes the full likelihood:

$$\mathcal{L}_{n,z,y} = \mathcal{L}_n * \mathcal{L}_z * \mathcal{L}_{y|z} \quad (13)$$

There is a second extension to CDS called mark-recapture distance sampling (MRDS), which also allows the detection function to vary with covariates (as above), but also relaxes the assumption that detection at the line is certain (e.g., $g(0) \neq 1$). This extension uses observations from dual-platform observers as a mark-recapture experiment that is used to estimate $g(0)$ (Marques et al. 2007). The first observer detects an animal, and then the second observer either *recaptures* (i.e., detects) the animal or not. Although the 2016 survey used a dual-platform observer set-up, there were too few recaptures of basking sharks to implement MRDS.

2.2.2.3. Fully Model-based Approach

When the conventional distance sampling hybrid design-based (Horvitz-Thompson estimator) and model-based (detection function) approach and its extensions were used, it was limited to modelling only the detection function, and then abundance was extrapolated from the plots to the entire survey region. If a fully-model based approach were incorporated, in which density can be modelled as a function of covariates, in addition to detection, it would allow the assumption that animal density can be directly extrapolated from the number of detections in the plots to be relaxed. The assumption that animal density in the study area can be extrapolated from the number of detections in the sampled area may not be appropriate if there is evidence of heterogenous habitat use within a region of the study area, which was found for basking sharks by Siders et al. (2013), or if there is evidence of aggregation behaviour as found by Crowe et al. (2018).

Royle et al. (2004) developed a multinomial-Poisson mixture model (hereafter “MPMM”) for distance sampling. The MPMM model allows both density and detection to be

modelled independently and as a function of covariates. This relies on a new assumption: that the number of animals available to detect are from a distribution, namely a Poisson distribution. A Poisson distribution is a discrete distribution used to develop a count model, to represent the number of events in a given time interval or unit space. It arises when the mean of the data is equal to the variance ($\mu = \sigma$). When this condition, is violated ($\mu < \sigma$) and variance increases faster than the mean, this is called *overdispersion*. While overdispersion is possible in this data, the replicate data is not available to evaluate it specifically. If there is good overall consistency from the multiple analysis approaches, it suggests that model estimates are not highly sensitive to distributional assumptions. Royle (2004) suggests that a Poisson distribution is a natural choice for abundance modelling because it assumes that animals are distributed randomly in space (described by a homogeneous Poisson point process), and departures from randomness can be explained explicitly by using covariates.

The Royle et al. (2004) MPMM is as follows. Let R be the number of sites (transects) visited J times and define Y_i as the number of individuals observed at site i . Then, the general form of this model is

$$N_i \sim \text{Poisson}(\lambda_i) \text{ for } i = 1, 2, \dots, R \quad (14)$$

$$Y_i | N_i \sim \text{Multinomial}(N_i, \pi) \quad (15)$$

where λ_i is the expected value of N_i , the abundance at site i and π is the vector of cell probabilities corresponding to the vector of counts Y_i .

Distance measurements are binned into k distance intervals (unlike CDS) which allowed them to be modelled as multinomial outcomes with cell probabilities $\pi_k(\theta)$. The distance classes have end points $(c_1, c_2), (c_2, c_3), \dots, (c_k, c_{k+1})$ with c_{k+1} is the maximum distance at which animals were counted, equivalent to w , the truncation distance from CDS. The cell probabilities were computed as the product of the probability of detection, $g(y)$, and the probability of occurrence in each distance interval, π_k . In general, π is determined by the specific sampling method (i.e., point or line transect), and $g(x)$ is either the half-normal or hazard-rate function of equations 4 and 5, above. λ_i is typically assumed to be linearly related to available covariates according to:

$$\log(\lambda_i) = \alpha_0 + \alpha_i z_i \quad (16)$$

where z_i is the value of the covariate measured at site i and α_0 is the intercept of the abundance model. The integrated product poisson likelihood is then

$$L(\alpha, \theta | y_i) = \sum_{k=1}^K \text{Poisson}[y_{ik}; \lambda_i(\alpha)\pi_k(\theta)] \quad (17)$$

and assuming that the data are independent across all sites, the joint likelihood for all data is then

$$L(\alpha, \theta | y_1, \dots, y_R) = \sum_{i=1}^R L(\alpha, \theta | y_i) \quad (18)$$

2.2.2.4. Estimation Options

The hybrid MCDS approach uses maximum likelihood to estimate the parameters. There are two estimation options for the fully model-based approach of the MPMM: maximum likelihood (MLE) and Bayesian methods. In addition, MCDS makes some simplifying assumptions to use a conditional likelihood (Eq 13) (Buckland et al. 2015), whereas the MPMM uses the full likelihood (Eq 17).

Both MLE and Bayesian methods use likelihoods to estimate the parameters of the model. A likelihood function represents the joint probability of the observed data as a function of the parameters. MLE is a method of estimating the parameters of a statistical model with given observations, by finding parameter values that maximize the likelihood of making the observations, given the parameters. Bayesian methods also use a likelihood, given in equation 16, to estimate the parameters of the model, but utilise a *prior* distribution in conjunction with it, to give the *posterior* distribution of each of the parameters (see McElreath 2015). The prior determines how strongly the likelihood is weighed in parameter estimation. While MLE methods gives a point estimate for each parameter, using Bayesian methods allows one to obtain a distribution for each of the parameter estimates.

There is an implementation of the MPMM model in a Bayesian context using a Hamiltonian Monte Carlo (HMC) algorithm, a Markov chain Monte Carlo method (MCMC) (Kellner 2021). The package was designed to allow for greater complexity in analyses by allowing for random effects and the implementation of non-traditional (i.e., other than half-

normal, uniform or hazard-rate) detection function shapes. Currently, only non-informative (uniform) priors are implemented in the estimation and the start values were the same as MLE. Therefore, the resulting parameter estimates are expected to be similar to those obtained from MLE. The use of this package was explored because it provided additional options for model validation that were not available in either MCDS or the MLE implementation of the MPMM, particularly using the Watanabe-Akaike information criterion (WAIC) to assess model fit.

2.2.2.5. Model selection and availability bias

All analysis was carried out in R 4.0.3 (R Core Team 2020). The main packages used were: (i) *distance* (Miller et al. 2019) for implementing CDS and MCDS, (ii) *unmarked* (Fiske and Chandler 2011) and (iii) *ubms* (Kellner 2021) for implementing the MPMM. *Ubms* extends *unmarked* with Bayesian models of abundance and occurrence via the *rstan* package, the R interface to the 'Stan' C++ library.

The best models from MCDS for each year were selected by Akaike Information Criterion (AIC) scores. The same model form (detection function and covariates) was then used for the MLE and Bayesian implementation of the MPMM model. Direct comparisons between the Maximum Likelihood and Bayesian implementations of similarly structured models cannot be made because they rely on different assumptions and different measures for validation (Burnham and Anderson 2002). For example, maximum likelihood methods typically base model selection on AIC scores (Burnham and Anderson 2002, Johnson and Omland 2004) whereas Bayesian methods use Watanabe Akaike information criterion (WAIC) for model selection, as well as \hat{R} , and effective sample size (ESS), as MCMC diagnostics (Roy 2020).

To account for the proportion of time spent at the surface (the *availability bias*), the estimates of abundance for each of the four regions in 2007 were divided by percentages from two different sources: (1) 36% from Sims et al. (2003a) and (2) 19% from Westgate et al. (2014).

2.3. RESULTS

2.3.1. PRELIMINARY EVALUATION

The collected data spans three surveys: TNASS and SNESSA in 2007 and NAISS in 2016 (Figure 2.1). In 2007, a total of 55,725 km of on-effort transects were flown between July 17 and August 24, 2007 and there was a total of 53 sightings of basking sharks (Table 2.1).

There were 14 basking shark sightings in 8,921 km of tracklines flown in the BoF in 2007 by SNESSA (Table 2.1). There were 5 sightings of basking sharks in NL from 23,261 km of on-effort transect lines (Table 2.1). The SS and GoSL portion completed a total of 23,443 km of transect line, including 9,111 km over the Scotian Shelf in 2007, with 15 sightings in the GoSL and 19 in the SS region (Table 2.1). In 2016, a total of 50,289 km of on effort transects were flown between August 1 to Sept 27, 2016 and there was a total of 206 sightings, for a total of 311 individual sharks (group sizes ranged from 1 to 12 individuals) (Table 2.2). There were 5 sightings in 1,059 km of tracklines in the BoF, 21 sightings in 14,820 km of tracklines flown in the GoSL and 14 sightings in 21,037 km of transects flown in NL (Table 2.2). In each of these regions (BoF, GoSL, and NL) all sharks were sighted as individuals. There were 166 sightings of basking sharks in the SS region for a total of 264 individual sharks in 13,373 km of on-effort transect lines (Table 2.2).

To help evaluate how detection probability should be characterized in the distance models, the distribution of sightings with respect to distance from the observer was plotted, both with data combined (Figures 2.2 and 2.3) and then separated by geographic region (Figures 2.4 and 2.5). Combined data from 2007 conformed to the detection pattern that is expected from line transect data, with a high number of detections at small distances (<200m) that falls off quickly with increasing distance (Figure 2.2, right panel). Conversely, in 2016 there is a noticeable peak in detections at a non-zero distance (~ 200-400m; Figure 2.3) with comparatively few detections at zero distance. In aerial surveys, this can occur when observers are unable to see directly under the plane (e.g., in Borchers et al. 2006) and leads to data that violates the first assumption of distance sampling, that detection on the line should be certain, i.e., $g(0) = 1$.

When the detection data was plotted relative to the four geographic regions (SS, GoSL, BoF and NL), there was comparatively little information from NL for both years and from the BoF in 2016 (Figures 2.4 and 2.5). Ideally, variability among sampling platforms and regions would be accounted for by estimating multiple separate detection functions (i.e., full geographic stratification) within a distance model (Thomas et al. 2010). However, there were not enough observations, especially in NL in 2007 (Figure 2.4) and BoF in 2016 (Figure 2.5) to support this, so detections from all regions were combined when estimating the detection function.

A thing to consider in the initial data exploration was the bin widths used, as a possible way to make the distribution of detection distance conform more closely to model assumptions. The MPMM relies on a multinomial distribution, which must meet the assumption of a finite number of possible values for x , whereas MCDS allows for either binned (i.e., discrete) or continuous values. Therefore, for the MPMM, the distances were manually binned into discrete intervals. Different bin widths can affect parameter estimates (Buckland et al. 2015) and as such a variety of bin widths were tested in the exploratory analysis, settling on bin widths that allows similar amounts of data in each bin. These bin widths were 50m for both years, similar to the output of histograms created by MCDS (Figure 2.2 and Figure 2.3 for 2007 and 2016, respectively).

Additionally, recall that the probability of detecting an animal may depend on factors other than the distance from the observer, factors such as habitat type, weather, observer platforms, animal behaviour or cluster size. They could be implemented in one of two ways: (i) in MCDS, covariates were added to vary the scale parameter of the detection function (Eq 11) or (ii) in MPMM, both density and detection could be modelled as a function of the covariates (Eq 16). Geographical regions, group sizes and Beaufort Sea-state were readily available from the survey data. As such, these factors were investigated as possible covariates for the model.

By using geographic region as a covariate on detection regionally specific estimates could be obtained, which allows for differences in abundance between habitat types/regions. It also allows information from one region to inform the detection function of another. For example, this is useful in the case of NL in 2007 (Figure 2.4), where the number of detections ($n=5$) is too low (Thomas et al. 2010) to give any useful information on its own. Additionally, as the original survey design was stratified by region and some regions were sampled differently than others, by putting 'like' with 'like' should reduce overall variability in estimates (Buckland et al. 2015). Differences among the planes used for sampling was not found to be a significant predictor in addition to the stratification. Stratification was tested as a covariate for both 2016 and 2007.

There were no observations of basking sharks in 2007 with a group size larger than one (Figure 2.6 left panel). In 2016, some basking sharks were detected in groups larger than one

(Figure 2.7 left panel). Thus, cluster size was assessed as a covariate for 2016 only. Recall that one of the key assumptions of distance sampling was that detections are independent events. Clustering violates this independence assumption, and as such, cluster size should be considered for incorporation into the distance sampling model. If clustering is not considered, and each detection were assumed to only represent one animal, then the model would likely underestimate the true density in the study area.

Beaufort sea-state was the last covariate that was investigated for incorporation into the model. There is a weakly decreasing trend of detectability with respect to increasing Beaufort sea-state in 2007 (Figure 2.6 right panel). This makes sense, as increasing the sea-state would be expected to decrease visibility because rougher conditions would make it harder to see basking sharks just under the surface from above. However, there is an opposing relationship with detectability in 2016, where increasing sea-state appears to increase detectability (Figure 2.7 right panel). This is contrary to expectation and may be due to some other process that was not accounted for in the analysis. Due to this confounding relationship between Beaufort sea-state and observation distances, sea-state was excluded as covariate for the models.

2.3.2. MODEL SELECTION

Recall that several different implementations of distance models were evaluated including: (i) the hybrid design-based and model-based Multiple-Covariate Distance Sampling (MCDS) approach from Buckland et al. (2015) implemented with Maximum likelihood estimation (MLE) in *distance* in R (Miller et al. (2019), as well as (ii) the fully-model based approach of the Multinomial-Poisson Mixture Model (MPMM) by Royle et al. (2004), implemented with either MLE via *unmarked* in R (Fiske and Chandler 2011) or a Bayesian Hamiltonian Monte Carlo (HMC) method via *ubms* in R (Kellner 2021).

The preferred models for each year from the MCDS were selected using Akaike Information Criterion (AIC) scores. The preferred model for TNASS 2007 survey data from the MCDS analysis, was the half-normal model (AIC 647.401, AICwt; 0.69, Table 2.3). AICwt refers to the Akaike weights, which can be interpreted as conditional probabilities for each model (Burnham and Anderson 2002, Wagenmakers and Farrell 2004). The predicted detection

function matches the observed data on detection distances, with no systematic deviations in model residuals (Figure 2.8).

The preferred model for the NAISS 2016 survey data from the MCDS analysis was the hazard-rate model with strata and group size as covariates (AIC 2256.597, AICwt: 0.92, Table 2.4). However, data exploration showed that the covariate ‘group size’ is highly unbalanced (Figure 7 left panel) as there were very few sightings with a group size larger than one. This model was excluded as a result of these data characteristics. The remaining model was the hazard-rate model with strata alone as a covariate (AIC 2261.368, recalculated AICwt 0.99; Table 2.4). While the wider shoulder region of the hazard-rate model can partially account for detections being low at zero distance (Buckland et al. 2015), model residuals show systematic deviations between the predicted detection function and observed detection distances. As expected from the preliminary evaluation of the data, the detection function overestimates detection probabilities at small distances from the transect line (Figure 2.9). The strength of the evidence was greater that the hazard-rate function was a better description of the 2016 than the half-normal (AICwt: 0.99 and AICwt: 0.01 for the hazard-rate and the half-normal detection functions, respectively). Therefore, the hazard-rate detection function was used for the 2016 data, whereas the 2007 data used a half-normal detection function because the 2007 data did not require the wide shoulder region that the 2016 data did.

Generally, the same combination of covariates on detection that was predicted from MCDS for the MPMM implementations were chosen. For the 2007 data, the preferred model for MCDS was a half-normal detection function (Table 2.3). Also, incorporating the covariate strata to the detection portion of the MPMM model was tested (AIC 599.26), and it gave a better fit than the half-normal alone (AIC 601.26) in both the MLE and Bayesian implementations of MPMM model. For the 2016 data, the preferred model from MCDS was a hazard-rate detection function with strata as a covariate. After testing other combinations of covariates and detection functions for the MPMM model implementations, the preferred model for the 2016 data remained the hazard-rate detection function with strata as a covariate.

Looking at the consistency in estimated abundances between approaches allowed for inference of sensitivity to model assumptions, in place of a simulation study. The MCDS and

MPMM models rely on different assumptions, and MLE and Bayesian are two different ways of estimating parameters. If the estimates are consistent among approaches, then it suggests that the model assumptions and parameter estimation options are not overly influential on the results. The model selection phase of the analysis suggests that for the 2007 data, the half-normal model is preferred for MCDS while the half-normal model with strata as a covariate on detectability is preferred for the MPMM. For the 2016 data, the preferred model across all three methods incorporates the hazard-rate detection function with strata as a covariate on detectability. Estimates from all three methods were retained and the range of abundance estimates are discussed in the following section.

2.3.3. ESTIMATES OF ABUNDANCE

In 2007, predicted abundance in Atlantic Canadian waters ranged from 1,296 (496-3,825) to 1,363 (744-2,563) from the three retained models (Table 2.7). Estimated densities (+SD; animals/km²) and abundances of basking sharks per strata are shown in Figure 10 and demonstrate a pattern of abundance with respect to region. In descending order, the highest abundances were predicted on the Scotian Shelf, then the Gulf of St. Lawrence, Newfoundland and Labrador, and lastly the Bay of Fundy (Figure 2.10). In the Bay of Fundy, estimated abundance ranged from 55 (26-117) to 57 (33-101) (Table 2.7). Predicted abundance in the Scotian Shelf region ranged from 579 (318-631) to 606 (368-997) (Table 2.7). Predicted abundances in the Gulf of St. Lawrence ranged from 384 (194-646) to 437 (103-2,029) (Table 2.7). In Newfoundland and Labrador, predicted abundance ranged from 226 (50-1,048) to 312 (127-769) (Table 2.7).

Recall that to account for the proportion of time spent at the surface, aka the “availability bias”, the estimates of abundance for each of the four regions in 2007 were divided by percentages from two different sources: (1) 36% from Sims et al. (2003a) and (2) 19% from Westgate et al. (2014) (Table 2.7). Using the Sims et al. (2003a) availability bias of 36%, predicted total abundance in Atlantic Canadian waters in 2007 ranged from 3,600 (1,378-10,625) to 3,786 (2,066-7,118) (Table 2.7). Using 19% availability bias from Westgate et al. (2014) predicted total abundance in Atlantic Canadian waters in 2007 ranged from 6,822 (2,611-20,131) to 7,146 (3,914-13,487) (Table 2.7).

In 2016, predicted abundance in Atlantic Canadian waters ranged from 4,876 (3,903-6,250) to 5,260 (2,493-11,496) from the three retained models (Table 2.8). Estimated densities (+SD; animals/km²) and abundances of basking sharks per strata are shown in Figure 2.11 and demonstrate the same pattern of abundance by region as in 2007 (Figure 2.10). In the Bay of Fundy, estimated abundance ranged from 91 (34-245) to 108 (30-235) (Table 2.8). Predicted abundance in the Scotian Shelf region ranged from 3,932 (1,990-7,769) to 4,051 (3,363-4,815) (Table 2.7). Predicted abundances in the Gulf of St. Lawrence ranged from 488 (318-748) to 680 (217-2,250) (Table 2.8). In Newfoundland and Labrador, predicted abundance ranged from 332 (197-561) to 557 (253-1,232) (Table 2.8).

As in 2007, the estimates of abundance for each of the four regions in 2016 were divided by two estimates of availability bias: (1) 36% from Sims et al. (2003a) and (2) 19% from Westgate et al. (2014) (Table 2.8). Using the Sims et al. (2003a) availability bias of 36%, predicted total abundance in Atlantic Canadian waters in 2016 ranged from 13,544 (10,842-17,361) to 14,610 (6,925-31,934) (Table 2.8). Using 19% availability bias from Westgate et al. (2014) predicted total abundance in Atlantic Canadian waters in 2016 ranged from 25,662 (20,543-32,894) to 27,682 (13,121-60,506) (Table 2.8).

2.3.4. MODEL VALIDATION

The HMC implementation in STAN (2020) gave a variety of tools for model validation which can be used for all of the Bayesian models. These validation tools look at sensitivity to starting points, autocorrelation, patterns of residuals and posterior checks (Roy 2020).

The first is \hat{R} , the potential scale reduction factor on split chains. This is a diagnostic of the convergence between the independent chains (Roy 2020). MCMC's run multiple independent chains, and \hat{R} is a measure to determine if the obtained distribution of parameters is similar between chains, otherwise known as *convergence*. The idea is that if a set of chains has not mixed well, then the variance of all the chains mixed together should be higher than the variance of individual chains (Gelman and Rubin 1992). This allows the sensitivity to starting points to be determined (Roy 2020). If the starting points are highly sensitive, then the chains will not converge. Roy (2020) suggests that \hat{R} should be <1.01 when there is good convergence between the four chains. \hat{R} values are all one for all parameters in the 2007 and 2016 models (Table 2.9).

Additionally, the trace plots are shown for the HMC MPMM in 2007 and 2016 in Figures 2.12 and 2.13 respectively. From visual inspection, it appears that the chains are mixing well in both years, as there does not appear to be any chain that is visually distinct from any other.

The second is Effective Sample Size, N_{eff} . This measures the amount that autocorrelation in the samples increases uncertainty relative to an independent sample (Roy 2020). The HMC:MPMM models for both years used 4 chains of 4,000 (3,000 post-warmup) iterations for a total, N , of 16,000 samples. Roy (2020) suggests that N_{eff}/N should be >0.001 . In 2007, N_{eff} is >7300 in all the parameters and in 2016 the lowest N_{eff} is >8200 (Table 2.9). Based on the target ratio of $N_{eff}/N > 0.001$ these values are acceptable. This suggests that there is not a concerning amount of autocorrelation in the samples.

Pearson residual plots follow the approach of Wright, Irvine and Higgs (2019) and calculate residuals separately for the count (i.e., ‘density’ submodel) and detection processes (Kellner 2021). The residuals for the MPMM model for 2007 data are shown in Figure 2.14. The residuals for the model for the 2016 data are shown in Figure 2.15, and include the ‘shape’ submodel, unique to the hazard-rate detection function. The residuals show a strong pattern in both the count and detection processes (Figures 2.14 and 2.15). In both years, low densities are under-predicted (‘density submodel’ of Figures 2.14 and 2.15). In 2016, there also appears to be under-predicted values at higher densities ($\sim 4-6$, lower panel of Figure 2.15), giving evidence that the density submodel fit is less than ideal in the tail regions. The ‘scale’ and ‘shape submodels’ (lower panel of Figure 2.14 and top panel of Figure 2.15) describe the fit of the detection functions. The ‘shape submodel’ (top panel of Figure 2.15) shows the bulk of residuals at low values, exhibiting a ‘funnel’ shape, similar to the density submodel, as well as an under prediction of values at an expected value of ~ 0.3 . The ‘scale submodel’ (lower panel of Figure 14) shows a similar pattern of under-prediction at the smallest expected values, but with an additional line that remains at zero because of the assumption that $g(0)=1$, as well as a under prediction of values at the expected value of ~ 3 . With all these residual plots demonstrating a pattern, this is evidence of a less than ideal fit.

The posterior predictive check is calculated as a N-mixture chi-squared test, based on Pearson’s chi-squared test (Pearson 1900, Kellner 2021). The statistic is calculated for each

posterior draw, for the actual data and for a simulated dataset, similar to Mackenzie and Bailey (2004). If the model fits well, the proportion of draws for which the simulated statistic is larger than the actual statistic, P , should be near 0.5. This posterior predictive check is shown in Figures 18 and 19 for the data from 2007 and 2016, respectively. The proportions indicate that the model for the 2007 data is a good fit, as it is very near 0.5 (Figure 2.16). The distribution of the points for 2007 is relatively even below and above the slope of 1, which indicates where $P = 0.5$, and as such suggest a good fit (Figure 2.17). There is no evidence for a lack of fit in the model for the 2016 data, and a larger proportion of the points in the test for 2016's model falls below the slope of 1 (Figure 2.19). However, P is closer to 0.5 for 2007 than it is for 2016, suggesting that the former does slightly better (Figures 2.16 and 2.17 for 2007 and 2016, respectively).

Full posterior distributions of each of the parameters of the abundance submodel are given for the models for the 2007 and 2016 data in Figures 2.18 and 2.19, respectively. They are all unimodal and normally distributed, which is indicative of a good fit (Figures 2.18 and 2.19).

2.4. DISCUSSION

A significant increase in abundance between 2007 and 2016 was predicted from all estimation methods, which give similar values with overlapping confidence/credible intervals for each year (Tables 2.7 and 2.8 for 2007 and 2016, respectively). There was a significant difference between the 2007 and 2016 estimates, in that their 95% confidence intervals do not overlap (Tables 2.7 and 2.8 for 2007 and 2016, respectively). This corresponds to an increase in abundance of approximately 270% in 9 years. Across years and the three methods used, SS consistently had the highest density of individuals per square kilometer, followed by BoF, GoSL and lastly NL.

There is very little existing information on the absolute abundance of basking sharks in the North Atlantic to compare these estimates to. Owen (1984) estimated that there may be as many as 2,800 sharks in the Gulf of Maine (GoM) and 3,700 in the waters of southern New England. Looking at those numbers, the estimates from this thesis for the total abundance do not appear to be unreasonable, although uncertainty is relatively high.

The COSEWIC designation of 'Special Concern' relied heavily on an abundance estimate derived by Campana et al. (2008) from the 2007 survey that was also analyzed in this

thesis. The Campana et al. (2008) study applied CDS without covariates and estimated that Atlantic Canadian waters contained 10,125 basking sharks, assuming a 36% availability bias. No confidence interval was given for this estimate, and it was considered highly uncertain (Campana et al. 2008, Rigby et al. 2019). Their regional estimates for the Scotian Shelf and Gulf of the St. Lawrence (N=5,342; 95% CI: 3,636-7,922), and Newfoundland (N=558; 95% CI: 116-2,694) (Campana et al. 2008) agree with the estimated range from this thesis for SS and GoSL (2,716 (95% CI: 1,482-4,355) to 2,821 (95% CI: 1,168-7,388)) as well as for NL (627 (95% CI: 116-2,694) to 867 (95% CI: 352-2,136)) when using the same value for availability bias. This agreement with Campana et al. (2008) was expected, as the same TNASS data was used. However, for the Bay of Fundy (BoF), Campana et al. (2008) estimated 4,200 basking sharks in 2007. For comparison, the estimates from this chapter for BoF in 2007 ranged from 152 (95% CI: 71-325) to 160 (95% CI: 91-281) when using the same availability bias as Campana et al. (2008). The estimates ranged from 289 (135-617) to 303 (172-533) in 2007 when using the 19% availability bias from Westgate et al. (2014). Westgate et al. (2014) estimated that there were 542 (95% CI: 198-1,482) and 632 sharks (95% CI: 377-1,058) in BoF in 2009 and 2011, respectively. A drop in absolute abundance from 4200 to 542 between 2007 and 2009 is improbable without serious changes to habitat availability or mortality, which have not been documented.

The estimates from this analysis for the BoF region differ greatly from Campana et al. 2008. Campana et al. (2008) did not use CDS methods for BoF, instead estimating basking shark abundance from sightings of North Atlantic Right Whales *Eubalaena glacialis*, from aerial- and boat-based survey sightings in the North Atlantic Right Whale Consortium (NARWC) database. A correlation factor between the relative visibility of right whales and basking sharks was created, and from that, they estimated that there were 4200 (CI not reported) basking sharks in the BoF in 2007 (Campana et al. 2008). This was done because sightings-per-unit-effort-data (SPUE) was very sparse and the proportion of data from aerial surveys was very low, leading to low accuracy in estimates from this region (Campana et al. 2008). There were many assumptions made in the estimate for BoF by Campana et al. (2008), as repeat sightings could not be taken into account, and factors affecting the relative visibility of basking sharks compared to right whales were, in their words, “arbitrarily” assumed without any existing literature. The

agreement in estimates of abundance for the Bay of Fundy from this analysis and the work of Westgate et al. (2014) suggests that the ratio method used by Campana et al. (2008) was inappropriate and could have significantly overestimated abundance.

Any abundance estimate for basking shark from aerial survey data critically depends on the chosen value for availability bias. Recall that the availability bias refers to the proportion of the time that the target species spends at the surface, and therefore is the proportion of time that it is *available* for detection. This was arguably the most influential parameter in these analyses, yet there is not a good consensus on what a reasonable value is for basking sharks. Time spent at the surface should be tightly correlated with zooplankton abundance, basking shark's preferred prey species (Sims et al. 2003a, Sims 2008). This suggests that vertical behaviour could vary considerably depending on the local conditions on any given day. Westgate et al. (2014) used an availability bias of 19%, estimated from 1252 h of time-depth recorder data from 13 free swimming sharks. Sims et al. (2003a) estimated availability to be 36% from 4 basking sharks in the Northeastern Atlantic. In addition, Siders et al. (2013) found from 833 hours of dive profiles that basking sharks spend on average between $15 \pm 10\%$ of their time between 0-2m from the surface in BoF. However, Curtis et al. (2014) found basking sharks spent 43% of their time at 0-10 m in the southern Gulf of Maine (N=7), which is comparable to the Sims et al. (2003a). The findings of absolute abundance are presented here with both 19% and 36% availability biases as equally plausible due to this lack of consensus, though future research would benefit greatly from assessing this in parallel to surveys for abundance. Vertical behaviour could vary considerably depending on the local conditions on any given day, and/or on a inter-regional scale. With enough tag data it could be possible to correlate daily environmental conditions to time-at-surface and estimate availability bias on a given survey day.

Operational Considerations

It is difficult to determine how representative the absolute abundance estimates are of true abundance in either 2007 or 2016. One major factor to consider is temporal differences in sampling. The 2007 surveys were carried out from July 17 to August 24, 2007; whereas the 2016 NAISS survey was carried out from August 1 to September 27, 2016 (Tables 2.1 and 2.2 for 2007 and 2016, respectively). In general, across all regions, 2007 sightings occur earlier in the

season than 2016. As 2016 has about 4x the number of sightings with approximately the same amount of effort, this could be a major factor affecting abundance estimations. There was good temporal overlap between the two years for the GoSL and NL regions, but the SS and BoF regions differ between years. The SS region was sampled in 2007 from August 10th to August 23rd by TNASS and in 2016 by August 24th to September 13th by NAISS (Tables 2.1 and 2.2 for 2007 and 2016, respectively). The BoF region was sampled in 2007 from July 31st to August 23rd by NOAA SNESSA, and in 2016 from September 15th to 16th by NAISS (Tables 2.1 and 2.2 for 2007 and 2016, respectively).

The low temporal coverage of BoF in 2016 is problematic. Most of the research on temporal patterns of basking shark abundance in Atlantic Canada comes from the Bay of Fundy. Siders et al. (2013) found that peak abundance in BoF is in July to September and concentrated in waters >100m deep, and then shifts into the Gulf of Maine (GoM) and waters >200m depth in October from 10 years (2002-2011) of presence-only sightings data (n=844). Siders et al. (2013) found that sightings seasonally varied, with ~10% sighted in July, ~63% in August, ~25% in September, and ~2% in Oct. Owen (1984) also observed a shift from shallow to deep water habitat in the GoM in September, but the Siders et al. (2013) model predicted the shift in August in BoF. Further, Hoogenboom et al. (2015) found that shark sightings peaked in August and early September in the BoF, based on a long-term sightings database (1994-2012). Even though surveys in the BoF in September miss peak abundance, re-distribution to other regions could still allow those individuals to contribute to the total abundance estimate.

Looking at another long-term sightings dataset supports the idea that the TNASS and NAISS surveys may not have been carried out at the optimal time to see basking sharks. The Shark Sightings Network (Sarah Wong, pers. comm.) has collected a long-term dataset from 1997-2016. The majority of basking shark sightings occurred in June (~2400 over the 19y period) that then drops off in July (~1000) and further in August (~320) and September (~210). It was considered that this may be a result of differences in effort as this dataset includes opportunistic whale-watch encounters, which may coincide with tourism increases in June-Aug. Upon further inspection of this dataset, the number of sightings from opportunistic whale-watch encounters peaked in August, suggesting that the differences in effort due to tourism may not have a strong effect, when compared to the high number of sightings in June from all data types

(aerial and boat based surveys, as well as the opportunistic sightings) Additionally, because basking sharks have been demonstrated to exhibit a high level of regional fidelity (Hoogenboom et al. 2015, Doherty et al. 2019, Lieber et al. 2020), these sightings may not represent an accurate index of abundance as the same individuals could be seen over and over or there could be regular immigration/emigration from the survey area. However, this long-term dataset suggests that June and July are the best time to sighting basking sharks in Atlantic Canada. Despite that, basking sharks are non-target species in these surveys (TNASS, SNESSA, NAISS) which focus predominantly on whales, and the temporal coverage of the surveys reflects that.

Other limitations and future recommendations

There is a strong need for further research to determine the suitability and evaluate potential sources of bias from aerial surveys for basking sharks, particularly given that surveys are typically designed for marine mammals who spend a large proportion of their time at the surface. This analysis encountered issues with the data violating the assumption that detection on the line is certain (i.e., $g(0) < 1$) and the potential for small-scale habitat heterogeneity. This analysis also assumed that the population was geographically closed, an assumption which is unlikely to hold. Here, possible solutions to alleviate those issues are proposed.

Future study should spend time looking at the shape of the detection function and here, a new detection function proposed: the double-logistic function. The double-logistic function is a six-parameter model, which normally is used to model selectivity (catchability) at length and is well known in the fisheries biology literature (Lipovetsky 2010). Similarly to catchability models, it is assumed that detectability starts at some value, then increases to 1, before falling off again. This is called dome-shaped selectivity and is the product of two logistic functions: one increasing and one decreasing. Detectability makes sense to follow this pattern from an aerial survey, as at small distances, glare and field of view limit the observer's ability to see animals directly under the plane, and then as distances get larger animals are less likely to be spotted given human eyesight. This would create an inflection point in the data, where the probability of detection is 1 at some non-zero distance, thereby relaxing the assumption that $g(0) = 1$. Implementing this novel method into the analysis was outside of the scope of this paper, but it

provides a promising avenue to explore for line-transect survey data that does not have perfect detection at zero distances.

Additionally, there is the potential for heterogenous habitat use. This analysis assumed that habitat use is homogenous/uniform across the entire study area and this assumption is also used in Campana et al. (2008). Homogenous habitat use is a fixed trait of any model that extrapolates local density from transect lines to density of an entire study region. While the orientation of the tracklines is thought to partially alleviate this problem, and stratification of the study area allows for predicted density to vary by region, this does not consider within-region-habitat use or patchy distributions of species. There is recent evidence of heterogenous habitat use in the BoF by basking sharks, with suitable habitat largely restricted to the deeper waters of the bay (Siders et al. 2013), as well as evidence to support that basking sharks may have a patchy distribution to maximize encounter rates when foraging for zooplankton (Sims 1999, Sims 2008, Miller et al. 2015). This would lower abundance estimates from surveys as the sharks would not have been available for detection. Additionally, while predicted habitat use and temporal patterns in occurrence have been well-studied for basking sharks in the BoF, they have not for other regions in Atlantic Canada, which could lead to overestimation of abundance. To improve this estimate to account for heterogenous habitat use across the study area, a recommendation would be to incorporate a species distribution model (SDM) or a density-surface model (DSM) as they are referred to in the distance sampling literature (Miller et al. 2013). For example, these have been successfully used to improve absolute abundance estimates for black-backed jackals (*Lupulella mesomelas*, Schreber 1775) (Farr et al. 2021), pantropical spotted dolphins (*Stenella attenuate*, Gray 1846) (Miller et al. 2013), and fin whales (*Balaenoptera physalus*, Linnaeus 1758) (Sigourney et al. 2020).

Finally, this population was assumed to be geographically closed when assessed in Canadian Waters. However, the surveys examined here do not sample the entire seasonal range (see Section 1.4.2). Tagging studies from Massachusetts demonstrate basking sharks making extensive north-south migrations (Skomal et al. 2004, 2009, Skomal 2005, Braun et al. 2018). Campana et al. (2008) suggests that it is likely that the Atlantic US and Canadian populations of basking sharks are continuous. It is possible then, that the abundance increase predicted here may be an artifact of immigration/emigration across the US-Canada maritime border, rather than a

large increase in absolute population size. It is difficult within the scope of this research to differentiate true population increases from distribution shifts and immigration from neighbouring areas. This analysis therefore may be tracking attendance of the northwest Atlantic basking shark population to Canadian waters, not tracking the total abundance of the broader population. Future abundance estimates would benefit from coordination among scientists from both Canada and the US, and continued monitoring across the entire range of basking sharks in the western North Atlantic.

2.5. CONCLUSION

Estimating the abundance of any marine species always presents challenges, especially with wide-ranging pelagic species. Even with what is considered “good” data – such as systematic surveys, compared to opportunistic sightings from whale-watching operations or fisheries dependant CPUE – considerable uncertainty remains in the estimates. In the case of basking sharks, this analysis would benefit greatly from the addition of habitat modelling, as well as a method for relaxing the $g(0)=1$ distance sampling assumption. Crucially, more work needs to be done to understand how basking sharks spend their time at the surface (as represented in the availability bias), and if this changes with factors such as time-of-year, time-of-day, zooplankton abundance, or habitat type. While this work suggests that the status of basking sharks is improving in Atlantic Canadian waters, it remains difficult to determine absolute abundance with precision and it is difficult to differentiate true population increases from distribution shifts and immigration from neighboring areas.

2.6. TABLES

Table 2.1 Summarized survey effort for the 2007 Trans North Atlantic Sightings Surveys (TNASS) conducted by the DFO.

Strata	Survey Dates	On effort (km)	Area (km²)	Sightings
Bay of Fundy	07/31 - 08/23	8,921	21,145	14
Scotian Shelf	08/10 - 08/23	9,111	167,745	19
Gulf of St Lawrence	07/21 - 08/23	14,332	246,623	15
Newfoundland and Labrador	07/17 - 08/21	23,361	741,699	5
Total	07/17 - 08/24	55,725	1,177,212	53

Table 2.2 Summarized survey effort for the DFO North Atlantic International Sighting Survey (NAISS), conducted in 2016.

Strata	Survey Dates	On effort (km)	Area (km²)	Sightings
Bay of Fundy	09/15 - 09/16	1,059	21,145	5
Scotian Shelf	08/24 - 09/13	13,373	280,238	166
Gulf of St Lawrence	08/02 - 08/30	14,820	246,376	21
Newfoundland and Labrador	08/02 - 09/25	21,037	741,699	14
Total	08/01 - 09/27	50,289	1,289,376	206

Table 2.3 Model selection for MCDS for the TNASS 2007 survey data, based on AIC scores. The lowest AIC score is the preferred model. Δ AIC is the difference between the specified model and the preferred model and AICwt is the weighted AIC scores.

Model	AIC	Δ AIC	AICwt
Half normal	647.401	0	0.6883
Hazard rate	649.614	2.213	0.2276
Half normal w/ Covariate: Strata	652.828	5.427	0.0456
Hazard rate w/ Covariate: Strata	653.171	5.77	0.0384

Table 2.4 Model selection for MCDS for the NAISS 2016 survey data, based on AIC scores. The lowest AIC score is the preferred model. Δ AIC is the difference between the specified model and the preferred model and AICwt is the weighted AIC scores.

Model	AIC	Δ AIC	AICwt	AICwt excluding group size
Hazard rate w/ Covariates: Strata, Group Size	2256.597	0.000	0.9156	-
Hazard rate w/ Covariate: Strata	2261.368	4.771	0.0843	0.9984
Hazard rate	2274.229	17.632	0.0001	0.0016
Half normal	2282.675	26.078	0.0000	0.0000
Half normal w/ Covariate: Strata	2290.610	34.013	0.0000	0.0000

Table 2.5 Abundance estimates (+95% confidence interval for MLE or 95% Bayesian credible interval for HMC) by region for basking sharks in Atlantic Canadian waters for the TNASS 2007 survey, uncorrected for availability bias.

Strata	MLE: MCDS	MLE: MPMM	HMC: MPMM
Bay of Fundy	55 (26-117)	57 (33-101)	57 (30-94)
Scotian Shelf	579 (318-631)	606 (368-997)	594 (340-922)
Gulf of St Lawrence	437 (103-2,029)	388 (216-695)	384 (194-646)
Newfoundland and Labrador	226 (50-1,048)	312 (127-769)	309 (98-649)
Total	1,296 (496-3,825)	1,363 (744-2,563)	1,344 (661-2,311)

Table 2.6 Abundance estimates (+95% confidence interval for MLE and 95% Bayesian credible interval for HMC) by region for basking sharks in Atlantic Canadian waters for the NAISS 2016 survey, uncorrected for availability bias.

Strata	MLE: MCDS	MLE: MPMM	HMC: MPMM
Bay of Fundy	91 (34-245)	105 (40-281)	108 (30-235)
Scotian Shelf	3,932 (1,990-7,769)	3,950 (3,349-4,659)	4,051 (3,363-4,815)
Gulf of St Lawrence	680 (217-2,250)	488 (318-748)	500 (306-735)
Newfoundland and Labrador	557 (253-1,232)	332 (197-561)	340 (186-549)
Total	5,260 (2,493-11,496)	4,876 (3,903-6,250)	4,999 (3,885-6,334)

Table 2.7 Abundance estimates (+95% confidence interval for MLE or 95% Bayesian credible interval for HMC) by region for basking sharks in Atlantic waters from the various models for 2007, assuming availability of 36% from Sims et al. (2003) or 19% from Westgate et al. (2014).

Strata	Uncorrected	36% Availability	19% Availability
<i>MCDS: MLE</i>			
Bay of Fundy	55 (26-117)	152 (71-325)	289 (135-617)
Scotian Shelf	579 (318-631)	1,607 (882-1,753)	3,046 (1,671-3,322)
Gulf of St Lawrence	437 (103-2,029)	1,214 (286-5,635)	2,300 (543-10,677)
Newfoundland and Labrador	226 (50-1,048)	627 (138-2,911)	1,187 (262-5,515)
Total	1,296 (496-3,825)	3,600 (1,378-10,625)	6,822 (2,611-20,131)
<i>MPMM: MLE</i>			
Bay of Fundy	57 (33-101)	160 (91-281)	303 (172-533)
Scotian Shelf	606 (368-997)	1,683 (1,023-2,770)	3,190 (1,939-5,248)
Gulf of St Lawrence	388 (216-695)	1,077 (600-1,931)	2,040 (1,137-3,659)
Newfoundland and Labrador	312 (127-769)	867 (352-2,136)	1,642 (666-4,048)
Total	1,363 (744-2,563)	3,786 (2,066-7,118)	7,174 (3,914-13,487)
<i>MPMM: HMC</i>			
Bay of Fundy	57 (30-94)	158 (82-262)	299 (156-497)
Scotian Shelf	594 (340-922)	1,649 (944-2,561)	3,125 (1,788-4,852)
Gulf of St Lawrence	384 (194-646)	1,067 (538-1,794)	2,021 (1,019-3,400)
Newfoundland and Labrador	309 (98-649)	859 (273-1,803)	1,627 (518-3,415)
Total	1,344 (661-2,311)	3,732 (1,837-6,420)	7,072 (3,481-12,164)

Table 2.8 Abundance estimates (+95% confidence interval for MLE or 95% Bayesian credible interval for HMC) by region for basking sharks in Atlantic waters from the various models for 2016, assuming availability of 36% from Sims et al. (2003) or 19% from Westgate et al. (2014).

Strata	Uncorrected	36% Availability	19% Availability
<i>MCDS: MLE</i>			
Bay of Fundy	91 (34-245)	253 (94-681)	479 (178-1,291)
Scotian Shelf	3,932 (1,990-7,769)	10,921 (5,527-21,582)	20,693 (10,471-40,892)
Gulf of St Lawrence	680 (217-2,250)	1,888 (602-6,249)	3,578 (1,141-11,841)
Newfoundland and Labrador	557 (253-1,232)	1,547 (702-3,422)	2,932 (1,330-6,483)
Total	5,260 (2,493-11,496)	14,610 (6,925-31,934)	27,682 (13,121-60,506)
<i>MPMM: MLE</i>			
Bay of Fundy	105 (40-281)	292 (110-779)	554 (208-1,477)
Scotian Shelf	3,950 (3,349-4,659)	10,973 (9,303-12,943)	20,790 (17,626-24,523)
Gulf of St Lawrence	488 (318-748)	1,355 (883-2,079)	2,568 (1,674-3,939)
Newfoundland and Labrador	332 (197-561)	923 (547-1,560)	1,750 (1,036-2,955)
Total	4,876 (3,903-6,250)	13,544 (10,842-17,361)	25,662 (20,543-32,894)
<i>MPMM: HMC</i>			
Bay of Fundy	108 (30-235)	299 (84-653)	566 (159-1,237)
Scotian Shelf	4,051 (3,363-4,815)	11,253 (9,342-13,376)	21,322 (17,701-25,345)
Gulf of St Lawrence	500 (306-735)	1,388 (850-2,043)	2,630 (1,610-3,870)
Newfoundland and Labrador	340 (186-549)	945 (516-1,524)	1,791 (978-2,887)
Total	4,999 (3,885-6,334)	13,886 (10,792-17,595)	26,310 (20,448-33,338)

Table 2.9 MCMC diagnostics for HMC MPMM models.

Parameter	Estimate	SD	N_{eff}	\hat{R}
2007				
<i>Density (log-scale):</i>				
(Intercept)	-5.675	0.253	7307	1
strata=BoF	-0.288	0.353	8830	1
strata=GoSL	-0.836	0.362	9079	1
strata=NL	-2.217	0.52	8302	1
<i>Scale (log-scale):</i>				
	-1.43	0.132	8195	1
2016				
<i>Density(log-scale):</i>				
(Intercept)	-4.24	0.0922	8948	1
strata=BoF	-1.17	0.5308	10242	1
strata=GoSL	-1.98	0.2372	10052	1
strata=NL	-3.48	0.2874	10509	1
<i>Shape (log-scale):</i>				
	-1.1	0.0479	8257	1
<i>Scale (log-scale):</i>				
	1.81	0.174	9753	1

2.7. FIGURES

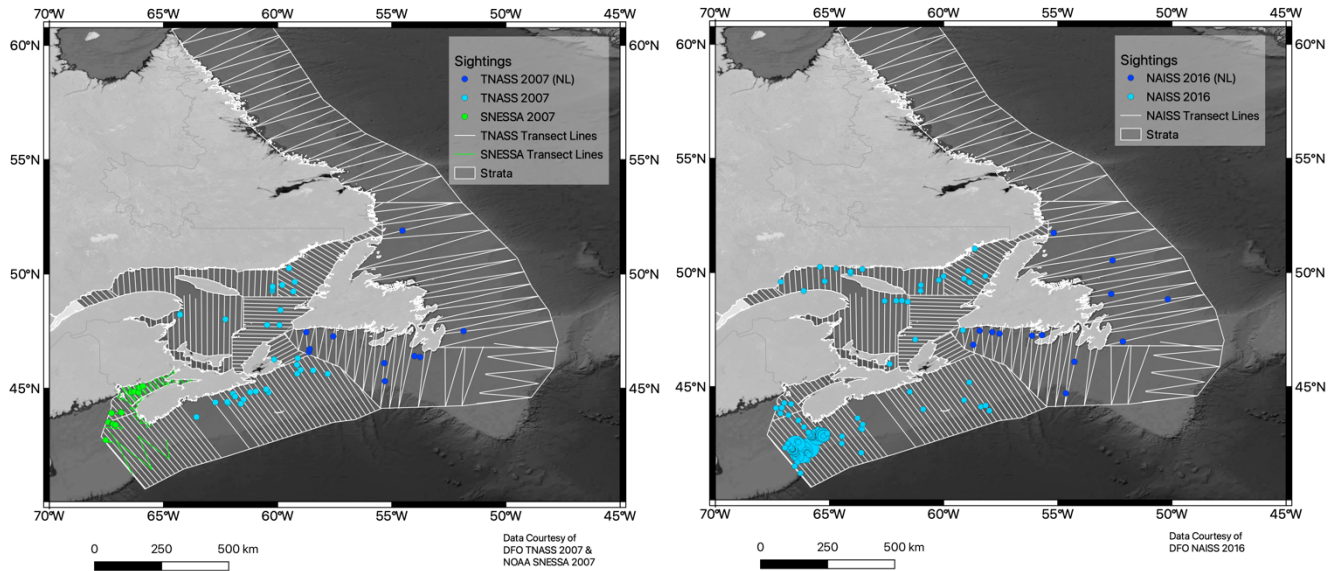


Figure 2.1 **Left:** Map of basking shark sightings from the TNASS and SNESSA 2007 surveys (N=53). *DFO TNASS 2007*: New Brunswick, Nova Scotia and Quebec (lighter blue); Newfoundland and Labrador (darker blue). *NOAA SNESSA 2007*: Bay of Fundy (green). **Right:** Map of basking shark sightings from NAISS 2016 Survey (N=213). Sightings from Nova Scotia, New Brunswick, and Quebec (light blue); Newfoundland and Labrador (dark blue). Size of marker indicates group size.

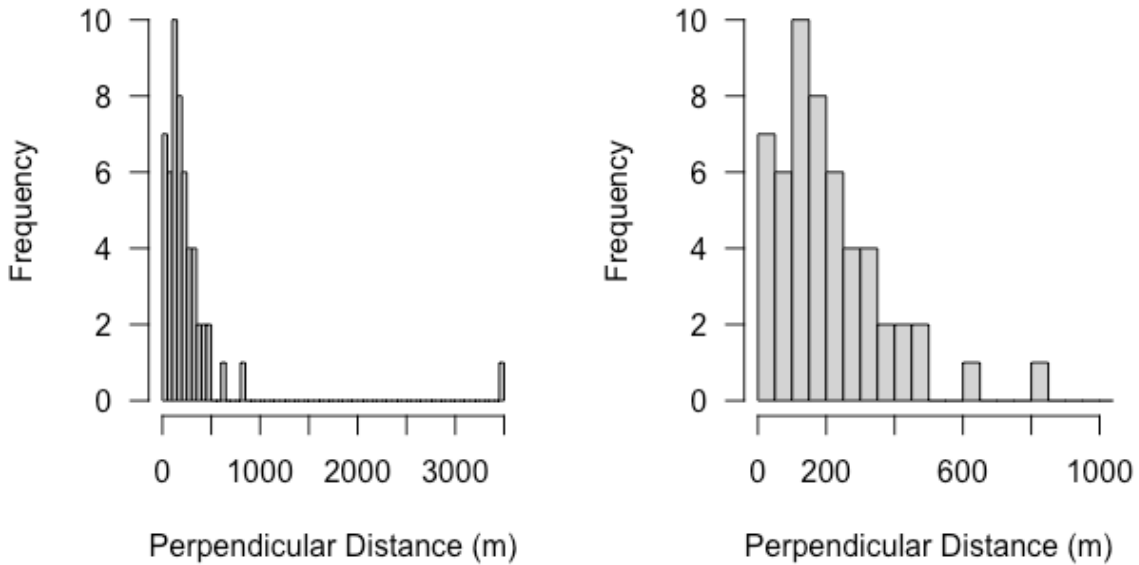


Figure 2.2 Histogram of perpendicular sighting distances (m) from the observer for the TNASS 2007 survey data. The original histogram (left) shows a clear outlier at 3473 m. After removal of the outlier the sightings ranged from 0m to 837m (right).

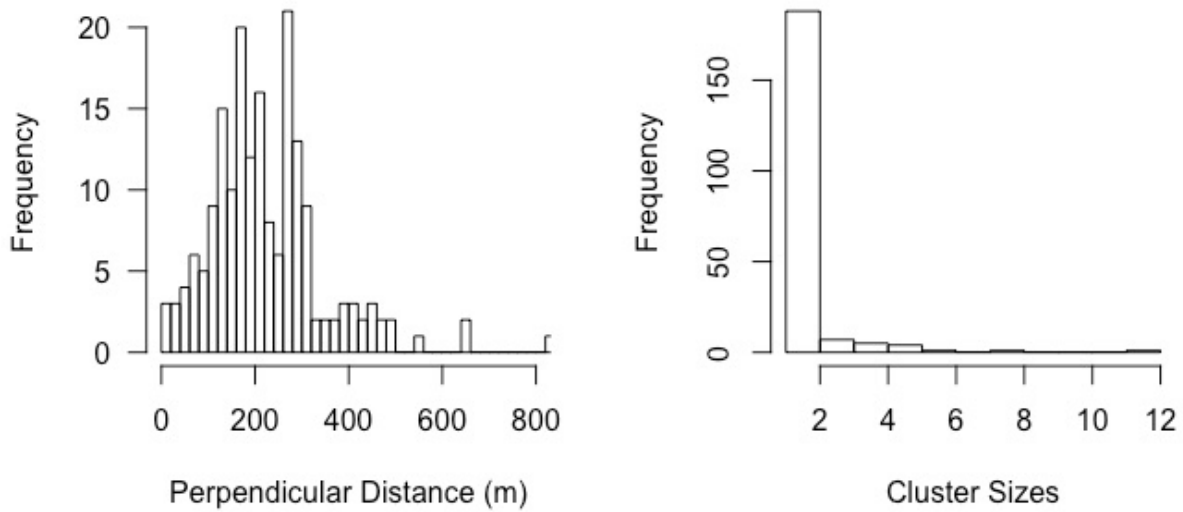


Figure 2.3 Frequency of perpendicular sighting distances from the observer (left) and cluster sizes (right) for the NAISS 2016 survey data. Sightings ranged in distances from 0 to 800m from the aerial observer, while cluster sizes ranged from 0 to 12, with a large majority of sightings having only one individual.

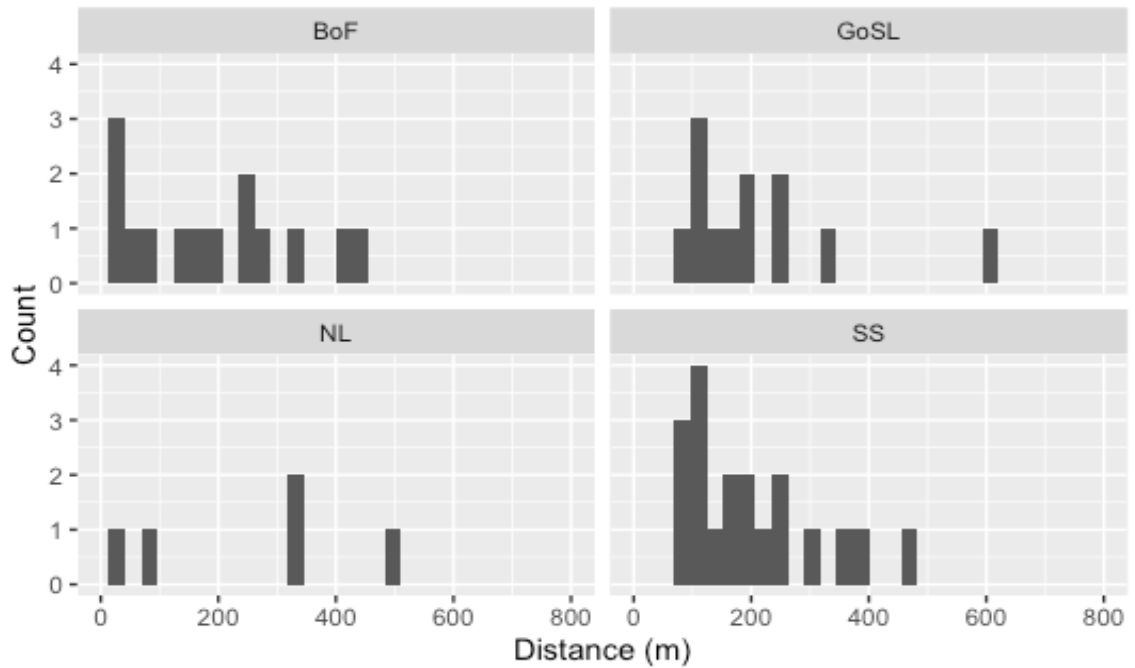


Figure 2.4 Number of sightings per distance (m) by geographic strata for TNASS 2007 survey data on basking sharks in Atlantic Canadian waters.

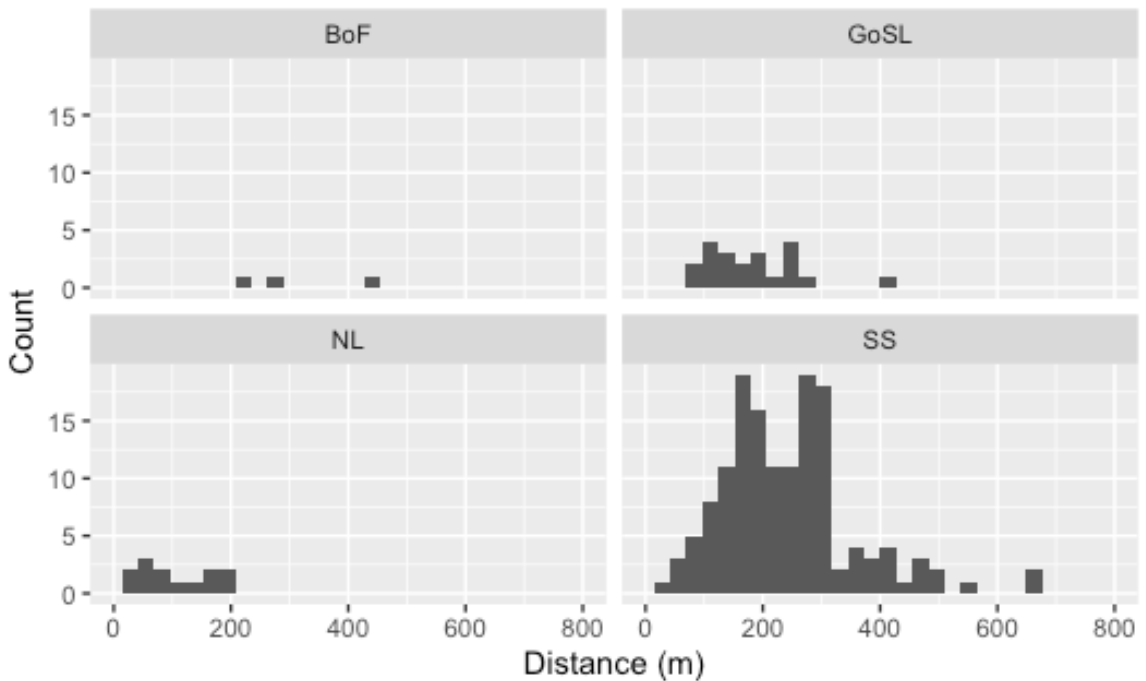


Figure 2.5 Number of sightings per distance (m) by geographic strata for NAISS 2016 survey data on basking sharks in Atlantic Canadian waters.

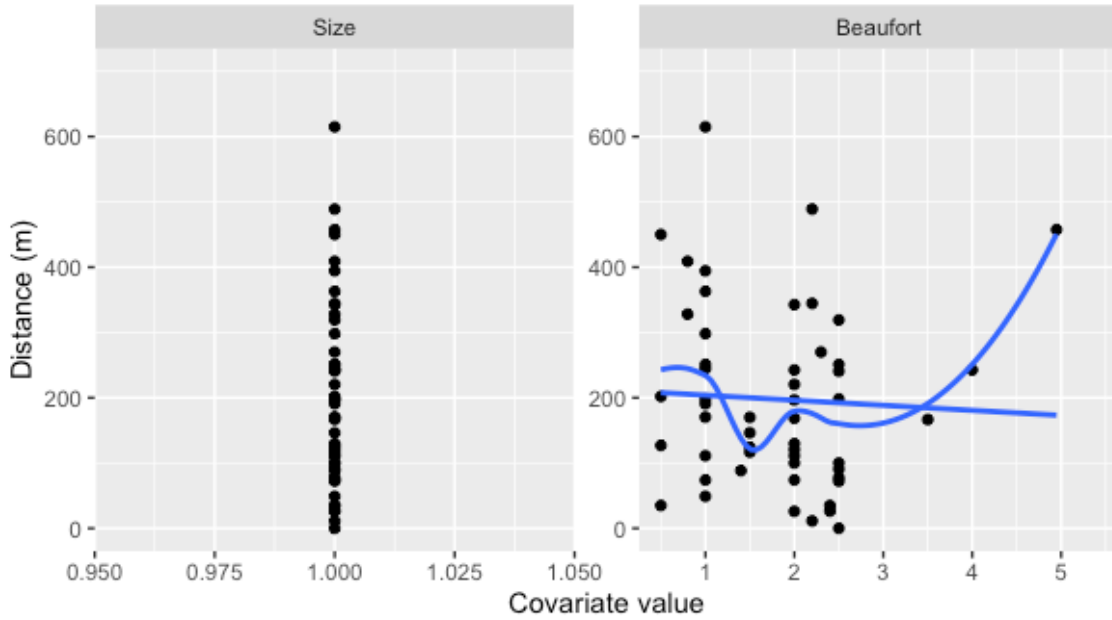


Figure 2.6 Linear model with LOESS smoother overlay of sighting distance versus cluster size (left) and Beaufort sea state (right) for TNASS 2007 survey data on basking sharks in in Atlantic Canadian waters.

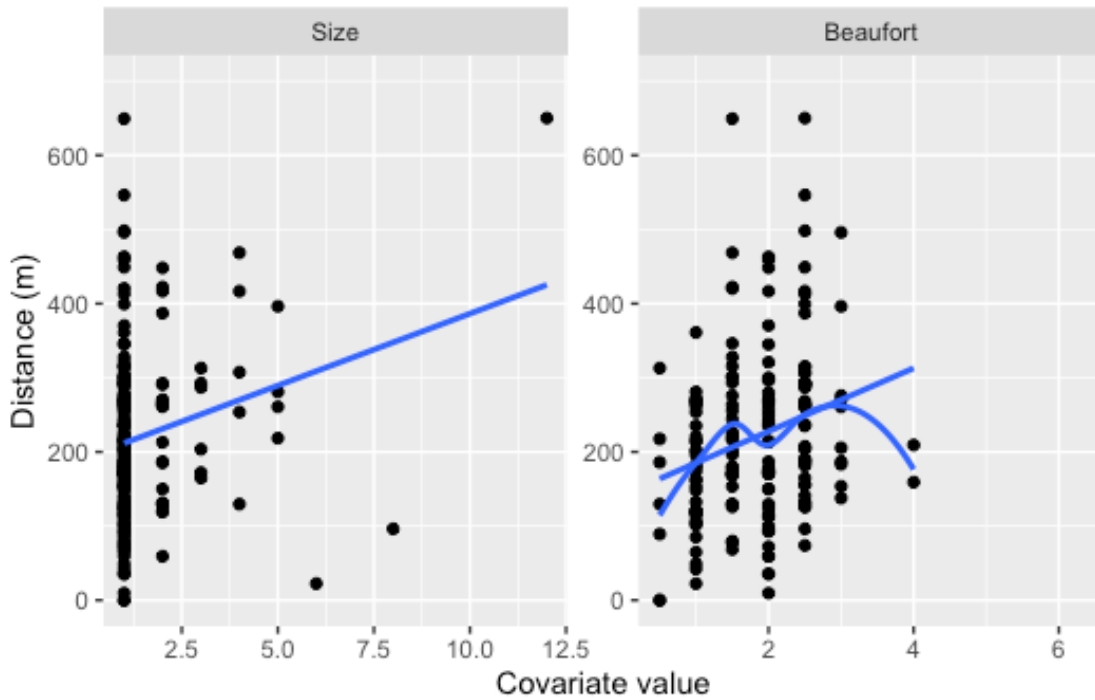


Figure 2.7 Linear model with LOESS smoother overlay of sighting distance versus cluster size (left) and Beaufort sea state (right) for NAISS 2016 survey data on basking sharks in in Atlantic Canadian waters.

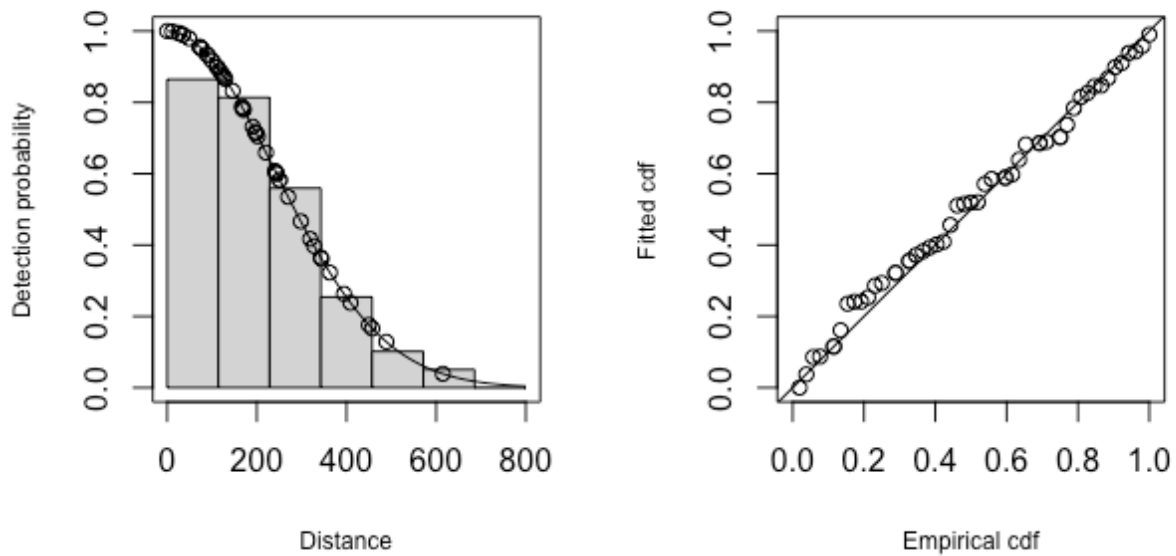


Figure 2.8 Half-normal detection function (left) for the TNASS 2007 survey data from MCDS model selection and associated goodness-of-fit test (right).

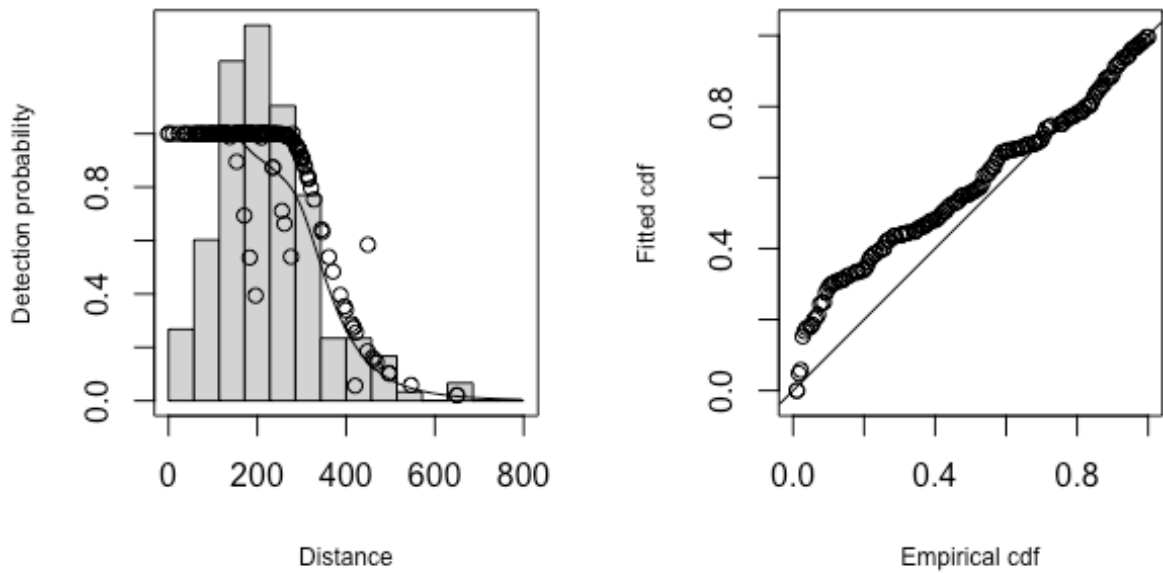


Figure 2.9 Hazard-rate detection function (left) with strata as a covariate for the NAISS 2016 Survey data from MCDS model selection and associated goodness-of-fit test (left).

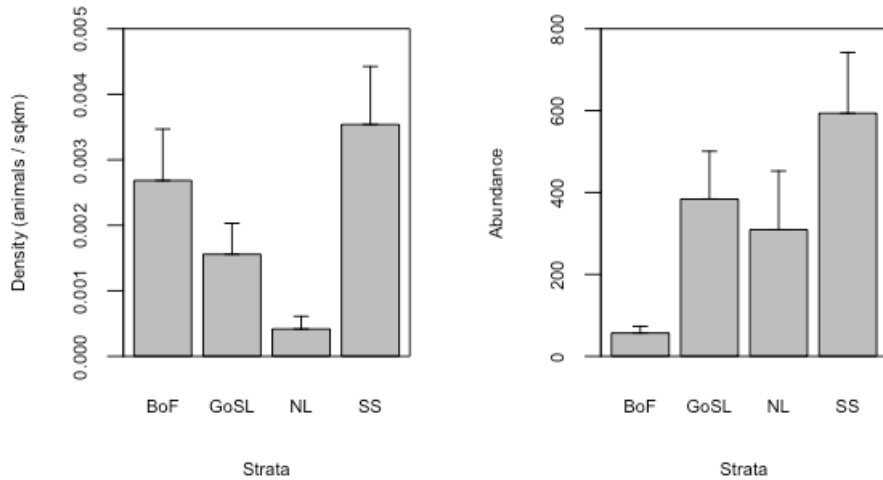


Figure 2.10 Estimated density (+SD; animals/km²) (left) and abundance (right) of basking sharks per strata (BoF: Bay of Fundy, GoSL: Gulf of St. Lawrence, NL: Newfoundland and Labrador, SS: Scotian Shelf) in Atlantic Canadian waters in 2007 from the HMC: MPMM.

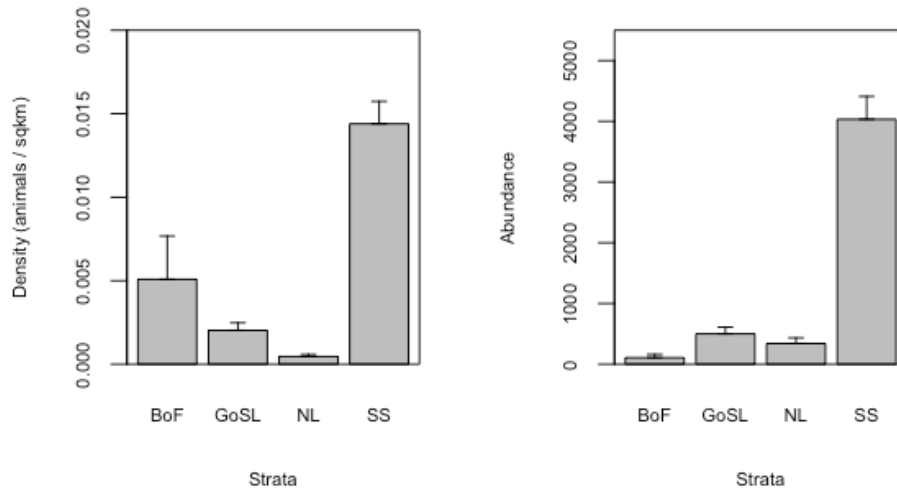


Figure 2.11 Estimated density (+SD; animals/km²) (left) and abundance (right) of basking sharks per strata (BoF: Bay of Fundy, GoSL: Gulf of St. Lawrence, NL: Newfoundland and Labrador, SS: Scotian Shelf) in Atlantic Canadian waters in 2016 from the HMC: MPMM.

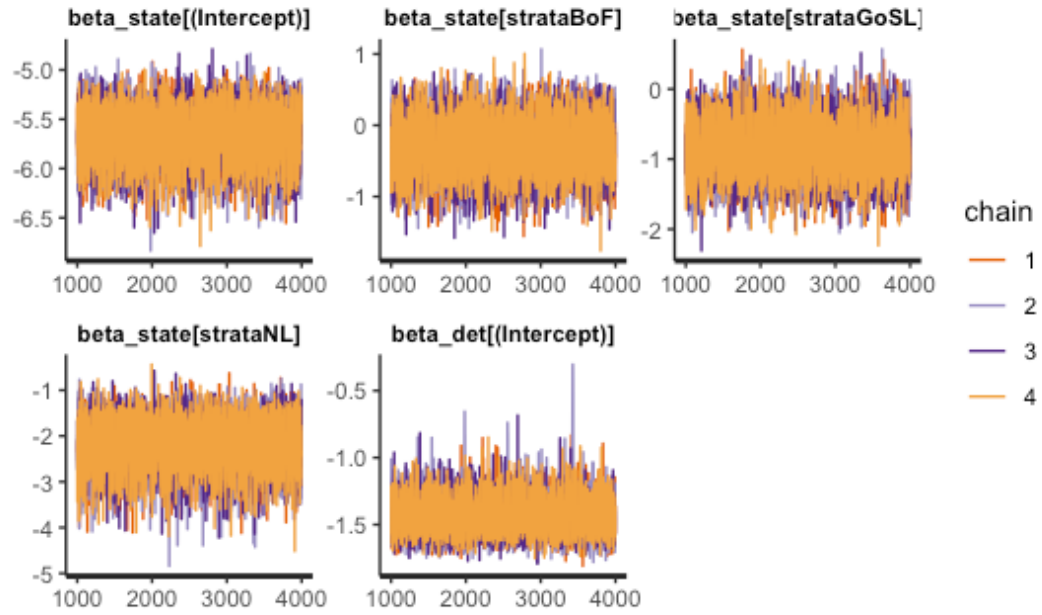


Figure 2.12 Trace plots for each of the parameters in the MPMM with data from 2007.

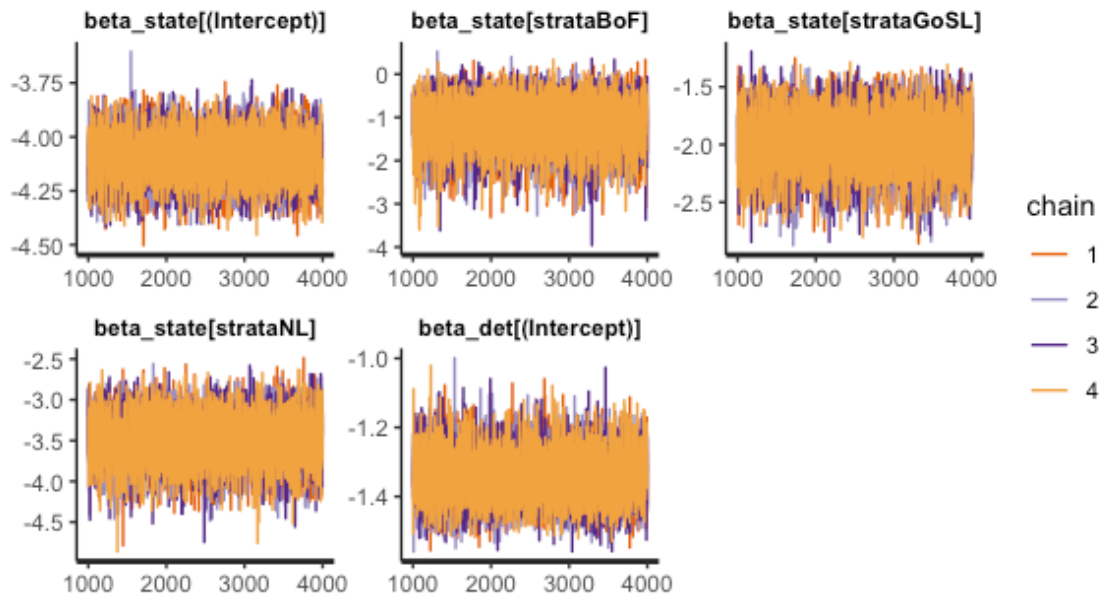


Figure 2.13 Trace plots for each of the parameters in the MPMM with data from 2016.

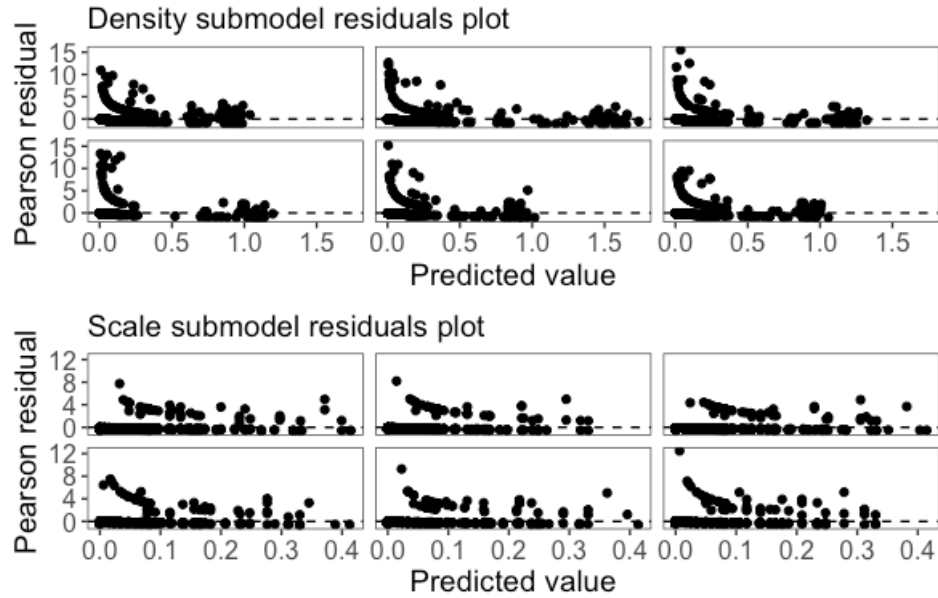


Figure 2.14 Pearson residual plots for submodels (density and scale, on top and bottom, respectively) used in the MPMM with data from 2007.

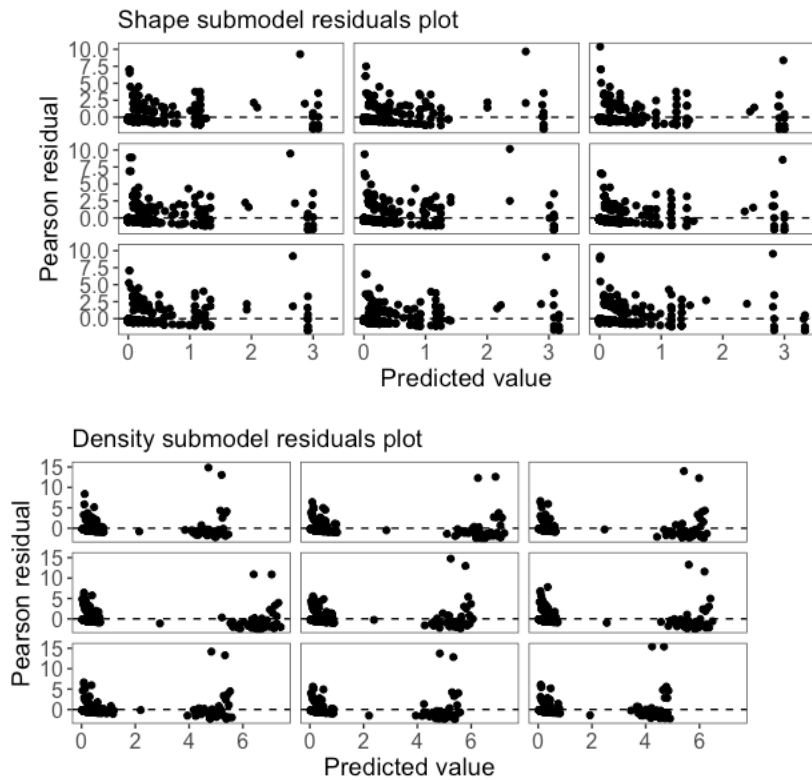


Figure 2.15 Pearson residual plots for the two submodels (shape and density, on top and bottom, respectively) used in the MPMM with data from 2016.

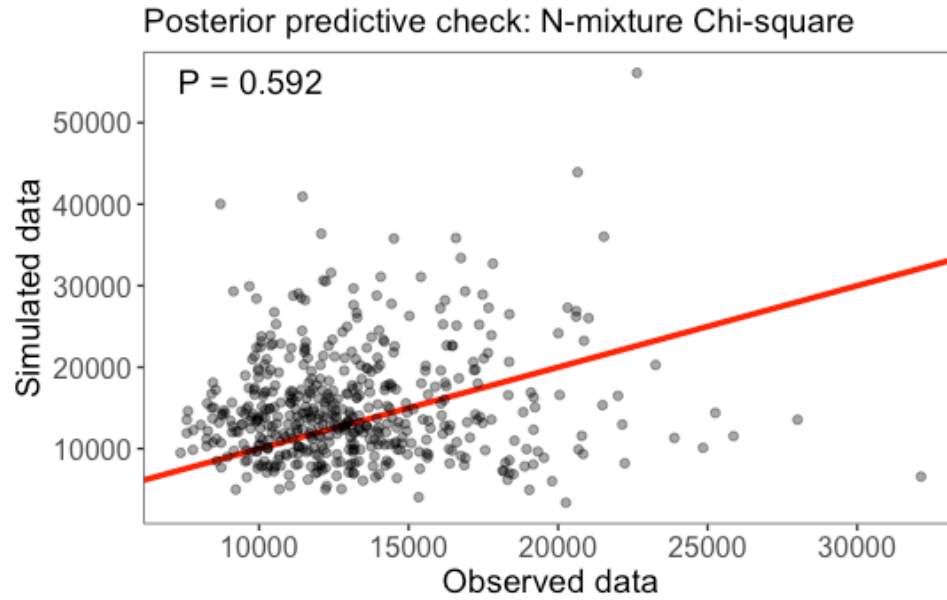


Figure 2.16 Posterior predictive check (N-Mixture Chi-Square) for the model built by the MPMM with data from 2007.

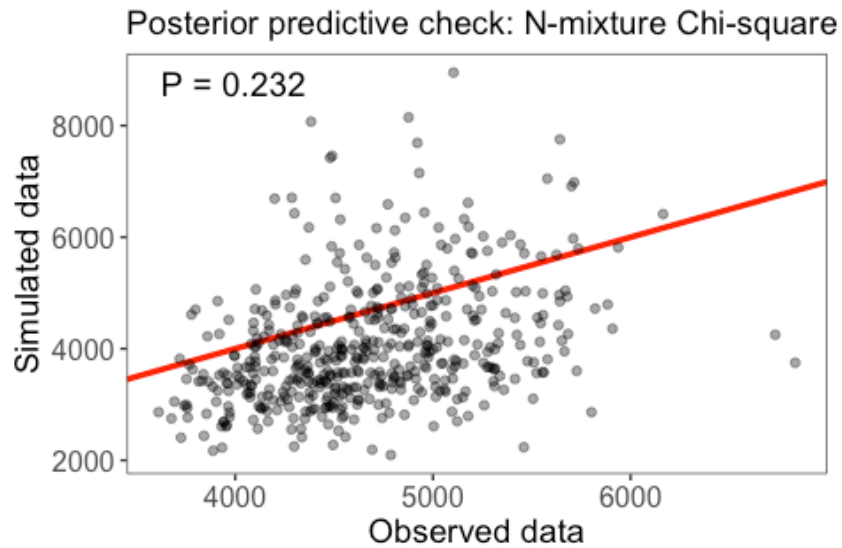


Figure 2.17 Posterior predictive check (N-Mixture Chi-Square) for the model built by the MPMM with data from 2016.

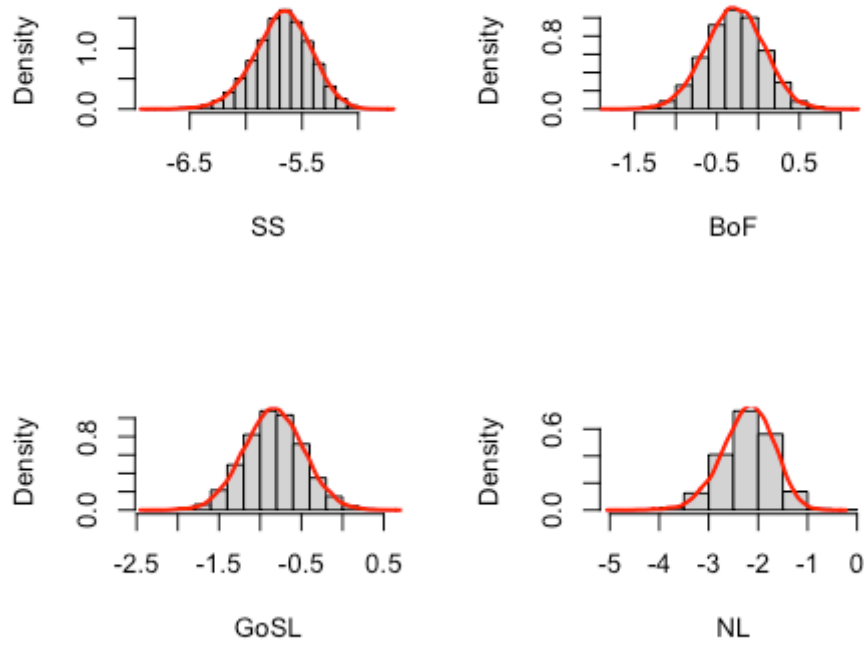


Figure 2.18 Posterior distributions of the shape parameter for each of the regions in the count portion of the MPMM with data from 2007.

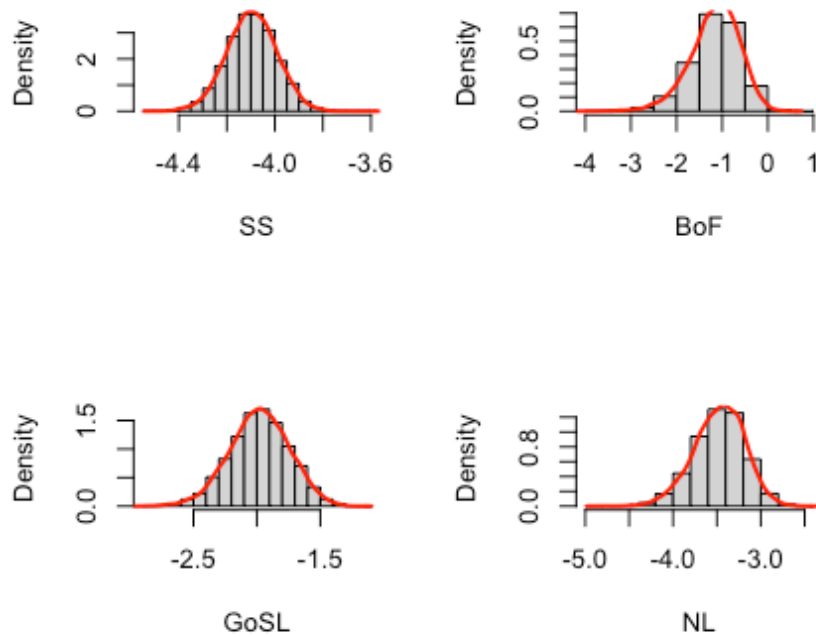


Figure 2.19 Posterior distributions of the shape parameter for each of the regions in the count portion of the MPMM with data from 2016.

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CHAPTER 3: LIFE TABLE ANALYSIS OF BASKING SHARKS

3.1. INTRODUCTION

To understand if an estimated trend in abundance is feasible based on what is known about the species, one can look to predict how a population changes over time. Populations are dynamic, shifting in size over time and space (Krebs 2001). Populations change in size as a result of four processes: birth, death, immigration and emigration (Cain et al. 2008, Kacev et al. 2017). As discussed previously, models that only take into account births and deaths are referred to as *closed* populations, whereas when immigration and emigration are accounted for, populations are considered *open* (Seber 1982). Populations can experience a wide range of growth patterns, including exponential growth (when conditions are favourable), logistic growth (how a population grows as it approaches an equilibrium), fluctuations and population cycles (Cain et al. 2008). Models of logistic growth are *density dependant*, whereas when exponential growth is modelled it is *density independent* (Seber 1982). These patterns are not mutually exclusive, and a single population could experience each of them at many different points in time (Cain et al. 2008). Additionally, populations can vary in their distribution within an environment with either random, regular (uniform) or clumped (patchy) distributions (Krebs 2001, Cain et al. 2008). Spatially isolated patches or populations can be linked through dispersal and/or migration (Bhaumik 2020).

Population trends can be influenced by a number of factors including fishing, biological interactions and environmental factors (Crawford 1991). Environmental factors include physical changes to the environment such as a shift in currents, temperatures or climate regimes whereas biological interactions encompass predator-prey relationships and competitive interactions (Crawford 1991). When conditions are unfavorable, whether it be due to fishing and bycatch mortality, biological interactions or environmental factors, a population's growth pattern may change, its growth rate may decrease, the population could shift its distribution to an area with more favorable conditions, or the distribution of the population within the environment may change (Krebs 2001, Cain et al. 2008). Additionally, if data collection methods are not standardized, an apparent trend in population size may be an artifact of methodology, rather than

a change in the true abundance of a species over time. This makes elucidating the exact causality of a change in population size very complicated, and often cannot be done with certainty.

Outside of biological and environmental changes, fishing can heavily influence population trends by increasing the total mortality that a species experiences over their lifetime. Total mortality, Z , consists of natural mortality, M , and fishing mortality, F . Fishing mortality often occurs through directed take, but can also affect non-target animals through bycatch, which in turn consists of non-directed take and discards. There is no directed fishery in Canada for basking sharks, and most bycatch is discarded at sea (Campana et al. 2008). As such, when fishing mortality for basking sharks is referenced in this analysis, it should be taken to mean discards from bycatch. Historical removals of basking sharks (1986-2007) in Atlantic Canada were estimated by Campana et al. (2008) and redfish and groundfish trawl fisheries on the Scotia Shelf account for the majority of the observed catch. In a density-independent model, bycatch would be expected to slow any population increase predicted by life history, due to increased total mortality.

Life table analysis (see Section 1.2.3.) relies on understanding patterns of reproduction and age-specific survival (Simpfendorfer 2005, Cortés 2016). Often, these life history parameters are not known with confidence. This is due to a lack of information, as many life history parameters cannot be estimated using non-lethal sampling (Heupel and Simpfendorfer 2010) and as there has been a contemporary move away from lethal sampling (Hammershlag and Sulikowski 2011). Often, this means that life history parameters can only be estimated from fisheries-derived specimens (Hammershlag and Sulikowski 2011) and are not regularly updated. For example, the only record of a pregnant female basking shark comes from Sund (1943). Other life history parameters (e.g., gestation period, age-at-maturity, longevity, etc.) for basking sharks are similarly uncertain (Sims 2008).

While these parameters remain uncertain, basking sharks are generally accepted in the literature to have long life histories (Sims 2008), and previous research suggests that populations would be expected to increase slowly in size (UK CITES 2002, Campana et al. 2008). Former estimates of basking shark population growth rates (r) predominantly come from life table analyses within population assessments (Campana et al. 2008, UK CITES proposal 2002). The

UK Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) proposal (2002) reported an r value of 0.020, with a range from 0.013 to 0.023. Campana et al. (2008) estimated intrinsic rates of population growth for an unfished population ranging from 0.032 (0.009-0.053) from MC sampling to 0.040 from a deterministic estimate. Earlier estimates cited in the UK CITES proposal (2002) from fishbase.org put population growth at $r=0.16$ but are considered significantly overestimated. These estimated values are very low compared to most fish species (Myers et al. 1999, Hutchings et al. 2012) and the UK CITES proposal (2002) states basking sharks have “among the lowest natural mortality and productivity yet calculated for a fished marine species”. This suggests that they would be expected to be inherently unproductive and experience very slow population growth. To see the estimated increase of ~19,000 (~270% increase) sharks in the 9 years between 2007 and 2016 as predicted in Chapter 2, basking sharks would be expected to have a population growth rate of $r= 0.159$, which would be significantly higher than any previous estimate.

Thus, the aim of this study is to estimate the maximum possible rate of population growth for an unfished population as well as the realized rate of population growth under fisheries mortality, and project it forward to 2016 from the estimated abundance for 2007 predicted in Chapter 2 to evaluate if the trend from Chapter 2 is feasible and consistent with what is currently known about basking shark life history. The abundance estimates of basking sharks from the distance sampling methods in Chapter 2 suggest a population increase of around 270% between 2007 and 2016. To evaluate the feasibility of the trend estimated in Chapter 2, a simulation model was used to model abundance changes over time. There were two components to this simulation; (i) life table analysis, which estimates the population growth rate, r , using the Euler-Lotka method and (ii) population projections, which model changes in abundance over a given period using a density-independent exponential growth model. A deterministic estimate of the per capita population growth rate (r) will be presented, along with an estimate from MC sampling, which is used to incorporate uncertainty into the life history parameters. Presented here are two equally possible population projections, based on the two estimates from Chapter 2 which were dependant on the chosen availability bias multiplier (19% from Westgate et al. (2014) or 36% from Sims et al. 2003a). The predicted population for 2016 from Chapter 2 will

then be compared with projected population from this method to evaluate the feasibility of the trend estimated in Chapter 2.

3.2. METHODS

3.2.1. OVERVIEW

Life table analysis was used to describe potential population growth for basking shark, based on life history characteristics. This was carried out using the most current estimates of key life history parameters (survival rate, age of sexual maturity, longevity and fecundity) for basking shark and allows the intrinsic rate of population growth (r_{max}) to be estimated. It was calculated first as a deterministic estimate, then Monte Carlo methods ($n = 1000$) were used to incorporate uncertainty into the life table analysis and the estimate of r . The population growth rates from Monte Carlo sampling were then used in a density-independent exponential population growth model to project the abundances of the population through time. These projections allowed for potential population response to be explored under various life history assumptions and levels of bycatch mortality.

The simulation model requires a population size estimate to initialize the projections. The estimate used was 7,072 (95% CI: 3,481-12,164) in 2007 from the Hamiltonian Monte Carlo implementation of the Royle et al. (2004) multinomial Poisson mixture model, with an availability bias of 19%, as the starting population (Chapter 2). This is referred to in this thesis as the “high abundance scenario”. This estimation method was chosen as it represented the middle of the range of the estimates from the three different methods (Chapter 2). The population estimate for 2016 from Chapter 2 (using the same method) was 26,310 (95% CI: 20,448-33,338). When using the availability bias of 36% from Sims et al. (2003a), the population estimates are 3,732 (95% CI 1,837-6,420) in 2007, and 13,886 (95% CI: 10,792-17,595) in 2016. This is referred to in this thesis as the “low abundance scenario”. If the population increase estimated in Chapter 2 is biologically possible with what is currently know about basking shark life history, then it would be expected to see the simulated population projections reflect that. Predicted abundance in 2016 would be within the range of uncertainty for the estimate determined in Chapter 2.

3.2.2. ESTIMATING THE POPULATION GROWTH RATE, r

While there are multiple methods for estimating the rate of population growth (Simpfendorfer 2005, Cortés 2016, see Section 1.2.3), a derivation of the Euler-Lotka equation, based on exponential population growth, was used (McAllister et al. 2001). The Leslie projection matrix was considered, but one requirement of that method is that when projecting into the future, the population converges to a stable age structure and a single estimate of r (McAllister et al. 2001, Kacev et al. 2017). This requirement was not met in Campana et al. (2008), and following their approach, the Euler-Lotka method was used in this analysis instead of a Leslie matrix.

This is a density independent model, in which r is taken to be the intrinsic rate of population growth (r_{max}), the maximum rate at which the population could increase from a severely depleted population size (Gedmke et al. 2007, Zhou et al. 2012). Here, using a density-independent model relies on the assumption that the population is at a severely depleted size in 2007. This assumption cannot be validated directly due to a lack of historical abundance information. Landings data from the eastern North Atlantic demonstrate a dramatic decline during the period 1946-2017 (CITES 2002, ICES 2018) and is believed to reflect a decline in population abundance (Rigby et al. 2021) though landings can be a poor indicator of relative abundance trends. Genetic results indicate one global population in the North Atlantic (Noble et al. 2007, Francis 2017) and tagging studies demonstrate that while basking sharks exhibit high regional fidelity, there is also evidence of trans-Atlantic mixing (Johnston et al. 2019, Gore et al. 2008) as well as trans-equatorial mixing (Skomal et al. 2009). As a result, it is plausible that basking shark in the Western North Atlantic are also depleted from their historic abundance, even though the Atlantic population was assessed as Special Concern by The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (2009).

The Euler-Lotka equation was used to approximate r :

$$1 = \sum_{x=0}^A e^{(-rx)} m_x l_x \quad (1)$$

where A is the maximum age, l_x is the proportion of female sharks surviving to age x ($l_0 = 1$) and m_x is the expected reproductive output at age x . The expected reproductive output at age x is

a function of the probability of being mature, fecundity and the sex ratio. This is a female-only model regarding reproductive output, which is calculated by the female age-at-maturity (a), the sex ratio (assumed to be 50:50) and the fecundity of females. The equation for r cannot be solved analytically, so it was instead solved through iterative minimization in R (R Core Team, 2020). Survivorship, l_x , is given by:

$$l_x = \prod_{i=0}^{x-1} \exp(-(M_i + F_i)) \quad (2)$$

where M and F are the instantaneous rates of natural and fishing mortality, respectively.

Fishing mortality (F) is a rate calculated from the mean number of removals (u) (i.e., historical landings and/or discards) over the known time series. Fishery selectivity was assumed to be knife-edged at age 2 (as in Campana et al. 2008; Table 3.2). Fishing mortality was calculated from the mean annual number of removals through the equation (Ricker 1975):

$$u = 1 - e^{-F} \quad (3).$$

A time series of total removals was derived by Campana et al. (2008) from a ratio estimator and fisheries observer records of basking sharks caught in commercial fisheries, spanning from 1986 to 2007 (Figure 3.1). This was the time period used for the backwards population projections. Observer coverage varies dramatically, with 100% observer coverage of foreign vessels, but observer coverage on domestic vessels is less than 5% (Campana et al. 2008). In general, most of the basking sharks caught as bycatch were caught in the Scotia-Fundy region, peaking in 1990 with 741 mt and averaging at 164 mt annually (Campana et al. 2008). The median weight (1000 kg per basking shark) from the observer database was used to transform biomass into numbers of animals (Campana et al. 2008) so that removals could be input into the simulation. The mean number of removals was 164 basking sharks per year, assuming 100% mortality of discards, although it appears to have decreased to a stable level around ~90 sharks per year after 1995 (Figure 3.1). Redfish and groundfish trawl fisheries on the Scotian Shelf accounted for most of the observed catch (Campana et al. 2008). However, there was limited coverage of inshore fishing gear (e.g., gill nets, cod traps) and bycatch from these gear types was not accounted for and may be larger than estimated.

Estimating the survivorship to age x requires an estimate of natural mortality rate (M) which can be estimated with a variety of methods (Kenchington et al. 2014). In this analysis, M was estimated from a function following Hoenig (1983). The Hoenig (1983) geometric mean regression natural mortality estimator for cetaceans is presented as a function of longevity (A):

$$M = 5.20A^{-1.04} \quad (4)$$

Using the Hoenig (1983) natural mortality estimator for cetaceans instead of the one for fish is appropriate in this situation, where basking sharks are thought to have long lives and a relatively low number of offspring compared to fish (Bowlby and Gibson 2020). For each sampled value of A in the simulations, a new value for M was calculated using Equation (4). The median natural mortality rate from Equation 4 was 0.089 (80% percentile: 0.0735-0.1121) (Table 3.2).

The life history parameters used for a deterministic base run of the intrinsic rate of population growth (r_{max}), following Campana et al. (2008), are given in Table 3.1. The most recent estimates or inferred values for life history parameters were used (Table 3.1.), though they are highly uncertain due to the lack of information available for basking sharks and the challenges in accurately determining these parameters (Campana et al. 2008, Sims 2008 review).

Monte Carlo (MC) methods were used to allow for uncertainty in the population growth rate (Bowlby and Gibson 2020, Campana et al. 2008). Minimum and maximum values were assumed for each life history parameter (Table 3.2), then sampled ($n=1000$) from uniform distributions defined by these bounds and used the resulting distribution of estimates in r in the following analysis. Abundance estimates from the simulations and values for r when fishing mortality was included or excluded were compared. When fishing mortality is excluded, r is equivalent to the intrinsic rate of population growth (r_{max}). Determining the population growth rate without fishing mortality gives an upper bound to the potential for population increase.

Age validation is difficult in some shark species (Caillet 2015) and estimates and methods used for basking sharks differ between studies. Parker and Stott (1965) based age-at-maturity and growth estimates off relating vertebral rings to body length (i.e., band pair counts), but did not estimate longevity. However, Natanson et al. (2008) found that band pair counts changed significantly along an individual vertebral column, suggesting that basking sharks cannot be aged using band pair counts. The findings by Natanson et al. (2008) suggest that the

Parker and Stott (1965) estimates should not be used. Pauly (2002) used a length-based growth model with different assumptions than the Parker and Stott (1965) study (namely, that basking sharks do not feed during colder months and therefore exhibit asymmetric growth throughout a year). Pauly (2002) estimated the longevity of basking sharks at around 50 y, but without consensus, the analysis incorporated bounds of 40-60 y for estimates of longevity (Table 3.2).

Similarly, there is very little information on basking shark reproductive parameters. Only one pregnant female was ever captured (Sund 1943) with a litter size of six pups. Assuming a 50:50 sex ratio, bounds of two to four for female litter size were used in this female only model (Table 3.2). Gestation period was estimated as high as 3.5y (Parker and Stott 1965) but length-frequency data by Holden (1974) estimated gestation as just over ~1 y. Gestation period was assumed to be between two to four years, as done in Campana et al. (2008) (Table 3.2). Following Campana et al. (2008), the lag (in years) between parturition and next pregnancy was set at a mean of 0.5, with limits at zero and one (Table 3.2). Age at maturity is the best-studied reproductive parameter (Matthews 1950, Matthews and Parker 1950, Sims 2008) with females reaching maturity around 18y. Bounds of 16-20 y for age at maturity were assumed (Table 3.2).

With these bounds on life history parameters (Table 3.2), values were randomly drawn ($n=1000$) from the distributions of each of the life history parameters and calculated r using the Euler-Lotka method (Eq 1). Campana et al. (2008) used a cut-off value of 0.057 as the upper threshold of r in the simulation, with values above this threshold being discarded. The Campana et al. (2008) cut-off value was based on the median value from a review of estimates of r for 21 shark species with a maximum length greater than 2 m from Cortés (2002). This cut-off value was tried with the data, as well as the suggestion of two times the deterministic estimate of r from Bowlby and Gibson (2020). The Bowlby and Gibson (2020) method of setting the upper threshold as two times the deterministic estimate ($r=0.044$) was used as it was slightly more conservative. Simulations that produced values of r that were above this threshold or less than zero were discarded.

3.2.3. POPULATION PROJECTIONS

3.2.3.1. Accounting for Bycatch Mortality

Historical bycatch could influence population growth rates by increasing the amount of total mortality the population experienced. An exponential population growth model was used to generate a time series of abundance by projecting backwards in time from a given, starting population size:

$$\frac{dN}{dt} = rN \quad (5)$$

where N is the population size and r is the rate of population growth, as before. Assuming exponential growth, the population size in a given year (N_y) equals the population size in the previous year multiplied by r , minus the number of removals in the previous year (D_{y-1}):

$$N_y = e^r N_{y-1} D_{y-1} \quad (6).$$

With the estimated r and a time series of human-induced mortalities, this equation can be arranged as:

$$N_{y-1} = \frac{N_y + D_{y-1}}{e^r} \quad (7).$$

This assumes that birth and natural mortality occur first and that deaths from fishing mortality occur afterwards. This assumption could exaggerate the effect of removals instead of modelling them as a continuous process, but this is not considered an issue by the other authors who have done this approach on basking sharks (Campana et al. 2008) and similar shark species (Bowlby and Gibson 2020), following the precautionary principle that prefers removals to be overestimated, rather than underestimated.

Chapter 2 provided two estimates, based on varying availability biases for basking sharks in aerial surveys. As such, in this analysis population growth rates and trends in population size will be presented relative to two scenarios of starting abundance. The model was initialized using the abundance estimate of 7,072 (95% CI: 3,481-12,164) in 2007 as the given starting population size in the “high abundance scenario” (Table 3.2). The “low abundance scenario” used an estimate of 3,732 (95% CI: 1,387-6,420) from results with an availability bias of 36% from Sims et al. (2003a); the former estimate uses an availability bias of 19% from Westgate et al. (2014).

This simulation was repeated for 1,000 simulated values for r . For each iteration, an abundance time series for the years 1986-2007 was back-calculated, based on a randomly drawn population size within the bounds for 2007 (Table 3.1), and accounting for fishing mortalities from 1986-2007. From this, a mean exploitation rate was determined, which was transformed into an instantaneous rate for fishing mortality and incorporated into the calculation of survivability (Eq 2) when estimating r . This gives a population growth rate for the forwards projections that incorporates the effect of fishing mortality.

3.2.3.2. Population Trends

Recall that the goal of this chapter is to predict the abundance increase between 2007 and 2016 to evaluate the feasibility of the trend predicted in Chapter 2. There are three scenarios being considered: (i) the unfished population, and then when fishing mortality is included from historical bycatch records, (ii) the high abundance scenario, as well as (iii) the low abundance scenario. Using the values of the population growth rate, the population was projected into the future (to 2030) from the randomly drawn population size for 2007. An exponential model (i.e., a lognormal regression) was fit to the time series to determine whether the forwards-projected abundance had been increasing or decreasing:

$$\ln(N_y) = \alpha + \beta y \quad (8)$$

with β as the instantaneous rate of change in population size, where positive values indicate an increasing population. The distribution of estimates for β were compared to the predicted level of population increase from Chapter 2. Based on the abundance estimates from Chapter 2, the annual rate of change would have to be approximately 0.3, regardless of which availability bias was used to estimate population size.

To further incorporate biological realism into the forward projections, autocorrelated annual variability was incorporated into r following the general approach of Hillborn (2001), similarly done by Bowlby and Gibson (2020). This allows for the simulated values of r to change slightly from year-to-year in the forward projections as reproductive output can vary from year-to-year. The deviates (w) were calculated as:

$$w_t = w_{t-1}d + w_t^* \sigma \quad (9)$$

where

$$w_t^* \sim N(0,1)$$

with annual variability (σ) and environmental autocorrelation (d) both given an assumed value of 0.005 and then the deviates were added to r . The low value for annual variability reflects that the variation in reproductive output is low in basking sharks compared to variability in other fish species with higher recruitment (Kindsvater et al. 2016). An extremely low level of annual variation in reproductive output can be expected for basking sharks based on their long lifespans and low levels of reproductive output (Kindsvater et al. 2016).

3.2.4. SENSITIVITY ANALYSIS

To assess sensitivity to model inputs, the simulations were repeated with a variety of alternate scenarios. Changing life history parameters in a way that increases lifetime reproductive output has the effect of increasing r , and vice versa. Parameters were chosen to change in ways that would increase r , to see if a specific parameter would have a large enough effect on r to give the magnitude of population growth predicted between 2007 and 2016 from Chapter 2. Any increases in the population growth rate (r) results in a greater proportion of populations showing increases (p) in the forwards projections.

The effects on r and the proportion of increasing populations (p) within the 1000 simulations were investigated by: (i) fixing the lag between parturition and next pregnancy at 0 (ii) reducing age at maturity (=14y), (iii) reducing age at maturity and setting $F = 0$ (no bycatch mortality), (iv) calculating mean exploitation from a shorter time period (1995-2007) and finally, (v) using no upper r -cutoff value. These alternate scenarios allow for greater reproductive output (i and ii), less impact from bycatch (iii and iv), and unbounded estimates for the population growth rate (v).

Lag between parturition and next pregnancy was initially assumed to be 0.5y (0-1), as in Campana et al. (2008). The interval between births for other species was looked at, either with similar ecological niches (filter-feeding on zooplankton), or from the same order (Lamniformes), to get an idea of what an alternate value could be. Whale sharks (*Rhiconodon typus*, Smith 1828) and Megamouth sharks (*Megachasma pelagios*, Taylor, Compagno and Struhsaker 1983), the two other large-bodied, filter feeding sharks, both lack an estimate of the lag between partition and next pregnancy in the literature. White sharks are thought to require a year or more between

pregnancies (Dewar et al. 2013, Domeier and Nasby-Lucas 2013). One of the most widely accepted estimates of birth interval for a Lamniform shark come from Porbeagle (*Lamna nasus*, Bonnaterre 1788) with a one-year lag, but they have a gestation period of less than a year (Natanson et al. 2002, Natanson and Gervelis 2013). Considering that gestation period is estimated at 3.5y for basking sharks (Parker and Stott 1965) and bounds of 2-4y on gestation were implemented, if the lag time were up to one year, that would correspond to a 5-year reproductive cycle, which would be the longest known for any shark species. As such, one of the alternate scenarios investigated was decreasing the lag time between pregnancies to zero, which in turn would increase r as reproduction would be more frequent.

The female age-at-maturity is thought to be approximately 18 years (16-20), based on two studies from the 1950s (Matthews 1950, Matthews and Parker 1950). Since then, there has been no recent work to determine age-at-maturity due to the contemporary move away from lethal sampling (Hammerschlag and Sulikowski 2011). Male age-at-maturity was estimated from total lengths (TL) of 5-7 m at ages between 12-16 years (Matthews 1950, Matthews and Parker 1950). As a result of difficulties aging basking sharks (discussed above) and a lack of a consensus on length-at-age growth curves (Sims 2008), there is still room for this parameter to be further explored. A 6.9m TL mature female basking shark with eggs in her uteri was recently captured (Ali et al. 2012) suggesting that maturation may occur at a smaller size than previously thought. Francis (2017) argues that estimates of age-at-maturity are “currently impossible” given the difficulty in aging basking sharks. If the female age-at-maturity was younger, then lifetime reproductive output could increase, thereby increasing r . For this reason, changing the female age-at-maturity to 14 years (12-16) to match male age-at-maturity was investigated. This was done for a population that did not experience bycatch mortality, and for one that did.

The longevity estimate of 50y by Pauly (2002) was used and bounds of 40-60y were incorporated. However, as previously discussed, age validation is difficult in shark species and there are very few re-sightings of female basking sharks that allow for validation of growth estimates (Sims 2008). A re-sighting of a 5m long female basking shark by Sims et al. (2000) three years after the initial sighting gave an estimate of an individual growth rate of 0.4-0.8m/yr, which was inconsistent with the results from the length-at-age growth curves of either Parker and Stott (1965) or Pauly (2002). Longevity is related to maximum length, with the largest measured

individual at 10.97m (Bigelow and Schroeder 1948). However, larger sharks have been reported but not formally measured (McClain et al. 2015), suggesting that longevity may be longer than 50 years. If longevity were greater, then there would be more time for reproduction, thereby increasing lifetime reproductive output and r . However, longevity and age-at-maturity are intrinsically linked because they are both derived from growth models fit to maturity-at-length data (see Caillet 2015 review). The formal sensitivity analysis varied age-at-mortality as it could lead to larger increases in r , therefore being more likely to be the parameter that could realize the rate of population growth required for the increase in abundance predicted between 2007 and 2016 in Chapter 2.

An additional alternate scenario that was looked at was to calculate the mean exploitation rate from a shorter time period. A change in the annual rate of exploitation would alter the amount of total mortality that the population experiences, thereby altering the estimates of r . Higher exploitation rates reduce r by a greater amount than lower. The time series of removals demonstrates a strong peak around 1990 (Figure 3.1). There was a collapse in commercial fisheries for Atlantic cod (*Gadus morhua*, Linnaeus 1758) throughout Atlantic Canada that came to a peak in 1992, when a moratorium was imposed on commercial exploitation (Myers et al. 1997). As groundfish trawling accounted for most of the observed removals of basking sharks, the reduction of trawling intensity due to the moratorium could lend explanation to the apparent peak in removals around 1990 and the later stabilisation at a lower level of exploitation. From 1989 to 1992 removals were much higher than average, with a mean number of annual removals of ~428 sharks/yr, peaking at 741 sharks in 1990 (Figure 3.1). Furthermore, the mean number of removals was ~252 sharks/year between 1986 to 1997 compared to ~90 sharks/yr between 1995 to 2007 (Figure 3.1). If there has been a significant drop in the number of fisheries removals since the mid-90's as the data suggests, then calculating the mean exploitation rate using the entire time series may overestimate the effect of historical fishing mortality on potential population growth rates, therefore inappropriately reducing the estimates of r . Additionally, when looking at overall trends in commercial fishing effort in these fleets, assuming that basking shark bycatch scales with fishing effort, due to regulations in the US and Canada, groundfish fisheries generally have declining effort over recent decades. For these reasons, an alternate

scenario in which the mean exploitation rate was calculated from the time series of removals for the period 1995 to 2007 was explored.

In the initial model formulation, bounds for r had been established on an unfished population between 0 and two times the deterministic estimate of $r = 0.044$ as suggested by Bowlby and Gibson (2020). Any simulated values of r that were above the upper threshold for r at 0.044 and below zero were discarded from the analysis. To test the effect of the truncation of r at 0.044, an alternate scenario was investigated in which this truncation was removed from the base model run, while maintaining the truncation at $r = 0$. If the maximum intrinsic rate of increase for a population was below zero, the population would have been driven to extinction long in the past, making values of $r < 0$ illogical.

3.3. RESULTS

3.3.1. POPULATION GROWTH RATE, r

Given the life history parameters in Table 3.1, life table analysis from the deterministic base run estimates the intrinsic rate of population growth (r_{max}) in an unfished population at 0.022 (Table 3.3). Incorporating life history variation through Monte Carlo sampling simulations, by using the life history parameters with assumed bounds (Table 3.2), slightly lowered the capacity of population growth across all three scenarios when compared to the deterministic estimate of r_{max} (Table 3). For an unfished population, the intrinsic rate of population growth became 0.0197 (80% percentile: 0.004 - 0.037) (Table 3.3).

Incorporating fishing mortality into the calculation of r decreased the population growth rate compared to both aforementioned estimates of r_{max} (Table 3.3). Using the calculated annual exploitation rates from the mean number of annual discards from 1986 to 2007 (164, Figure 3.1) and the starting population of 7,072 (95% CI: 3,481-12,164) in 2007 (i.e., the “high abundance scenario”), gave a median r value of -0.017 (80% percentile: -0.046 – 0.013) (Table 3.3). This is lower than the estimate of $r = 0.0197$ from an unfished population (Table 3.3) and implies that the population would be decreasing in abundance over time in the forwards projections. Similar calculations from the lower starting population of 3,732 (95% CI: 1,387-6,420) in 2007 (i.e., the “low abundance scenario”, gave a median r value of -0.037 (80% percentile: -0.076 – -0.002). Historical removals represented a larger proportion of total population size when abundance was

lower, leading to a greater effect on r (Table 3.3) because the exploitation rate is calculated as a proportion of the total population size.

3.3.2. POPULATION PROJECTIONS

The forward population trajectory for an unfished population is shown in Figure 3.2, with the median of the simulations showing an increase in abundance over time. The distribution of r values generally follows a normal distribution with data roughly symmetric around the median (Figure 3.3). When the population is growing at its theoretical maximum rate, 99% of simulated populations show an increase between 2007-2016 (Table 3.4). The projected abundance was estimated to be 8,273 (80% percentile: 4,716 – 12,667) in 2016 (Table 3.4). The distribution of the annual rates of change is almost entirely positive, with a mean of 0.019 (bottom right panel, Figure 3.3)

The population trajectory from 1986 to 2030 of the high abundance scenario is shown in the top panel of Figure 4, with the median of the simulations showing a decrease in abundance over time. In the backwards portion of the simulation (1986-2007) the largest decline is around the year 1990. This corresponds to a peak in discards in 1990, with 741 removals in that year (Figure 1). The histograms for population size in 2007, the population size in 2016, r and the instantaneous rate of change in the population show uncertainty in the present and future population sizes, as well as the uncertainty in r (Figure 3.5). The annual rates of change are generally lower than in the unfished scenario, with a median at -0.014 (bottom left panel, Figure 3.5). Accounting for fishing mortality markedly affects the predicted population growth rate, with only 25% of simulated populations showing an increase between 2007-2030 (Table 3.4). The abundance in 2016 (the year of interest) was estimated to be 6,402 (80% percentile: 3,386 – 10,795) (Table 3.4).

The population trajectory projected to 2030 of low abundance scenario is shown in Figure 3.4, in the middle panel, with the median of the simulations showing a decrease in abundance over time. The proportion of increasing populations in the simulation was lower relative to the base model, with 9% of populations showing an increase for the period 2007-2030 (Table 3.4). The results of the analysis of this scenario compared to the base model are shown in Figure 3.5 (middle panel) with histograms of population sizes predicted for 2007 and 2016, as

well as the annual rate of change. As r under this scenario was predicted to be more negative than in the base model, the annual rates of change are generally lower, and a larger proportion (~80%) of the histogram of r values falls below zero with a median at -0.035 (Figure 3.5). The projected abundance was estimated to be 2,981 (80% percentile: 1,194 – 5,381) in 2016 (Table 3.4).

The predicted magnitude of population increase from Chapter 2 was transformed into an annual rate of change and plotted relative to the distribution of annual rates of change from the forward projections (Figure 3.5). The annual rate of change between the two abundance estimates from Chapter 2 would have to be ~0.3 (indicated by the blue line on Figures 3.5 and 3.6), regardless of which availability bias was used to estimate population size. Across both scenarios, the estimated annual rate of change fell between -0.1 and 0 (Figure 3.5).

3.3.3. SENSITIVITY ANALYSES

The rate of abundance increase predicted in Chapter 2 did not fall within the distribution of values from the forward simulations in any of the alternate scenarios (Figure 3.6). If lag time was decreased to 0 instead of 0.5, r would increase slightly and the proportion of populations trending upwards increased to 0.28 (Table 3.5). The estimated abundance for 2016 would increase to 6,524 (80% percentile: 3,198 – 10,900) (Table 3.5) but remains much lower than the abundance of 26,310 (95% CI: 20,448-33,338) estimated in Chapter 2. If the age at maturity was younger (~14y), then r would increase, and p would increase to 0.52 (Table 3.5). The estimated abundance for 2016 would increase to 7,417 (80% percentile: 3,588 – 12,940) (Table 3.5) and while this is the largest increase of abundance from changing one life history parameter, this estimate remains substantially lower than what is estimated for 2016 in Chapter 2. If the age at maturity was younger, and the population was increasing at its theoretical maximum rate, then r would be substantially higher and 100% of populations would be trending upwards. However, the predicted abundance for 2016 would be 9,936 (80% percentile: 5,708 – 16,973), less than half of the abundance estimate from Chapter 2. If mean exploitation rate was calculated from the time series of removals over the period 1995-2007 instead of 1986-2007 then r would increase, and the proportion of populations increasing would increase to 0.41 (Table 3.5). An abundance of 6,865 (80% percentile: 3,768 – 11,387) (Table 3.5) would be estimated for 2016, higher than the base model but much lower than the estimate for 2016 from Chapter 2. Additionally, because

limits had been established for r , with values outside of it being discarded. Removing the upper threshold on r increased r and increased the proportion of populations showing an increase to 0.47 (Table 3.5). The estimated abundance in 2016 increased slightly to 7,075 (80% percentile: 3,876-11,709) (Table 3.5).

3.4. DISCUSSION

The results of this analysis suggest that aerial surveys are extremely unlikely to accurately estimate abundance, because the magnitude of predicted change from Chapter 2 is biologically implausible with what we know about basking shark life history. Furthermore, estimating a trend from only two points (2007 and 2016) is inadvisable as there is likely interannual variability in distribution and prey abundance that was not taken into account in this analysis. There is a need for more long-term data, with a better monitoring plan to accurately assess trends. The unfished population model – the only scenario that was not experiencing negative population growth over time – estimated an abundance of 8,273 (4,716 – 12,667) basking sharks in 2016, significantly smaller than the estimate from Chapter 2 (Table 3.4). When fisheries mortality was incorporated, the rate of population growth was negative, and only 9 to 25 % of forward projections were found to be experiencing increases in abundance over time (for the “low” and “high” abundance scenarios, respectively) (Table 3.4). Across both scenarios that included fisheries mortality, the median annual rate of change fell between -0.1 and 0 (Figure 3.5) and in the unfished population the median annual rate of change was ~ 0.02 (Figure 3.3). The required rate of change to see the abundance increase predicted in Chapter 2 would be ~ 0.3 . The population growth rate that would be required to see that level of increase in 9 years is 0.159, close to eight times the estimated value for r from life table analysis. While this analysis explored a wide-range of biologically-plausible scenarios, it was not possible to reach the predicted level of increase from Chapter 2 based on basking shark life history.

It is unlikely that the capacity for population growth in basking shark has been markedly underestimated. Basking sharks are often cited as having extremely low biological productivity (e.g., Sims 2008, Hoogenboom et al. 2015, Braun et al. 2018, Rigby et al. 2019, etc) and the estimates support this idea. Compared to the existing literature, a population growth rate of 0.0197 for an unfished population supports the idea that basking sharks are inherently unproductive and experience very slow population growth relative to most fish species (median

$r=0.43$, Hutchings et al. 2012), most Chondrichthyans (median $r=0.26$, Hutchings et al. 2012) and is more similar to estimates for cetaceans (median $r=0.07$, Hutchings et al. 2012). The estimate of r is within the range of r values given in the UK CITES proposal (2002). However, this estimate is quite a bit lower than the 0.040 population growth rate predicted by Campana et al. (2008). The lack of agreement with the Campana et al. (2008) estimate stems from the difference in the value used for natural mortality, when all of the other parameters were kept the same. Campana et al. (2008) used a natural mortality rate of 0.068 as per Pauly (2002) whereas this analysis used the median estimate from the Hoenig (1983) geometric mean regression natural mortality estimator based on longevity, estimated at 18y (16-20y). The median natural mortality rate was estimated as 0.089 (0.0735-0.1121) (Table 3.2) which is much closer to the assumption of $M=0.091$ used in the CITES calculation, and as such explains the conformity between this estimate of r and the one from the UK CITES proposal (2002). This supports the idea from CITES (2002) that basking sharks have “among the lowest natural mortality and productivity yet calculated for a fished marine species”. However, even if natural mortality is lower, it would not result in population growth rates needed to get the trend predicted from Chapter 2.

The life history parameters that were used in the life table analysis constitute large sources of uncertainty in this analysis. A sensitivity analysis was carried out by varying the ranges of some of the parameters to show if there are ways that could cause the conclusion to be wrong, i.e., that population did in fact increase by the amount suggested in Chapter 2. The largest effect came from decreasing the female age at maturity to 14 (12-16) years to match male estimated male age-at-maturity (Matthews 1950, Matthews and Parker 1950), instead of 18 (16-20) years old. However, even though decreasing the female age at maturity corresponded to the largest increase in r out of the parameters tested in the sensitivity analysis, the abundance estimate for 2016 increased to only 7,417 (3,588 – 12,940), remaining lower than the estimated abundance in 2016 from Chapter 2 (Table 3.5). If female age-at-maturity was younger *and* the population was unfished, then r significantly increased to 0.047 (0.018-0.085), close to the estimated growth rate of 0.040 from Campana et al. (2008) (Table 3.5). Nevertheless, this still corresponds to an estimated abundance of 9,936 (5,708 – 16973) in 2016, which remains substantially lower than the predicted value from Chapter 2 (Table 3.5).

If future research suggests vastly different life history characteristics for basking shark, there would be a need to revisit the effect of removals on the population. The time series of removals comes from fisheries observer records of commercial fisheries, spanning 1986 to 2007, and Campana et al. (2008) used a ratio estimator to infer the total number of annual removals. A ratio estimator relies on the assumption that there is a linear relationship between the target and bycatch species (Edwards et al. 2015). If a positive linear relationship does not exist, then ratio estimators are not a valid method for estimating bycatch (Edwards et al. 2015). Campana et al. (2008) did not evaluate for linearity but without access to this raw data, it is effectively impossible to recreate and is outside the scope of this analysis. Much of the contemporary work on estimating bycatch has moved towards using model-based estimators instead of simple ratio estimators (Moore et al. 2021). Model-based estimators of bycatch include spatio-temporal models (Thorson et al. 2015, Thorson 2019), a random-forest machine learning approach based on relationships between observed bycatch and a set of fishery-characteristics (e.g. location, bathymetry, gear characteristics, etc) (Caretta et al. 2019) and generalized linear or generalized additive modeling (GLMs or GAMs) which can be implemented in either a frequentist (Cruz et al. 2018) or Bayesian framework (Martin et al. 2015). Stock et al. (2019) evaluated a variety of spatio-temporal models for predicting bycatch, including Gaussian Markov random fields, generalized additive models and random forests, and found that random forests had better performance than the other models. Future research quantifying basking shark bycatch should move past simple ratio estimators and investigate model-based estimators of removals. Additionally, I looked at shortening the time period in which exploitation was estimated (1995-2007 instead of 1984-2007). While this information does not lend any support to the population estimate for 2016 from Chapter 2, it may be useful to consider a shorter time period over which exploitation is estimated for future research.

Other recommendations for future research outside of estimating exploitation mostly focus on improving the understanding of basking shark life history. To use life history parameters as a main data source for evaluating species at risk requires robust estimates of those parameters. There is considerable uncertainty in the life history parameters. While it is unlikely that any would change the conclusion that the trend from Chapter 2 is not feasible, improving the estimates of these parameters is essential to better understanding these species. Heupel and

Simpfendorfer (2010) make a strong argument for the need for lethal sampling of sharks to obtain life history data. The authors reason that non-lethal methods to collect the same data are in the process of being developed, but not yet accessible in the near term. For this reason, Hammershlag and Sulikowski (2011) argue for the need to prioritize development of non-lethal methods to collect life history data and the results of this study emphasize this need. Developing non-lethal methods to estimate life history parameters should be a priority, as this data is crucial for monitoring populations and developing effective conservation strategies. Additionally, more could be done to coordinate among regional scientists to maximize the biological sampling of occasionally stranded or bycaught specimens.

3.5. CONCLUSION

Life table analysis indicates that the trend predicted by Chapter 2 between 2007 and 2016 is not feasible with what is currently known about the biology of basking sharks. A population growth rate of 0.0197 (80th percentile: 0.004 - 0.037) for an unfished population is very low compared to most fish, but not unlikely given previous estimates of r in the literature. When fisheries mortality was included in the calculation of population growth rate, r decreased to -0.017 (80th percentile: -0.046 – 0.013) and 25% of the population projections between 2007 to 2030 show an increase over time. Using a lower starting population further lowered the population growth rate and decreased the percent of populations showing an increase to 9%. Recommendations for further research include improving methods for estimating bycatch and developing methods for non-lethal sampling of life history data to enhance population level assessments. Other factors outside of their biology should be considered to explain the trend predicted by Chapter 2. These simulations provided a mechanism that could be used to assess the scope for abundance changes over time.

3.6. TABLES

Table 3.1 Life history parameters used for a deterministic base run to estimate r .

Parameter	Estimate	Source
Age at maturity (yrs)	18	UK CITES Proposal (2002)
Female litter size	3	Compagno (2001)
Gestation period (yrs)	3	Compagno (2001)
Lag between parturition and pregnancy (yrs)	0.5	Assumption from Campana et al. (2008)
Maximum age (yrs)	50	Pauly (2002)
Natural mortality	0.089	Equation 4
Selectivity	2	Assumption from Campana et al. (2008)

Table 3.2 Life history parameters with assumed bounds for the Monte Carlo sampling used in the life table analysis to estimate r .

Parameter	Mean	Minimum	Maximum
Population size in 2007 ¹	7,072	0	12,164
Age at maturity (yrs)	18	16	20
Female litter size	3	2	4
Gestation period (yrs)	3	2	4
Lag between parturition and pregnancy (yrs)	0.5	0	1
Maximum age (yrs)	50	40	60
Natural mortality ²	0.089	0.0735	0.1121
Selectivity	2	1.5	2.5

¹ The “low abundance” scenario used the estimate of 3,732 (1,387-6,420) from Chapter 2 with a 36% availability bias

² Hoenig (1983) geometric mean regression natural mortality estimator for cetaceans, as a function of longevity; Equation 4

Table 3.3 Estimation of the population growth rates (r) for each of the three estimation methods. Values of r are the medians, with the 10th and 90th percentiles in brackets.

Scenario:	Method of estimating r		
	Deterministic estimate	MC Sampling: unfished	MC Sampling: fishing included
High Abundance	0.0217	0.0197 (0.004 - 0.037)	-0.017 (-0.046 – 0.013)
Low Abundance	0.0217	0.0197 (0.004 - 0.037)	-0.037 (-0.076 – -0.002)

Table 3.4 Summary of the population projections relative to the life history variability in the population growth rate (r) from MC sampling, population sizes in a given year (N_y) and the proportion of increasing populations (p) in the 1000 simulations from the forward projections. Values for r and N_y are the medians, with the 10th and 90th percentiles in brackets.

Scenario:	r	N_{2007}	N_{2016}	p
Unfished	0.0197 (0.004 - 0.037)	7026 (4183 – 11183)	8273 (4716 - 12667)	0.99
High Abundance	-0.017 (-0.046 – 0.013)	7026 (4183 – 11183)	6402 (3386 – 10795)	0.25
Low Abundance	-0.037 (-0.076 – -0.002)	3726 (1875 – 5942)	2981 (1194 – 5381)	0.09

Table 3.5 Examples of alternate scenario runs for the simulation model to evaluate sensitivity to model inputs. Values for the population growth rates (r) and N_{2016} are the medians, with the 10th and 90th percentiles in brackets. p is the proportion of increasing populations in the 1000 simulations.

Scenario:	r	N_{2016}	p
High abundance	-0.017 (-0.046 - 0.013)	6402 (3386 - 10795)	0.25
Lag time = 0	-0.015 (-0.049 - 0.017)	6524 (3198 - 10900)	0.28
Younger age at maturity (14y)	0.002 (-0.04 - 0.043)	7417 (3588 - 12940)	0.52
Younger age at maturity + unfished population	0.0474 (0.018 - 0.085)	9936 (5708 - 16973)	1.00
Exploitation calculated from 1995-2007	-0.006 (-0.034 - 0.023)	6865 (3768 - 11387)	0.41
No upper threshold on r	-0.002 (-0.030, 0.027)	7075 (3876-11709)	0.47

3.7. FIGURES

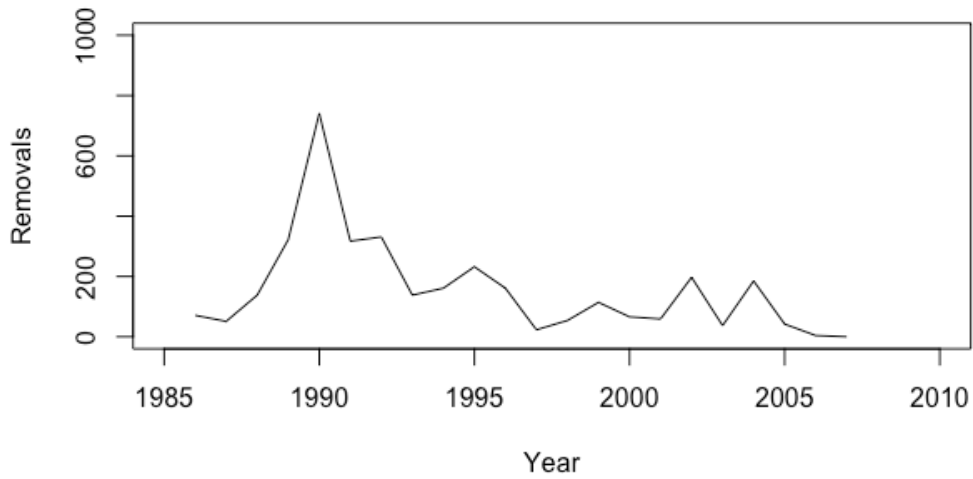


Figure 3.1 Removals (no. of animals) per year from 1986-2007 for basking sharks in Atlantic Canada. Data comes from the Scotia-Fundy and Newfoundland fisheries observer program databases, as estimated by Campana et al. (2008).

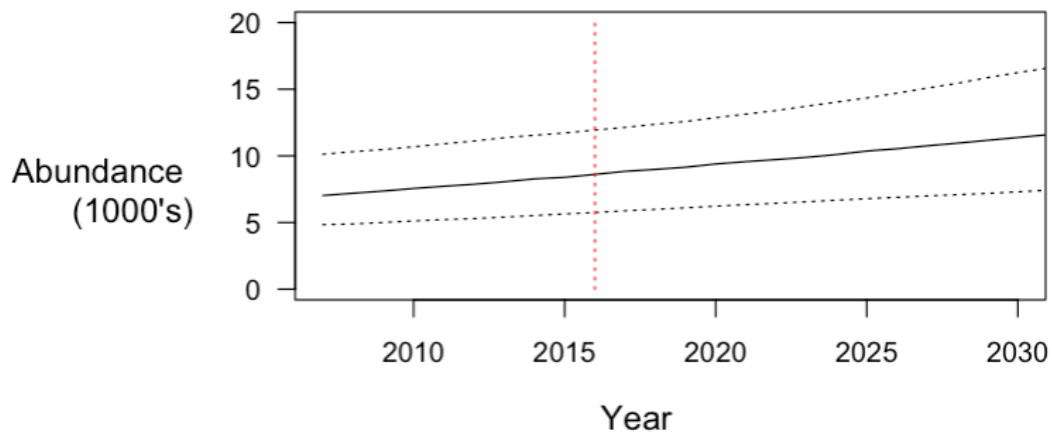


Figure 3.2 Simulated forward population trajectories (median + 80th percentiles) from 2007 to 2030 for an unfished population. The red dotted line indicates 2016.

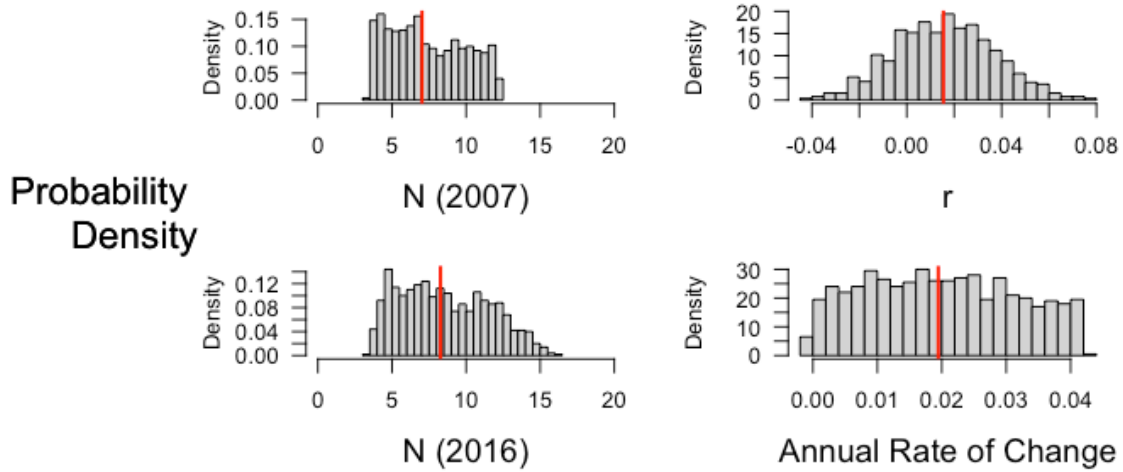


Figure 3.3 Histograms, based on 1000 simulations, of population size in 2007 and 2016, r , and the rate of change in the population size (positive values indicate an increasing population) for an unfished population. The red lines indicate the medians.

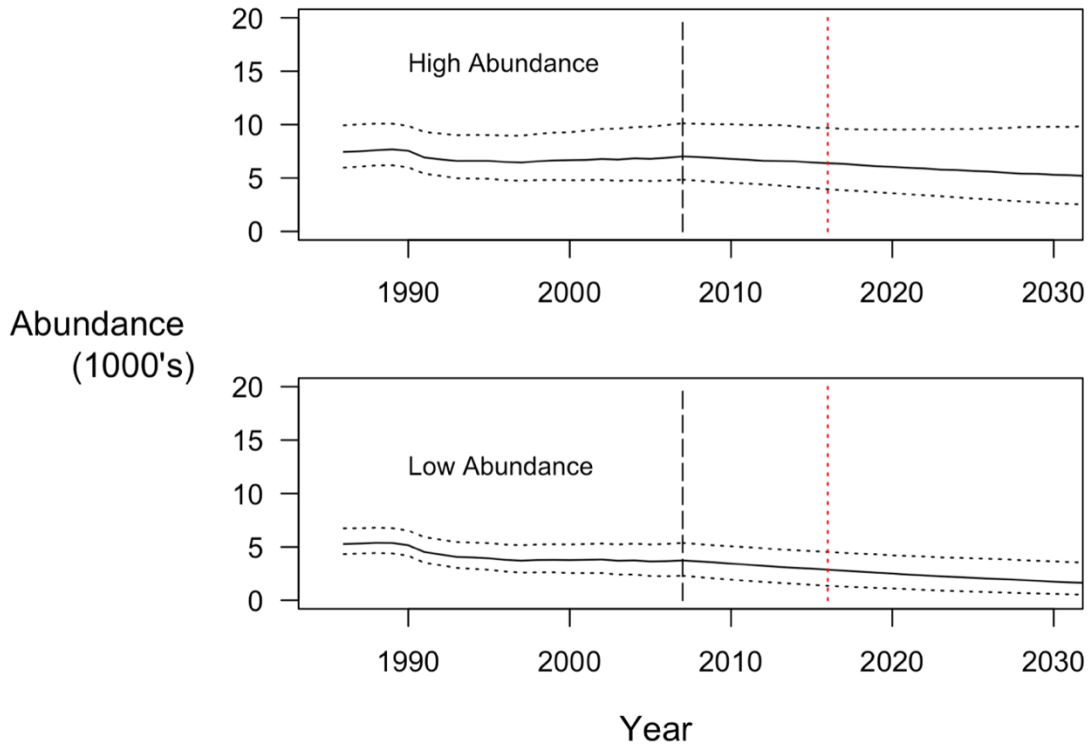


Figure 3.4 Historical declines (1986-2007) and predicted population trajectories (2007-2030) (median + 80th percentiles) based on 1000 simulated populations, of both scenarios: the higher (top) and lower (bottom) abundance scenarios. The vertical lines indicate years of interest: the given starting population in 2007 is indicated by the black dashed line, and the red dotted line indicates 2016.

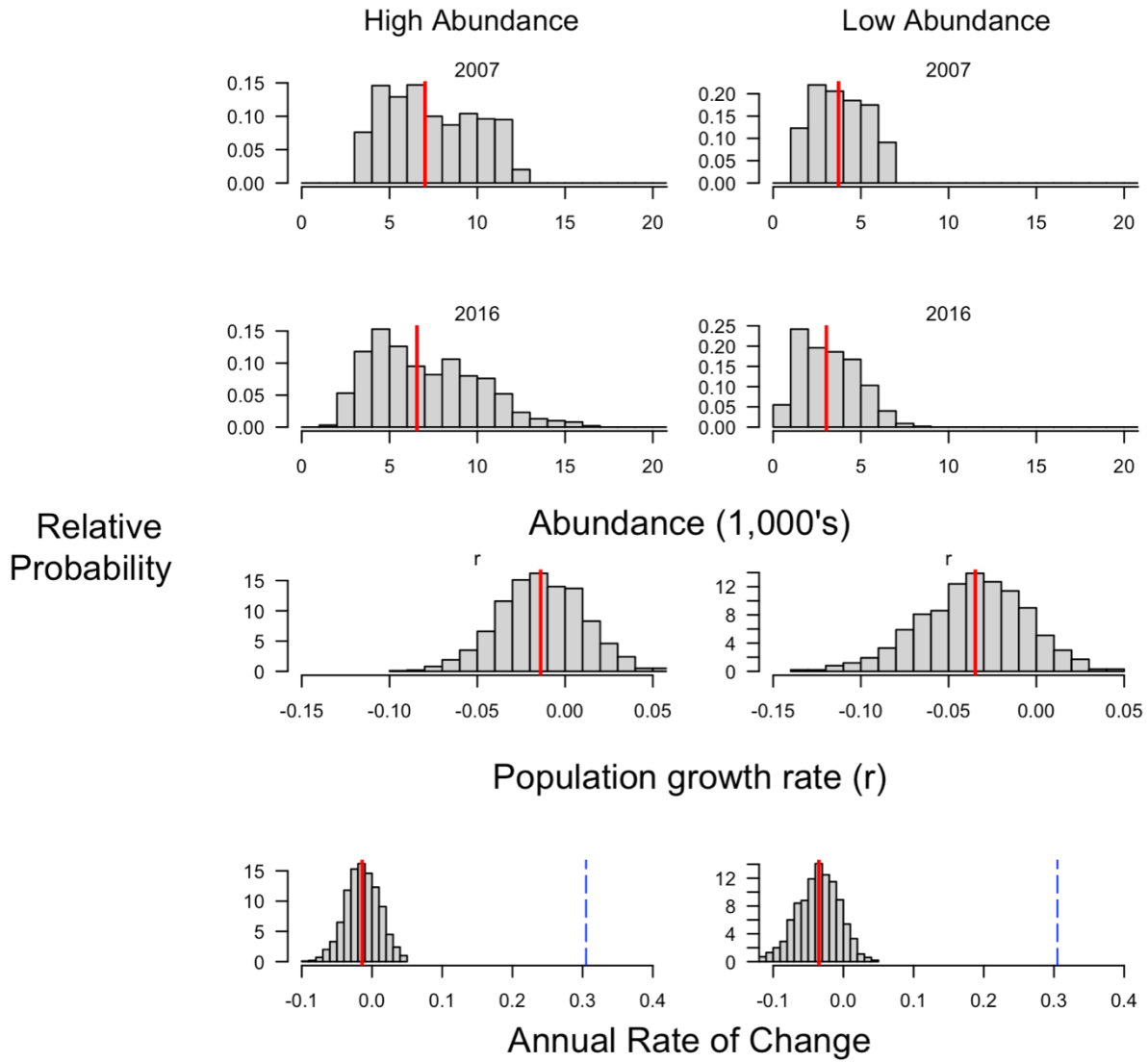


Figure 3.5 Histograms of population size (in the 1,000s) in 2007 and 2016 as well as the population growth rate (r) and the annual rate of change (positive values indicate an increasing population) for both scenarios: the higher (left) and lower (right) abundance scenarios. The red lines on the histograms indicates the medians, while the blue dashed line on the rate of change histograms indicates the level of annual change required for the abundance estimate from Chapter 2.

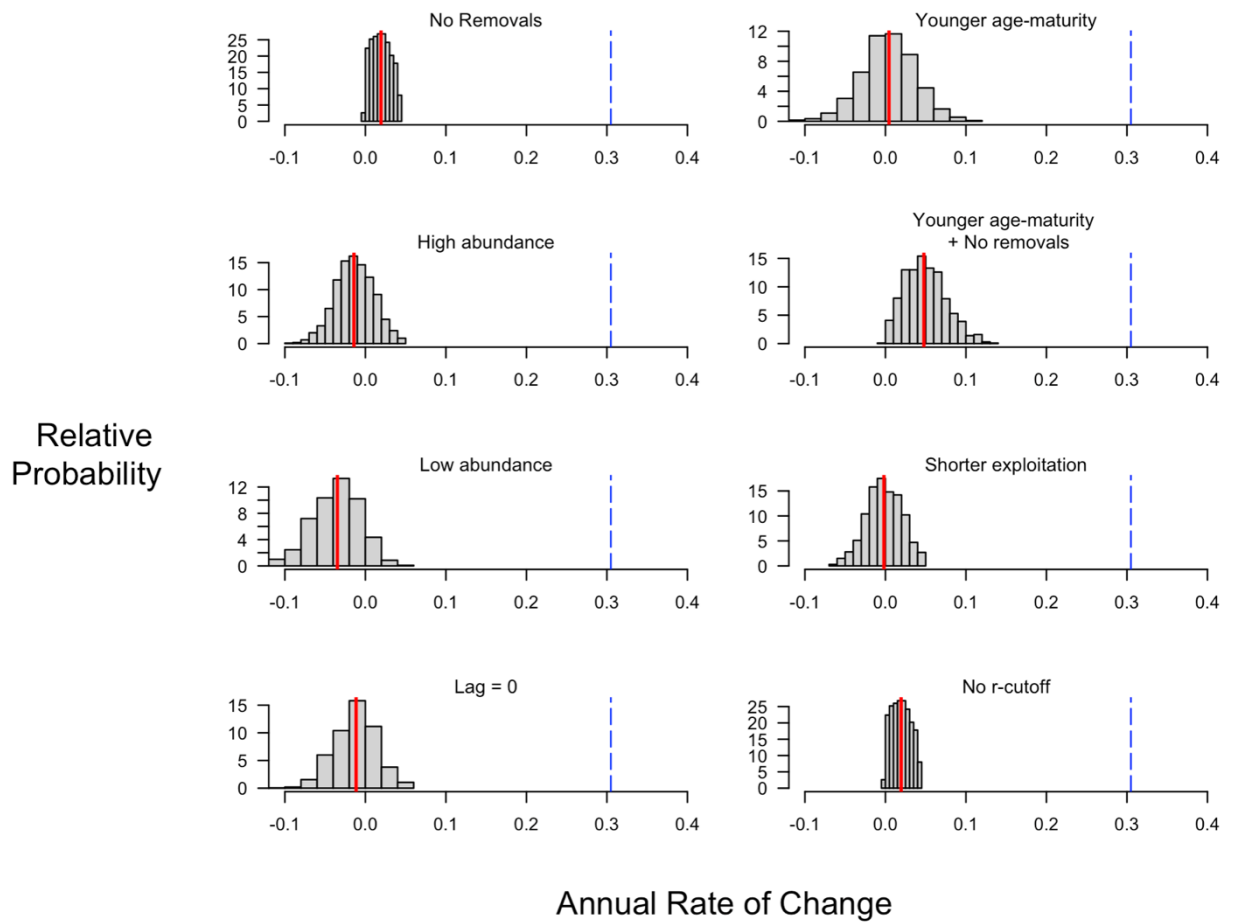


Figure 3.6 Histograms of the annual rate of change (positive values indicate an increasing population) for all scenarios. The red lines on the histograms indicates the medians, while the blue dashed line on the rate of change histograms indicates the level of annual change required for the abundance estimate from Chapter 2.

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CHAPTER 4: GENERAL DISCUSSION AND CONCLUSIONS

4.1. OVERVIEW

This work presented in this thesis estimates the abundance of basking sharks in Atlantic Canadian waters in 2007 and 2016, and then attempts to infer the validity of the predicted trend in abundance with what is currently known about basking shark life history. Understanding the abundance and trends in abundance is crucial for effective management and is required as, in 2022, it has been over ten years since the last COSEWIC assessment (2009). The Atlantic Canadian population of basking sharks is designated Special Concern by COSEWIC (2009). These results highlight the need for continued monitoring, collaboration between regional scientists along the coast of the western North Atlantic, improvement in methods to estimate abundance, and the development of non-lethal sampling for determining life history parameters.

It is not immediately obvious if one or both of the abundance estimates from Chapter 2 is inappropriately high or low, or if other factors outside the scope of this analysis are influencing the results. If abundance in 2007 was underestimated for example, a good estimate from 2016 could lead to an inappropriately high trend. As it stands, the trend predicted by Chapter 2 was shown not to be feasible within the constraints of what is currently known about the life history of basking sharks in Chapter 3. This chapter explores possible reasons and other factors that may account for the nonconformity between the two chapters. Discussed here are the strengths and weaknesses of both methods of population monitoring (i.e., (i) aerial surveys with distance sampling and (ii) life table analysis), as well as other factors that were not taken into consideration that could explain the trend predicted by Chapter 2. We need robust methods to evaluate abundance and to track changes over time for species at risk to make effective conservation decisions.

4.2. ABUNDANCE ESTIMATION FROM AERIAL SURVEYS

The abundance estimate of Chapter 2 comes from fisheries-independent data from aerial surveys, widely considered to be higher-quality than fisheries-dependant data (Pennino et al. 2016). Fisheries-independent data is often standardized and designed with the target species in mind (Pennino et al. 2016). However, surveys are extremely costly and are often restricted in spatial and temporal coverage. For example, as discussed in Chapter 2, the lack of temporal

coverage of the Bay of Fundy (BoF) region in 2016 is problematic and could suggest an underestimation of the true abundance of basking sharks in the BoF region (Section 2.4.). Additionally, while surveys are considered more reliable than opportunistic sightings (e.g., from whale watching operations), it is still unclear if one or both of the estimates from Chapter 2 is inappropriate.

A number of simplifying assumptions had to be made to make use of the aerial survey data. Surveys are specifically designed to sample randomly with respect to the distribution of the study animal and contain a sufficient number of lines (Strindberg et al. 2004). The designed pattern of the transect lines and their orientation across the study area are assumed to ensure equal inclusion probabilities (Buckland et al. 2015, Thomas et al. 2010). Distance sampling is then preferred over strictly design-based estimation (Section 2.2.2.1) to lessen the reliance on perfect survey design and deal with *perception bias*, the assumption that all animals present are detected (Thomas et al. 2010). However, this relies on the assumption that detection with respect can be modelled as either a half-normal or a hazard-rate shaped detection function. This analysis went one step further and also tested a fully-model based estimation method (Section 2.2.2.3) that allowed density to be modelled as a function of covariates, instead of directly extrapolating the density of animals in the study area from the number of detections in the sampled area. While this method may be more appropriate when there is evidence of heterogenous habitat use (as in Siders et al. 2013) or aggregation behaviour (as in Crowe et al. 2018), it relies on the assumption that the numbers of animals available to detect are from a Poisson distribution (Royle et al. 2004).

The characteristics of the data available for this analysis had limitations that should be considered and improved for future studies. Both methods of distance sampling (hybrid- and fully-model based) relied on the assumption that detection on the line should be certain (Buckland et al. 2015). The data from 2016 violated this assumption and both models struggled to account for it. In the discussion of Chapter 2, a new detection function shape was recommended, the double-logistic, and restated here is the importance of investigating alternate shapes for the detection function in future research to improve estimates when incomplete detection on the transect. Becker and Quang (2009) successfully used a gamma-shaped detection function for line transect data of brown bears (*Ursus arctos*, Linnaeus 1758). Additionally,

Buckland et al. (2001) suggest that at least 60-80 animals should be detected for the reliable estimation of abundance through transect-based distance sampling. The 2007 data only had 53 sightings in total, suggesting that sample size may be too small to provide a robust estimate of abundance. Lastly, in the 2007 data, all basking sharks were detected as individuals, and there were very few sightings in 2016 with a group size larger than one (2-12 individuals: <20%), suggesting that using group size as a covariate for the 2016 data may be highly unbalanced. As a result, group size was excluded as a covariate for the models for both years. This goes contrary to published observations of large but infrequent aggregations (Kenney et al. 1985, Skomal et al. 2004, Crowe et al. 2018) and anecdotal knowledge (Heather Bowlby, pers. comm.) and suggests that data that shows basking sharks as entirely solitary may underestimate abundance. For these reasons, the survey data may not be an accurate representation of status.

The assumed availability bias parameter is a key limitation in accurate abundance estimation from aerial survey data for basking sharks. Recall that availability bias refers to the proportion of time spent at the surface, and is used in the analysis as a multiplicative factor. This analysis presented two equally plausible estimates of abundance based on availability biases from Sims et al. (2003a) and Westgate et al. (2014), however this parameter is nonidentifiable and uncertain from the literature. Direct estimates of basking shark availability bias range from $15 \pm 10\%$ (Siders et al. 2013) to 36% (Sims et al. 2003a). Curtis et al. (2014) found that basking sharks spent 66.4% of time in the upper 25 m of the water column, with 43% of that time spent between 0 to 10 m. Additionally, they found that primary productivity and depth are the strongest predictors of basking shark movement (Curtis et al. 2014). Sims et al. (2005) found that basking sharks near frontal zones spent 60% of their time near the surface during the day, and <1% of their time near the surface when in well-stratified waters. All of this is to say that availability bias is highly uncertain, highly influential on abundance estimates and may be dependant on physical/bathymetric factors or zooplankton abundance. To combat this, a spatially-varying availability bias is recommended to be investigated for future studies of this nature. If basking sharks spend more time near the surface near frontal zones, in areas of high zooplankton concentrations or in areas with high primary productivity, then it would be logical to have the availability bias reflect that instead of assuming homogenous habitat use. While it

outside the scope of this analysis, a spatially-varying availability bias could be a promising avenue for future research and has applications beyond basking sharks.

4.3. LIFE TABLE ANALYSIS

The life table analysis method is well-established and often used in shark research (McAllister et al. 2001, Cortés 2002, Campana et al. 2008, Hutchings et al. 2012, Cortés 2016, Kacev et al. 2017, Bowlby and Gibson 2020). Compared to data from aerial surveys, which is more often than not used for mammals in the marine environment that rely on the surface to breathe, life history analysis is a staple of fisheries science and has been widely tested for a variety of fish species (Hutchings et al. 2012). As such, there is a wealth of research on the strengths of this method and its major limitations center more on the selection of data put into the model.

For basking sharks, there is a limited understanding of life history. While the idea that basking sharks have long life histories is well accepted (Sims 2008) and previous research suggests that populations would be expected to increase slowly in size (UK CITES 2002, Campana et al. 2008), there is considerable uncertainty around the individual life history parameters (age-at-maturity, fecundity, mortality and survivorship, longevity) (Sims 2008). Most of these parameters are difficult to collect data on without lethal sampling (Heupel and Simpfendorfer 2010) and even when specimens are collected, estimation of certain parameters can prove challenging (e.g., aging; Natanson et al. 2008, Calliet 2015). The parameterization of the model used in this analysis is described in detail in section 3.2.2, but it remains important to underscore the lack of confidence around each parameter. This analysis used Monte Carlo (MC) sampling to incorporate the uncertainty around parameter values. A sensitivity analysis was carried out to investigate the effects of changing individual parameters on the population growth rate to alleviate the reliance on the estimated parameters and see if the predicted trend from Chapter 2 was possible under alternate scenarios. However, this analysis should be revisited if new information on basking shark life history is published as this raises questions on the utility of using life table analysis when so many fundamental parameters are uncertain.

Additionally, as discussed in section 3.4, if future research updates life history characteristics for basking sharks, there would be a need to revisit the removals series and the

effect of removals on the population. This analysis used the removals series from Campana et al. (2008), based on a ratio estimator from fisheries observer records spanning 1986 to 2007 (described in section 3.2.3). Much of the contemporary work on estimating bycatch has moved beyond ratio-estimators and towards model-based estimators (Moore et al. 2012) and future research on basking shark removals should do the same. Quantifying fisheries mortality (in this case, bycatch mortality) accurately is imperative to understanding not only the effects of fisheries on basking sharks, but also to effectively monitoring the trends in abundance.

4.4. OTHER CONTRIBUTING FACTORS

Considering the exceptionally high population estimate of Chapter 2, the conclusion from Chapter 3 that the predicted trend between 2007 and 2016 is not feasible within what is known about the reproductive biology of basking sharks. If this magnitude of increase is not feasible within the rate of intrinsic population growth, then one should look to consider if there are other factors that may cause the predicted increase in abundance. One of the major limitations to this analysis is that the population was assumed to be closed (i.e., no immigration, emigration). It is not outside of the realm of possibility that the estimated increase in abundance from Chapter 2 could be due to increased immigration into the population as a result of abiotic and biotic factors that were not taken into account in this thesis.

While basking sharks were previously thought to exhibit a high regional fidelity and form local populations, as previously discussed, there is also evidence that populations may freely mix and migrate (see Sections 1.4.2. and 1.4.4.). Campana et al. (2008) suggests that it is likely that basking sharks in Atlantic Canada are part of the same population as ones in the US. Basking sharks have been tracked moving rapidly between regions over a period of a few weeks (Sims et al. 2003b) and their movements were shown to primarily be driven by foraging for high densities of zooplankton (Sims et al. 2006). Basking sharks tracked in the UK were shown to freely mix (Sims et al. 2003b) and tracking studies on the eastern coast of the US found basking sharks making extensive north-south migrations (Skomal et al. 2004, 2009, Skomal 2005). Basking sharks have been found spending late winter and early spring moving southward and in deeper waters than normal (>600m) (Braun et al. 2018, Doherty et al. 2019). Evidence of trans-Atlantic mixing has been reported by Gore et al. (2008) and Johnston et al. (2019). It is therefore not likely that the population of basking sharks in Atlantic Canada can be considered a truly

geographically closed population. As such, it may not be appropriate to use a survey on a component of the population to understand the trends in abundance across the entire population of basking sharks along the Atlantic coast of North America. In the future, more could be done to coordinate among regional scientists and conduct surveys all along Atlantic coastline of North America within the same time frame. Continued monitoring across the entire range of basking sharks in the western North Atlantic should help to determine if the predicted increase in abundance from this thesis is truly demonstrating that the population is rapidly increasing in abundance or if this is a result of a distributional shift.

Population trends can be influenced by a number of factors including fishing, biological interactions and environmental factors (Crawford 1991). Recall that when conditions are unfavorable, whether it be due to fishing and bycatch mortality, biological interactions or environmental factors, an apparent shift in abundance could occur. This could be due to change in a population's growth pattern, its growth rate may decrease, the population could shift its distribution to an area with more favorable conditions, or the distribution of the population within the environment may change (Krebs 2001, Cain et al. 2008). Discussed over the next few paragraphs are possible biological and environmental factors that may contribute to the trend predicted by Chapter 2.

One of the major factors that was not incorporated in this analysis is the tight association between basking sharks and their zooplankton prey. Their preferred prey is Calanoid copepods (Sims and Quayle 1998, Cotton et al. 2005) and the rate of basking shark observations per hour has been related to prey density (Sims 2008). The sharks spent twice as long in areas with zooplankton densities $>3 \text{ g/m}^3$ then in areas with $<1 \text{ g/m}^3$ (Sims and Quayle 1998) and there is evidence to suggest that the amount of time basking sharks spend at the surface is proportional to zooplankton density in surface waters (Sims et al. 2003a). Sims and Quayle (1998) tracked basking sharks responding to zooplankton gradients and selectively choosing the patches with the highest density. In his review of basking shark biology and ecology, Sims (2008) goes as far to say that “the abundance of zooplankton must be assessed in parallel with surveys for basking sharks if the method of finding sharks depends on their surface occurrence”.

It may be then, that the increased number of basking sharks sighted in 2016 was due to enhanced surface zooplankton abundance rather than deriving from any other factor. This could mean that if surface zooplankton abundance was not as high in 2007, the sharks could have been spending more time offshore or at depth, both of which would make them unavailable for detection in the aerial surveys. There is also the potential that zooplankton were more plentiful in the Gulf of Maine (i.e., outside of the study area) during the summer of 2007 and the sharks simply followed it. Conversely, sharks that would have been in US waters in 2007 may have followed high zooplankton densities to Atlantic Canadian waters in 2016. However, Sorochan et al. (2019) suggests that copepod abundance has declined in the last two decades in Atlantic Canadian waters and in the Gulf of Maine. Without an assessment of zooplankton abundance (or of chlorophyll-*a* as a proxy) in parallel with the surveys, it is nearly impossible to know if the population of basking sharks is truly increasing rapidly in abundance or if a combined US-Canadian population is simply migrating back and forth across the maritime boundary.

Furthermore, because basking sharks are so tightly associated with zooplankton, other related biological interactions may influence the abundance of basking sharks in a particular year. For instance, both herring (*Clupea harengus*, Linnaeus 1758) and North Atlantic right whales (*Eubalaena glacialis*, Müller 1776) also feed on Calanoid copepods, and as such, changing levels of competition with either of these species may also affect basking shark abundance in a given year. Herring are commercially fished in Atlantic Canada (DFO 2011), so increased take of herring in a given year in say, the Bay of Fundy, may have increased the availability of copepods during that year. North Atlantic right whales are considered endangered in Canada (COSEWIC 2014) and critically endangered by IUCN (Cooke 2020) and there is evidence of a distributional shift out of the BoF (Davies et al. 2019). Reduced competitive pressure on copepods from N.A. right whales in the BoF may increase availability of copepods for basking sharks. Increased availability of copepods in a given year could increase abundance estimates of basking sharks for that year.

Additionally, climate change has been predicted to change the distribution and abundance of copepods (Richardson 2008) which could lead to significant changes on the distribution of basking sharks, and therefore the assessed abundance in Atlantic Canadian waters. Increased nutrient outflow from cities along the St. Lawrence River (Shindler and Valentine 2008), and

from along the eastern US seaboard and up the Gulf Stream, may also locally increase zooplankton abundances due to increased fertilization, which in turn would affect abundance estimates of basking sharks. Further, Cotton et al. (2005) found that basking sharks were highly correlated with sea-surface temperature (SST) on long time scales, and suggest that climate-driven change in SST could alter basking shark distribution and therefore abundance in a local area. Climatic oscillations are also correlated with basking shark presence (McInturf et al. 2022), which suggest that predicting trends in abundance from a time series of only two years may be highly inappropriate. Future studies that aim to predict trends in abundance should consider a larger sample size. Further, future research could be focused on how climate change may alter the distribution and abundance of basking sharks in coastal regions.

4.5. CONSERVATION EFFECTIVENESS AND RECOMMENDATIONS

Many recommendations for future research and management efforts have been made throughout this thesis. This includes increased temporal coverage of surveys, collaboration between regional scientists along the western North Atlantic coastline, accounting for heterogenous habitat use, exploring an alternative shape for the detection function in distance sampling methods (double-logistic, see section 2.5), exploring model-based estimators of bycatch, and developing non-lethal methods for life history sampling. In this chapter, a spatially-varying availability bias was also proposed, either based on physical factors (bathymetry) or biological interactions (e.g., zooplankton distribution and abundance). Outside of these suggestions that have already been discussed in previous chapters, the most pressing recommendation is to incorporate information on zooplankton alongside estimates of basking shark abundance. Information on copepod abundance and distribution could also be used as a covariate on the count model in a density-surface modelling (DSM) distance sampling analysis. This is easier said than done, as the methods for surveying copepods are not the same as those for surveying basking sharks, and the coverage of copepod abundance in the Atlantic Canadian study area is not complete, and real-time monitoring is expensive. However, it would greatly improve the reliability of basking shark abundance estimates.

It appears that a significant change in fishing mortality occurred after the 1992 moratorium on cod fishing (Myers et al. 1997). Regardless of these environmental and behavioural conditions, at the estimated rate of removals from 1995-2007 (90 animals/yr) life

table analysis in Chapter 3 suggests that, if the 2007 population estimate is correct and the population is indeed closed, without further intervention, the population is declining over time. Management efforts therefore should be focused on eliminating the last vestiges of mortality due to bycatch in fisheries. Fortunately, as basking sharks generally tend to inhabit coastal regions which typically fall within the exclusive economic zones (EEZ, 200 nmi) of countries including Canada, management efforts have a higher probability of success compared to species that live predominantly outside of EEZ's and are subject to unregulated fisheries in international waters.

The results of this analysis suggest that overall, the population of basking sharks in Atlantic Canada are increasing, despite the predicted negative trend with the inclusion of fishing mortality in the life table analysis. It is unclear if the estimated abundances of either (or both) 2007 or 2016 from Chapter 2 are inappropriately high or low, and if the removals series from 1986 to 2007 as estimated from Campana et al. (2008) is representative of the current level of removals. If abundance was higher than ~7000 individuals in 2007, or if fishing mortality is now effectively negligible, then all simulated populations of basking sharks would show an increase in abundance over time. Given the long generation time of the species, a lag between enacted conservation measures and a quantified increasing trend is to be expected. The predicted increasing trend therefore could be a result of the CITES listing in 2002 and the CMS listing in 2005, or conservation actions taken to protect other species, tighter fishing regulations, and global efforts to protect ocean ecosystems and reduce pollution. This suggests that current conservation measures have been effective thus far, though the continued monitoring of this species remains crucial.

4.6. CONCLUSIONS

Taken together, Chapters 2 and 3 present a somewhat confounding picture of the abundance of basking sharks in Atlantic Canada. It is unclear if the estimates of abundance for 2007 or 2016 or both are inappropriately high or low as a number of assumptions were invoked in this analysis, or if the trend is a result of factors outside of the scope of this analysis.

As the trend predicted by Chapter 2 was not feasible within the constraints of what is known about the biology of basking sharks, other factors must be taken into consideration. The analysis in this thesis assumed a closed population, with no immigration or emigration. It is more

than likely that the Atlantic Canadian and US populations of basking sharks are continuous, and the sharks freely migrated across the maritime border, possibly following their zooplankton prey. The distribution and abundance of their preferred prey may be responding to climatic shifts by altering their distribution, increased eutrophication by nutrient outflow may be inflating zooplankton abundance, or there may be shifts in competitive interactions with other species that prey on zooplankton that may be advantageous to basking sharks.

To improve future estimates of basking shark abundance in Atlantic Canada, it is imperative to assess zooplankton abundance in parallel, to truly understand if predicted trend from Chapter 2 is indeed representative of significant growth in the population size of basking sharks, or an artifact of year-to-year variation in their preferred prey. A spatially-varying availability bias was also proposed for future research.

When historical removals were included into the calculation of the per capita population growth rate, only 25% of projected population were showing an increase in abundance over time, suggesting that the population is declining. Management actions should therefore focus on continuing to monitor and eliminate bycatch, as the life history parameters of basking sharks make it so that they cannot sustain even moderate levels of fishing mortality. However, the results of this analysis suggest that basking sharks in Atlantic Canadian waters are increasing in abundance, and that conservation measures thus far have been effective. Basking sharks in Atlantic Canada are considered Special Concern by COSEWIC, continued monitoring of this species is vital.

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