STRIPED BASS *MORONE SAXATILIS* (WALBAUM,1792) POPULATION

DEMOGRAPHICS AND MIXING IN THE BAY OF FUNDY

by

Lita L. O'Halloran

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The examining committee for the thesis was:

_____

Dr. Rebecca Casey, Chair

_____

Dr. Roger A. Rulifson, External Examiner

_____

Dr. Anna Redden, Internal Examiner

_____

Dr. Trevor Avery, Supervisor

_____

Dr. Rodger Evans, Department Head

This thesis is accepted in its present form by the Division of Research and Graduate Studies as satisfying the thesis requirements for the degree Masters of Science in Biology.

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_____

Author

_____

Supervisor

_____

Date

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Abstract

The use of population dynamics in fisheries management is a crucial tool to understand trends and appoint sustainable harvest rates. In the Bay of Fundy (BoF), Striped Bass *Morone saxatilis* is a highly prized recreational fishery and aboriginal FSC fish. Striped Bass are found throughout Minas Basin, where they are believed to mix with U.S.A. Striped Bass populations. Mixing of these populations creates difficulties in determining population structure which is required for implementation of effective conservation actions for Canadian stocks. Here we use catch data from 1981–2019, as well as mark-recapture to answer information gaps on population structure. Specifically, we address information gaps on movement, length frequency, weight-length relationships, and estimating growth using tag data. Our data suggests that 99.5% of bass tagged over 7 years did not leave the Minas Basin. Growth models were comparable to traditional length-at-age models with Francis and Wang models outperforming Fabens models. 183 tissue samples were analyzed using next generation sequencing (NGS), single nucleotide polymorphisms (SNP)s and microsatellites and summary of mark-recapture studies since the 1930s to determine the presence and abundance of other populations in the Minas Basin, and genetic origin of bass in Labrador and Annapolis River. Of the bass chosen for higher probability of migrancy analyzed using SNPs, 99% were of Shubenacadie River origin, with one U.S.A. migrant, and no hybridization detected. Proportions in Annapolis River were 2.4% for both Saint John River and U.S.A. origin and 95.2% Shubenacadie River origin. Labrador bass (n=8) were of Miramichi River origin, which is the first genetic evidence of Striped Bass expanding past its native northern range. Across the entire Atlantic coast into the BoF 48 (0.002%) transboundary recaptures have occurred from published studies using over two million external tags. These results indicate that U.S.A. migrants present in the Minas Basin are insignificant and the adjustment necessary for the Shubenacadie River population would be negligible.

Abbreviations and Symbols

AIC	Akaike's Information Criterion
ALS	American Littoral Society
A-R	Albemarle Sound-Roanoke River
ASMFC	Atlantic States Marine Fisheries Commission
BoF	Bay of Fundy
cm	centimeters
CMR	Capture-Mark-Recapture
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CPUE	catch per unit effort
DFO	Department of Fisheries and Oceans Canada
ddRAD	double-digest restriction-site associated DNA
DU	Designatable Unit
EtOH	ethyl alcohol
FL	Fork length
FSC	Food, Social, and Ceremonial
GSMFC	Gulf States Marine Fisheries Commission
IUCN	International Union for Conservation of Nature and Natural Resources
K	Brody growth rate coefficient; provides shape of model of length-at-age
Kg	Kilogram
L_∞ / Linf	Asymptotic mean length
Lm	Length at marking
Lr	Length at recapture
L_t	expected or average length or weight at time (or age) t
M	metre
Mg	microgram
mtDNA	Mitochondrial DNA
NB	New Brunswick
NGS	Next-generation Sequencing
NOAA	National Oceanic and Atmospheric Administration
NS	Nova Scotia
PEI	Prince Edward Island
QC	Quebec
RFA	Recreational fishing area
RFLP	Restriction Fragment Length Polymorphisms
SARA	Species at Risk Act
SBRT	Striped Bass Research Team
SGoSL	Southern Gulf of St. Lawrence
SNP	Single Nucleotide Polymorphisms
t_0	Theoretical time at which mean length is zero (0)
TL	Total length
µL	microlitre
U.S.A	United States / United States of America
YOY	Young-of-year

Acknowledgements

Chapter 1

Striped Bass

Focus

The focus of this thesis is on populations of Striped Bass present in the Bay of Fundy (BoF), specifically Minas Basin, Canada. Aspects of morphology, physiology, distribution, significance, and other characteristics were summarized for the broader geographic range of the species.

Morphology and Function

Striped Bass, *Morone saxatilis* (Walbaum, 1792*)*, is an anadromous fish in the Order Perciformes, and one of six species in the Family Moronidae, which represents temperate basses (Heemstra, 1995). Perciformes have more evolutionarily-derived morphological forms with deep bodies (dorso-ventrally elongated) and lateral compression. The pectoral fins are placed more dorsally on the body, and the pelvic fins are located thoracically beneath the pectoral fins; these positions allow for rapid turning and maneuvering (Bone & Moore, 2008). Striped Bass have two dorsal fins, one spiny with 9–11 spines, and one soft with 10–13 rays, separated at the base and approximately equal in length. There is no adipose fin, and the anal fin has 1–3 spines and 9–12 rays. The caudal fin is large, slightly forked, and homocercal (Hart, 1973). The fusiform body shape, fin placement, and powerful musculature allows streamlined, fast swimming with cruising swimming speeds of 0.41 m/s (Freadman, 1981; Bone & Moore, 2008). Spines are present on the posterior edge of the operculum to help pass water over the gills and, as with other spines, provide protection from predation. Ctenoid scales provide resistance

against penetration and abrasion and have miniature spines on the exposed edge that help maintain laminar flow (Zhu *et al*., 2011; Hauser, 2014).

Striped Bass range in colour dorsally from light green to olive, blue, brown to almost black, ventrally they are white (Fay *et al*., 1983). Laterally they are silver with seven to eight stripes that run longitudinally from behind the operculum to the base of the tail, one of which always overlays the lateral line. This striped pattern is a disruptive coloration, which breaks up the shape or outline of the body. The dark to light colouration provides camouflage as countershading. Striped Bass sometimes have a variable stripe pattern: in some individuals the stripes are broken, and this is anecdotally and previously believed to differentiate stocks (Eldridge, 1988), but no genetic analysis has been completed to confirm this idea. However, broken stripes can indicate hatchery-raised bass in the U.S.A. and for Striped Bass and White Bass (*M. saxatilis* x *M. chrysops*) hybrids (Fullner *et al*., 2007; Waldman and Vecchio, 2011).

Striped Bass have a triangular shaped head with its lower jaw projecting slightly anteriorly over the upper jaw and extending posteriorly below the eye (Fay *et al.*, 1983). The eyes are rather large in comparison to the size of its head, because feeding is primarily assisted with sight, and are located slightly dorsally allowing better upward vision for surface feeding or hunting prey from below (Pennsylvania Board of Fishery Commissioners, 1892). Bass mouths are large for enabling them to consume large prey and are set on an oblique angle for improved feeding from below (Henshall, 2015). Inside its mouth is has three small bristle-like sets of teeth -- two parallel patches of teeth at the base of the tongue, numerous small vomerine teeth, and maxillary teeth along the jaw -- all of which are used for securing prey rather than biting or tearing (Maine Board of

Agriculture, 1862; Fay *et al*., 1983; Kahnle *et al.*, 1991; Burton & Burton, 2017). The perciform jaw is ideally modified to produce a suctioning effect when the lower jaw protrudes, and this action is used in prey capture (Burton & Burton, 2017).

Native Canadian and U.S.A. populations of bass share the above characteristics, but some size and sexual maturity traits vary between bass that are found in its northern range of Canada, and its U.S.A. counterparts. In all populations, bass are a long-lived fish, living up to 35 years. Females grow larger than males in all populations and bass over about 14 kg in U.S.A. coastal populations are likely female (Bigelow and Schroeder, 1953). In the U.S.A., sexual maturity is reached at an earlier age whereas Canadian bass tend to reach sexual maturity 1–2 years of age later than U.S.A. bass (Setzler *et al*, 1980; Rulifson and Dadswell, 1995; Bradford *et al*, 2015). World records of bass have reached as high as 56.6 kg, with many others over 45 kg in North Carolina in 1891, but in Canadian waters the documented weight record is 28.5 kg in the Saint John River in 1979 (Seeley, 2016). In the U.S.A. bass can reach lengths of 2 m, but they rarely reach 1 m in Canada as many do not survive long enough to grow longer (COSEWIC, 2004; ASMFC, 2016; DFO 2016).

Distribution

Striped Bass are native to the Atlantic coast of North America ranging in the north from the St. Lawrence River estuary in Canada south to the St. Johns River in Florida, U.S.A (Figure 1; DFO, 2016a). Bass are also native to the Gulf of Mexico but are characterized separately due to its limited coastal interactions (GSMFC, 2006). Within its native range, cultured progeny from geographically and genetically distinct populations have been introduced to increase abundance in other native rivers, including

the Gulf of Mexico, throughout the Atlantic U.S. coast, and the St. Lawrence River (Rulifson and Laney, 1999; GSMFC, 2006; Robitaille *et al*., 2011; Woodroffe, 2011).

Striped Bass has recorded to expand from its native range (Karas, 2016), but in August 2017 individuals were discovered in commercial salmon nets along the coast of Labrador (Trevor Avery, pers. comm., 2017; Bartlett, 2017; Andrews *et al*., 2018; DFO, 2018a; NunatuKavut, 2018; Andrews *et al*., 2019). One of these vagrants was tagged as part of the Department of Fisheries and Oceans Striped Bass monitoring program in the Miramichi River. In March 2018, dead bass were found in rivers and estuaries in northern Labrador, suspected to not survive overwintering (Corey Morris, Department of Fisheries and Oceans Canada, pers. comm., 2018), but live ones were found in similar areas about a week later (Patricia Nash, NanatuKavut, pers. comm., 2018).

Striped Bass have been successfully introduced along the U.S.A.-Canada west coast, and freshwater lakes in U.S.A., Ecuador, Russia, Iran, Mexico, Hawaii, South Africa, and Turkey (Scott and Crossman, 1973; Rulifson and Laney, 1999; Robitaille *et al*., 2011; Woodroffe, 2011; Rainer, 2016). Unsuccessful introductions have also occurred in Latvia, Argentina, Japan, USSR, China, and Israel (Rainer, 2016). In Canada, the Miramichi River population of bass was used to populate a declining population in the Gulf of St. Lawrence (Robitaille *et al*., 2011). Other than this introduction, no other known anthropogenic introductions of bass have been recorded in Canada.

Populations and Management Units within Canada and the U.S.A.

Population and Management Unit Terminology

The word "population" in fisheries literature is not always used in a consistent manner. For Striped Bass, population refers to geographically distinct areas or describe

bass originating from different spawning rivers. Generally, populations are genetically

distinct (Robinson and Courtenay, 1999). In Canada, populations are typically referred by

their spawning river (e.g., St. Lawrence River population), but for management purposes,

populations are often combined in regions where genetic populations intermix because of

the highly migratory nature of bass. These mixed populations are referred to most often

as DFO management units, by designatable units (DU), or, generally, as 'stocks', but in

many documents, these same DUs are referred to as populations. DFO management units

correspond with geographically and genetically distinct populations with one spawning

river, except for the Bay of Fundy (BoF) DU, which has three historical spawning rivers,

each of which was genetically distinct (Government of Canada, 2016). A DU is a term

used by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and

is defined as a "taxonomic unit below the species level to conserve biological diversity of

geographic and genetically distinct populations" (COSEWIC, 2016). For this thesis, the

term population is used for a distinct genetic population and DU for both DFO

management units and COSEWIC designatable units.

Canada and U.S.A. populations

Along the U.S.A. Atlantic coast, Striped Bass spawn in the Roanoke River,

Chesapeake Bay, Delaware River, and Hudson River, all of which are currently viable

and have a sustainable population (ASMFC, 2013). South of the Roanoke River, bass are

not known to undertake coastal migrations, whereas the Albemarle Sound-Roanoke River

(A-R) management unit and northward to Maine are considered coastal migrants

(ASMFC, 2013). Thus, bass occupying this range are managed as one trans-boundary

(i.e., trans-state) coastal migratory stock due to its migratory nature (ASMFC, 2013;

Essig *et al*., 2019). Within the management unit, the A-R and Chesapeake Bay stocks have separate management programs. The A-R stock is managed as a non-coastal migratory stock by Atlantic States Marine Fisheries Committee (ASMFC) because they contributed minimally to the coastal migratory population. The Chesapeake Bay stock, which is comprised of multiple spawning populations, is managed separately due to its population abundance. The ASMFC manages the entire Atlantic U.S.A range and all stocks within it (ASMFC, 2013; Essig *et al*., 2019).

In Canada, there are three DUs: The Southern Gulf of St. Lawrence (SGoSL) DU, the St. Lawrence River DU, and the BoF DU. The SGoSL DU ranges from Gaspe, Quebec (QC), throughout the Northumberland Strait, surrounding Prince Edward Island (PEI), to the northern point of Cape Breton Island, Nova Scotia (NS). The spawning river for this DU is the Miramichi River in New Brunswick (NB) (DFO, 2016b; DFO, 2016c). The St. Lawrence River DU ranges from Montreal, QC, to Rimouski, QC. Striped Bass previously spawned in the St. Lawrence River at Lac St. Pierre, but this genetic population became extirpated in the 1960s due to dredging and fishing pressure (Robitaille *et al*., 2011). After rearing cultured bass originating from Miramichi River and stocking them between Saint-Pierre-les-Becquets and Rivière-Ouelle, QC, they now spawn naturally further downstream in the Rivière-du-Sud basin at Montmagny (Government of Quebec, 2008; Robitaille *et al*., 2011; DFO, 2016d; DFO, 2016c). The BoF DU includes the entire BoF, the Atlantic coast of NS, up to Cape North on Cape Breton Island, NS. This DU has three historical spawning rivers: the Annapolis River, NS (extirpated), the Saint John River, NB (previously deemed extirpated, but recently questioned; LeBlanc *et al*., 2018), and the Shubenacadie River, NS (Figure 2; DFO,

2016a; DFO, 2016c). Rulifson and Dadswell (1995) suggested the Nepisiguit River, Tabusintac River, Kouchibouguac River and Richibucto Rivers in New Brunswick historically sustained spawning populations, but there has been no confirmation of spawning in these rivers recently. More recently, Andrews *et al.* (2019) proposed that the eastern shore of NS and Cape Breton be considered as a separate new DU due to presence of Striped Bass in Bras d'Or Lake, Mira River, Framboise, and Inhabits rivers that could support reproducing populations and lack of tag recapture records in the area from existing DUs. However, these regions are less studied, and to date only one genetic study of Striped Bass from the Mira River and Bras d'Or lake has been completed and determined they are of SGoSL origin (same samples: Buhariwalla, 2018; Leblanc *et al.*, 2020).

Although Striped Bass young spend time in natal rivers during early life stages and return for spawning with high river fidelity, there is population overlap during the summer and fall and bass occupy many habitats throughout the year (DFO, 2014). Thus, population and habitat overlap makes population estimates difficult (DFO, 2006; COSEWIC, 2012). A coastal area where bass from the SGoSL DU and the St. Lawrence DU mix (Figure 2) runs from Rimouski, QC to Gaspe, QC (COSEWIC, 2004; DFO, 2016c). It is also unknown what populations frequent the Northern point of Cape Breton Island, NS. Some fishers suggest bass they are a part of the SGoSL DU, and others believe they are migrants from the BoF DU or U.S.A.. Preliminary molecular work by Leblanc *et al.* (2020) suggests that individuals within this range (Bras d'Or) are of SGoSL origin. Within the BoF DU, genetic mixing occurs between the Shubenacadie River and Saint John River populations (Bentzen and Paterson, 2016; Andrews *et al.*,

2017; LeBlanc *et al*., 2018), with occasional migrants from the U.S.A. populations (Bentzen and Paterson, 2016). Andrews *et al*. (2020a) acoustically tagged 44 bass and showed 4 individuals in the Saint John River migrated to the Shubenacadie River during spawning season and then promptly returned to the Saint John River. The Petitcodiac River in South-Eastern New Brunswick, draining into Chignecto Bay, had a causeway permanently opened in 2010 and the reappearance and steady increase in bass abundances and sizes classes may indicate a recolonization event in that river (Redfield, 2018), but genetically these bass were of Shubenacadie River origin (Mazerolle, 2014).

Tag data have shown bass tagged in the BoF migrating into coastal U.S.A., but no molecular work was completed to determine if tagged individuals were originally of U.S.A. origin (Dadswell *et al*., 1986; Rulifson *et al.*, 1987; Rulifson *et al*., 2008), and no recent tagging studies have documented migrations on this scale (Bradford *et al*., 2012; Broome, 2014). In contrast, north of the Roanoke River, U.S.A., bass are known to complete coastal migrations northward into the BoF in search of food in the summer (ASMFC, 2013). Through tagging studies, it is reported that most migrate back to the U.S.A. in the fall, but there is some evidence of overwintering in Canadian waters and some questions are raised about whether these U.S.A. origin bass are spawning with Canadian populations creating hybrids (Nichols and Miller, 1967; COSEWIC, 2012; ASMFC, 2013; Andrews *et al*., 2017). Recent molecular evidence from Bentzen and Paterson (2016) suggests that a low proportion of bass in the Minas Basin are from other populations, including the U.S.A.

Habitat Preference

Striped Bass is anadromous and spend most of its lifecycle in coastal areas within the neritic zone with sand or rocky bottomed substrates (Scott and Crossman, 1973). It can tolerate temperatures of 0–30° C and salinities ranging 0–33.7 ppt, and optimum temperatures range 16–23° C depending on fish length (Tagatz 1961; Bogdanov *et al*., 1967; Westin and Rodgers, 1978). In winter, bass metabolism is reduced, and it is known to retreat to deeper coastal waters, or freshwater lakes and rivers until temperatures increase in the spring (DFO, 2016; Keyser *et al*., 2016).

Life Cycle

Striped Bass occupies different habitats throughout its lifecycle. It was previously believed that Canadian bass were restricted to deeper freshwater lakes and rivers during overwintering but, Keyser *et al*. (2016) showed through acoustic telemetry that some larger bass (52–87 cm FL**;** n= 6 of 17 tagged) overwintered in Minas Passage, a high-flow saltwater passage, in the inner BoF, NS, Canada, indicating bass may use coastal areas as well as fresh water for overwintering habitat. In addition, abnormal overwintering behaviour is observed in both Canada and the U.S.A. at power plants generating thermal discharges, creating an artificially warm environment for bass to continue to feed and grow (Marcy and Garvin, 1973; Buhariwalla *et al*., 2016).

Increased water temperatures in the spring encourages movement from overwintering grounds to spawning grounds in brackish water or fresh water (DFO, 2016a). Males are usually the first to arrive to the spawning grounds, followed by females shortly before spawning begins in May and almost all spawning is complete by mid-June (Holland and Yelverton, 1973; Paramore and Rulifson, 2001; Bradford *et al*., 2012).

Males reach maturity sooner than females at an age of 3–4 years (>32 cm TL), whereas females can reach sexual maturity at 4 years (>50 cm), but many do not mature until 6 years (>68 cm) (Scott and Crossman, 1998; Paramore and Rulifson, 2001; Bradford *et al.*, 2012; DFO, 2016a). Females are iteroparous, generally spawning once per year, rarely spawning more than once in a year, and do not always spawn every year (Lewis, 1962; Scott and Crossman, 1998). Spawning can last three to four weeks and appears to commence when water temperatures exceed 15° C (Bradford *et al.*, 2012). Spawning takes place at the surface with one female surrounded by many males (Setzler *et al.*, 1980; DFO, 2016a).

Females can lay 58,000 to 1.3 million eggs (depending on female weight) (McInnis, 2012). Eggs are released at the surface and are slightly negatively buoyant. Eggs hatch after 2–3 days depending primarily on water temperature (Clemon *et al.*, 1983; Bradford *et al.*, 2012; Rainer, 2016). Larvae feed on yolk sacs for the first five days, then feed on zooplankton and copepods until its transition into Young-of-Year (YOY) 35–40 days after hatching (Reesor, 2012; Duston *et al.*, 2018). YOY remain in the river and estuarine areas where they were spawned to feed until late summer, thereafter they are known to migrate to other estuaries to continue to feed (Clemon *et al.*, 1983; Robinson and Courtenay, 1999; Bradford *et al.*, 2012; Reesor, 2012; Duston *et al.*, 2018). Based on otolith calcium and strontium levels YOY overwinter in estuarine and saline waters, but not fresh water (Bradford *et al.*, 2012). As YOY become immature and mature adults, overwintering occurs in either freshwater lakes or saltwater (Paramore and Rulifson, 2011; Keyser *et al.*, 2016). In early summer, post-spawning, these individuals leave estuaries and move into marine water and tidal parts of rivers in search of prey until late fall (DFO, 2016a). For this thesis, the

term YOY refers to individuals less than one year old or less than 12 cm TL, juvenile refers to immature individuals from 12-35 cm TL and adults are described as >35 cm TL and mature.

Diet

Feeding Behaviour

Striped Bass is a voracious, opportunistic predator. It feeds primarily by sight, which is adapted for a wide colour range in both daylight and low light conditions, and with increased visual acuity, makes bass efficient day and night feeders (Horodysky *et al*., 2007). To assist in finding prey at night and in areas with high suspended sediments, bass also use olfactory cues to detect predators and prey from kilometers away (Karas, 2016). Both YOY and juveniles tend to school together by size cohorts and follow other schooling prey fish. In these schools, YOY and juveniles feed simultaneously (Clemon *et al*., 1983). Conversely, adult bass travel and feed individually or in small groups (Clemon *et al*., 1983). Upon finding food, bass do not eat steadily, rather they gorge on prey and drop in the water column after feeding until digestion is completed (Setzler *et al*., 1980). For an unknown period before spawning, and during the actual spawning process, bass typically do not eat (Trent and Hassler, 1966).

Prey

YOY feed on small shrimp and crustaceans. In the spring, juveniles and adults feed on coinciding fish species present as they migrate down river. Some of these species include Rainbow Smelt *Osmerus mordax* (Mitchill, 1814), Alewife *Alosa pseudoharengus* (Wilson, 1811), and Blueback Herring *Alosa aestivalis* (Mitchill, 1814) (DFO, 2016b). In the summer bass feed on a variety of fish including smaller bass, Alewife, Rainbow Smelt, American Eel

Anguilla rostrata (Lesueur, 1817), multiple species of flounder, Mummichog *Fundulus heteroclitus* (Linnaeus, 1766)*,* Rock Gunnel *Pholis gunnellus* (Linnaeus, 1758), Sand Lance *Ammodytes americanus* DeKay, 1842, Atlantic Silversides *Menidia menidia* (Linnaeus, 1766), multiple species of hake, other fishes, macroinvertebrates (squid, sea worms and amphipods), and crustaceans (lobsters and crab) (DFO, 2016b; Rainer, 2016).

Predators

Striped Bass larvae may be preyed upon by Atlantic Tomcod *Microgadus tomcod* (Walbaum, 1792), Silver Hake *Merluccius bilinearis* (Mitchill, 1814), Bluefish *Pomatomus saltatory* (Linnaeus, 1766), large copepods *Cyclops bicuspidatus*, and larger bass (Scott and Crossman, 1973; Rainer, 2016). As juveniles and adults, spiny defences and larger size make bass difficult to be preyed upon. Sharks, mammals, bald eagles *Haliaetus leucocphalus*, Sea Lamprey *Petromyzon marinus* (Linnaeus, 1758), and conspecifics will occasionally feed on adult bass, but its main predators are humans (Scott and Crossman, 1973; MPT, 2005; Rainer, 2016).

Ecological Importance

All life stages of Striped Bass are important ecologically and can be indicators of ecosystem health. Early life stage success can be an indicator of estuarine ecosystem health, as larvae remain in estuarine waters for its first year and survival is highly dependent on an abundance of aquatic organisms, as well as favourable temperature and dissolved oxygen levels (Robitaille *et al*., 2011). Bass egg survival to hatching is dependent on the physicochemical properties of rivers, specifically temperature, dissolved oxygen and a moderate current (Cooper and Polgar, 1981). Bass eggs require flow to remain suspended in the water column, otherwise they sink and can become covered in sediment,

suffocating the eggs. Thus, high hatch rates of eggs and larvae can indicate healthy

physical characteristics of rivers (Robitaille *et al.*, 2011).

As adults, Striped Bass are an important top predator of coastal marine habitats

and given its anadromous life cycle, provides a link among freshwater, estuarine, and

marine habitats (COSEWIC, 2012). As an apex predator, it fills many ecological roles

within the ecosystem. Apex predators can increase biodiversity by maintaining prey

abundance and therefore reduce interspecific competition (Sergio *et al.*, 2006; Robitaille

et al., 2011). They can also assist in maintaining healthy populations of prey by removing

diseased and weak individuals from prey populations (Temple, 1987).

Social Importance

Striped Bass is important commercially, recreationally, and for aboriginal food,

social, and ceremonial (FSC) needs (COSEWIC, 2012; Dennys *et al.*, 2013). Commercial

catches of bass are sold for food and historically had high economic returns, for example

bringing in over five million dollars for 1,740 tonnes in 1981 in the U.S.A. (Clemon *et

al.*, 1983). Peak catches in the U.S.A. were 6,335 tonnes in 1973 (Clemon *et al.*, 1983).

Historically, Canada had directed commercial fisheries of bass that peaked at 61 tonnes in

1917 (COSEWIC, 2004; Andrews *et al.*, 2017). By 1996 all Canadian directed

commercial Striped Bass fisheries were closed (DFO, 2017). Currently, the only directed

commercial fishery in Canada is with the Eel Ground Mi'kmaq First Nations in New

Brunswick and this fishery was only recently granted (Chilibeck, 2017).

Recreationally, Striped Bass is a popular recreational fish because they reach

large, "trophy" sizes and are strong fighters while on rod and reel (Karas, 2016). Ease of

access to fishing locations and the lack of licensing for coastal fishing also contributes to

its popularity (DFO, 2015). In aboriginal FSC, striped bass is used for food sustenance among community members; it is socially valued for providing a sense of social pride in being able to harvest such a large fish to share with others in the community (Denny *et al*., 2013). Culturally, the presence of bass emerging from overwintering grounds and spawning is loosely used as an environmental calendar, coinciding with other species emerging, e.g., barn swallows, June bugs, and spring peepers (Denny *et al*., 2013). Striped Bass is so highly prized in the U.S.A that it is the state fish for Maryland, Rhode Island, South Carolina, and marine state fish for New Hampshire, New York, and Virginia (State symbols USA, 2018).

Canadian Population Trends

St. Lawrence River DU

The abundance of Striped Bass in the St. Lawrence River fluctuated largely following a decadal cycle (COSEWIC, 2004). Commercial fisheries were reported since 1920 with annual catches of 5–50 tonnes reported from 1920 into the 1950s until in 1957 catches dropped to below 3 tonnes annually; in 1965 the commercial fishery was closed. The only population abundance estimate is from 1967, where it was estimated that there were between 600–1,300 two-year-old bass along a 60 km coastal segment on the south shore of the river (COSEWIC, 2004). Subsequently no bass were reported commercially or recreationally after 1968 and a recovery plan was initiated. The St. Lawrence River was stocked with bass from the Miramichi River starting in 2002 and hatchery raised bass in 2006 (COSEWIC, 2004; Robitaille *et al*., 2011). From 2002–2009 almost 6.5 million bass were re-introduced into the St. Lawrence River (Robitaille *et al*., 2011).). There is evidence that re-introduced bass spawned naturally in the St. Lawrence River in 2008 and

have started to colonize new areas in 2013; current threats and historical spawning fluctuations required stocking for several years (Bérubé *et al*., 2017).

Southern Gulf of St. Lawrence DU

The SGoSL DU historically had the largest directed commercial fishery with a maximum of 61 tonnes in 1917 (Leblanc and Chaput, 1991; COSEWIC, 2004). Commercial landings dropped in 1934 and no landings were recorded for 33 years until interest increased and catches increased to 48 tonnes in 1981 (Douglas *et* al., 2003; COSEWIC, 2004). After that peak, the fishery crashed with less than 1 tonne in landings in the early 1990s (COSEWIC, 2004). Abundance estimates in the Miramichi River began shortly after and showed less than 5,000 spawners in the late 1990s (DFO, 2017). Due to conservation concerns, the commercial fishery closed in 1996 and the recreational and aboriginal fisheries were closed in 2000. A small number of FSC fisheries were reinstated in 2012 and allocations of bass to aboriginal communities have gradually increased since. The recreational fishery reopened in 2013 after meeting the recovery target of achieving spawner abundances greater than 31,000 adult spawners for three out of five consecutive years (Douglas *et al*., 2006; DFO, 2017). Spawner abundance has been estimated annually since 1993 and in 2016 the median estimated spawner abundance was 318,000 (DFO, 2017). Adjustments to the spawner abundance model to account for the daily distribution of spawners in the system and the catchability of the gaspereau trap nets used were introduced in 2017 by using the behaviour of acoustically tagged bass. In 2017, the median spawner abundance estimate was 994,000 for total spawners with a wide 95% confidence interval (486,400–2,063,000) (DFO, 2018a). In

2018, the estimate dramatically dropped to 333,000 for total spawners, again with high

uncertainty (95% confidence interval 154,000-623,000) (DFO, 2019).

Bay of Fundy DU

The BoF DU historically consisted of three spawning rivers: the Annapolis River,

the Saint John River, and the Shubenacadie River. The Annapolis River population has

been considered extirpated since 1979 and the Saint John River population, until recently,

was considered a remnant genetic population (COSEWIC, 2012; LeBlanc *et al*., 2018).

Historically, this DU had the lowest catches of the three DUs annually catching 0.5–15

tonnes between 1870 and 1990 with only one large peak in 1888 of 55 tonnes (Jessop,

1991). The sport fishery in the Shubenacadie River declined from 1950 to 1975, but then

appeared to stabilize (COSEWIC, 2004). It is unknown what proportion of bass caught

over that period were U.S.A. migrants. Population abundance estimates have been

restricted to the Shubenacadie River population. Recreational angler surveys and juvenile

presence studies have been done in the Saint John River and the Annapolis River. Based

on historical tagging studies, anecdotes, and few genetic studies, U.S.A. migrant bass are

considered to mix with the BoF bass, and anecdotally may occasionally overwinter in

Canadian waters.

The first population estimate was completed by Rulifson and Tull (2009) in 1994

for total spawners in the Stewiacke River, NS. The only spawner abundance estimate on

the BoF DU completed by DFO was assessed in 2002; it estimated 15,000 total spawners

of ≥ 3 years old migrating out of Grand Lake, NS (Bradford *et al*., 2015). A median

population estimate of 1,500–2,520 bass was also made for the localized area of Grand

Pre, NS spanning 2008–2010 (Broome, 2014). Bentzen and Paterson (2016) completed a

genetic analysis on 294 bass sampled from this location and the Stewiacke River, of which

291 were of Shubenacadie River origin, two bass were of mixed ancestry, and one bass was

a U.S.A. migrant. Uncertainty in migration and mixing between populations in the BoF

imposes problems with estimating abundance for the BoF DU. With recent evidence of

bass overwintering in saltwater, the identification of a discrete genetic population in the

Saint John River, some of which migrate to the Shubenacadie River to spawn, and an

unknown proportion of bass migrating and potentially overwintering in Canadian waters,

these estimates are likely confounded. More generally, it is unknown to what extent

population mixing confounds abundance estimates of native BoF DU bass; thus, the

mixing rate is considered an important information gap (DFO, 2014).

Conservation Status

Ranking systems

Species status can be determined at global, national, and subnational levels. The

International Union for Conservation of Nature and Natural Resources (IUCN) Red List

classifies species conservation status at the global level through a widely standardized

system, with most of their information gathered through partner organizations and other

ranking systems. Their classifications are only applied to wild populations inside natural

ranges, and to populations resulting from benign introductions (IUCN, 2001).

In Canada, the most popular ranking system is at the subnational level by the

Committee on the Status on Endangered Wildlife in Canada (COSEWIC). COSEWIC is

a committee of experts that reviews research information on population and habitat

status, trends, and threats; utilizes community and Indigenous traditional knowledge; and

applies assessment criteria based on international standards. Once COSEWIC assesses a

population it makes a recommendation to the Canadian federal government for consideration to be listed and therefore protected under the Species at Risk Act (SARA) (Government of Canada, 2018a). If a species is SARA listed, recovery strategies and action plans are developed and implemented to protect critical habitat and prevent further decline by mitigating harm. In the extreme case, a SARA listing can make it illegal to kill, harass, capture, or harm the identified population (DFO, 2009a).

Striped Bass Conservation Status

As of 2019, Striped Bass are designated as Least Concern by the IUCN (NatureServe, 2019). This designation reflects the status of bass populations in the Roanoke, Hudson, Chesapeake, and Delaware Rivers of the U.S.A. that are doing well. The National Oceanic and Atmospheric Administration (NOAA) reported a female spawning stock biomass of 4,535 tonnes on the U.S.A. Atlantic coast in 2012 (NOAA, 2015). In Canada, all three DUs are designated as at-risk by COSEWIC. The St. Lawrence River DU is designated as Extirpated, SGoSL DU is Special Concern, and BoF DU is Endangered (COSEWIC, 2012; Government of Canada, 2019). The St. Lawrence River population assessment was initially downgraded from Extirpated (COSEWIC, 2004) to Endangered following successful re-introduction of bass broodstock originating from the Miramichi River, NB to historical areas in 2011 and 2012; however, it was reassessed in 2019 and upgraded to Extirpated as the re-introduced bass were from another population, and not considered to be part of the original St. Lawrence River population; thus, the genetically distinct St. Lawrence River population no longer exists. (COSEWIC, 2012; Government of Canada, 2019). The SGoSL population assessment was also downgraded from threatened (COSEWIC, 2004) to special concern (COSEWIC,

2012) due to an increased abundance, but lists poaching and commercial by-catch as continued threats as the Miramichi River is only known spawning river. The Bay of Fundy (BoF) DU was assessed as endangered in 2012 (COSEWIC, 2012), from its prior assessment as threatened in 2004 (COSEWIC, 2004). This change is due to continued habitat degradation in historical spawning rivers, unknown population abundances, and unknown exploitation from recreational fishing, commercial by-catch, and poaching. From these assessments, the St. Lawrence River DU was the only DU amended to the SARA after a delayed review period, where it was listed as extirpated in 2011 based on the 2004 COSEWIC assessment, then updated to its current SARA designation as endangered in 2019 based on the 2012 COSEWIC assessment (Government of Canada, 2018b; Government of Canada, 2019).

Project Scope

The lack of knowledge in population size of Striped Bass in the BoF has led to information gaps that have impeded informed conservation actions for this DU. Without any consistent population abundance data, it is not possible to establish abundance targets for either the BoF DU or individual river populations. Monitoring of adults has been mainly focused on the Shubenacadie River during the descent from overwintering in Grand Lake, NS (Bradford *et al*., 2012). However, recent evidence from Keyser *et al*. (2016) has shown bass overwinter in the Minas Passage, meaning that total spawner abundance and thus population size is underestimated. In addition, there is evidence of Saint John River resident bass travelling to the Shubenacadie River during spawning seasons (Andrews *et al*., 2017). Although there is genetic evidence of a remnant Saint John River population, no direct observations of spawning in the Saint John River have been observed for

decades (Andrews *et al*., 2017). The Shubenacadie River is currently reported as stable; however, if spawning or juvenile habitat were destroyed in the Shubenacadie River or estuary, a risk of extirpation of the BoF DU would increase, likely dramatically, because this is the only remaining stable spawning river in the DU.

To estimate population size, the basic population demographics that are used in population dynamics analysis are necessary. Population demographics include estimating the composition of the population for size and age structure, population density, age or size-specific mortality, fecundity, and sex ratio. These metrics are used to develop population dynamics models. Furthermore, growth rate, recruitment, immigration, emigration, and other metrics are useful in population dynamics analysis. Population mixing confounds estimations of parameters in both demographics and dynamics. The DFO (2014) recovery potential assessment for bass outlines current knowledge gaps in the BoF DU: sex ratios, size/age structure, recruitment, and abundance of adult Shubenacadie River bass, annual removals of bass from authorized activities, Saint John River population status and location of habitat, potential availability of overwintering habitats affecting demographics, and possible mitigation of the negative impacts of the Mactaquac Dam and the Annapolis River Causeway. To assess whether population mixing is confounding population estimates, population discrimination through molecular methods is used to determine the proportion of individuals belonging to each population present within a geographic area where population size is estimated.

For this thesis I have addressed knowledge gaps in the BoF DU by assessing population demographics through capture-mark-recapture (CMR), and population mixing through molecular analysis. Since the BoF DU contains only one stable spawning

population – the Shubenacadie River – and the primary habitat of the Shubenacadie River

population is the Minas Basin, the focus of this study was on the Minas Basin.
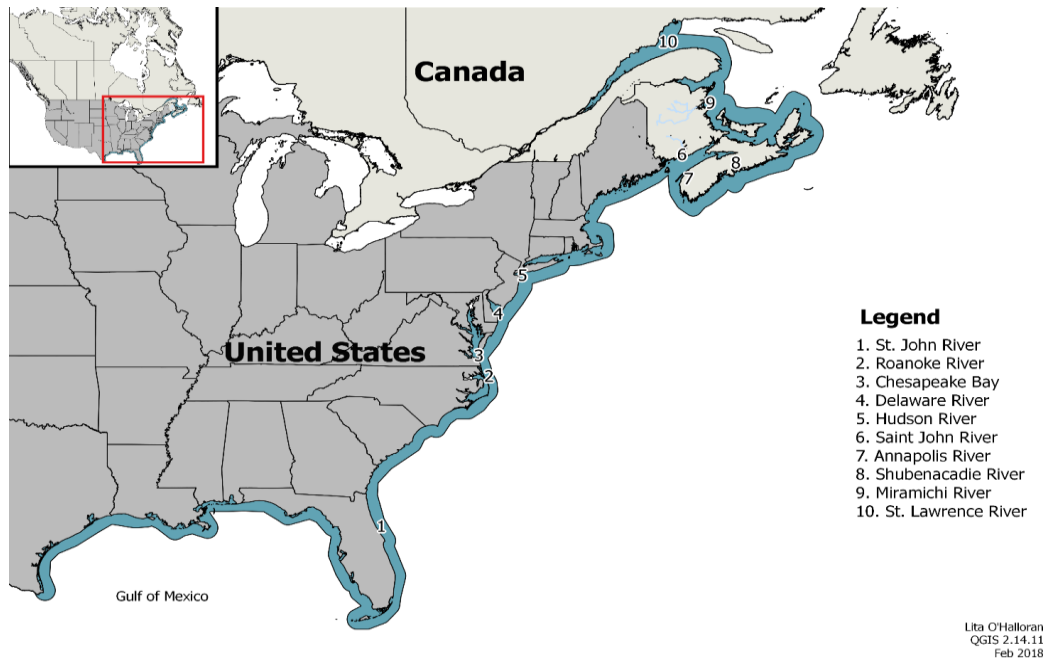
Figure 1. Native distribution and spawning rivers of Striped Bass *Morone saxatilis* (Walbaum, 1792).
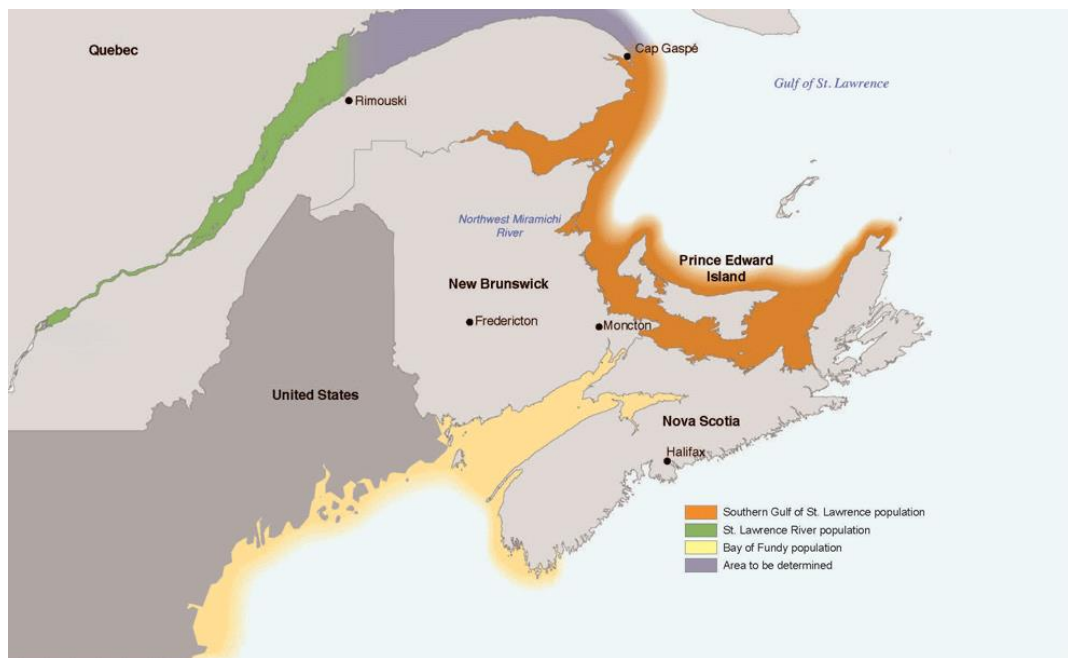
Figure 2. Department of Fisheries and Oceans Canada Atlantic Canada management units and undetermined geographic range of Striped Bass *Morone saxatilis* (Walbaum, 1792) (source: DFO, 2016c)

Chapter 2

Bay of Fundy Population Structure and Characterization of the Fishery

Bay of Fundy DU

The BoF is located at the northern extent of the Gulf of Maine and between the Canadian provinces of NB and NS (Figure 3). It consists of the outer BoF to the south, and the inner BoF to the north. The inner BoF is subdivided into Chignecto Bay to the northeast and the Minas Basin to the east (Figure 4). The inner BoF is a well-mixed, hyper-tidal estuarine system that has the highest tides in the world (16 m) due to geomorphological features and resonance time of the semi-diurnal tides (12.42 hours) (Thurston, 1990). Catch reports of bass from research herein have occurred throughout the entirety of the inner BoF and the rivers draining into it.

Minas Basin

The Minas Basin is connected to the BoF by the Minas Channel and adjacent Minas Passage. The Minas Channel located closest to the outer BoF is on average 15 km wide and is characterized by high rocky shoreline. The Minas Channel lies west of the Minas Passage, which narrows to 5.5 km before opening into the Minas Basin. The Basin itself is comprised of three ecoregions: the central basin, Cobequid Bay, and the Southern Bight (Figure 5; Thurston, 1990). The Minas Passage exhibits flow speeds of up to 5 m · s^{-1} (Ashall *et al*., 2016). High current speeds and the high tidal range creates elevated levels of suspended sediment on ebb tides, which distribute variably throughout the basin (Ashall *et al.*, 2016). There are about 17,900 hectares of mudflats within the basin with almost half in Cobequid Bay; 7.5% of the mudflats feature salt marsh, which is largely concentrated in

the Southern Bight (Percy, 2001). At low tide, 20% of the salt marshes are exposed (Daborn and Redden, 2016). The natural warming of the exposed mudflats increases the temperature of the tidal waters during the summer months deterring adult bass from the intertidal zone and potentially attracting juveniles through thermal habitat division and food availability (Coutant, 1977; Broome, 2014). During the winter months, high numbers of bass are found overwintering in Grand Lake, NS, which is connected to the Shubenacadie River (DFO, 2016b), but bass also overwinter in tidal waters in the Minas Passage (Keyser *et al*., 2016).

Management in the Bay of Fundy

In the Bay of Fundy non-tidal waters are managed by the provincial Department of Fisheries and Aquaculture in NS, and the Department of Natural Resources in NB, and tidal waters are managed federally by the DFO. Anadromous species such as Striped Bass are managed and protected federally by the DFO in Canada under the Canadian Fisheries Act (Bradford *et al*., 2012). Recreational angler licenses are required by law for fishing bass in non-tidal waters only; volunteer catch reporting is encouraged through a reporting 'stub' program provided to license holders. No license is required for recreational angling in tidal waters, so participation in the 'stub' program is not easy. In NB, there are three non-tidal recreational fishing areas (RFA) that surround the BoF: inner BoF, lower Saint John River, and the Southwest. Out of these three fishing areas in 2020, only the lower Saint John River RFA is open to inland bass fishing for spring through fall, closing after 15 October (Province of New Brunswick, 2020). In inland waters of NS RFAs 3,4,5 and parts of 1,2,6 flow into BoF DU. The open season for bass in inland waters corresponds to the open season for sportfish in the waters of each RFA. During spawning season in

the Shubenacadie River, angling of any species is closed from 1 April–9 May and additionally from 10 May–10 June the following regulations are put in place to prevent harm and overexploitation of the fishery: (1) catch and release only from Grand Lake and Pollock Bridge to the Shubenacadie-Stewiacke River Confluence, (2) only artificial flies and unbaited lures with a single hook are permitted from the CN Railway Bridge at East Milford and Pollock Bridge to the Shubenacadie-Stewiacke River confluence (NS DFA, 2020). Tidal waters in NS and NB are open all year except in Annapolis River, NS from Hebbs Landing upstream to the highway bridge at Lawrencetown from 1 April until 30 June, when it is closed (Province of Nova Scotia, 2020). Fishing regulations in the DFO Maritimes Region limit angling to five fishing line and a maximum of six hooks per line. In both inland and tidal waters of NB and NS, retention of one bass per day and possession limit of one bass is permitted for the BoF DU. The current regulations of the retention of one bass greater than 68 cm total length (TL) per day is intended to allow for survival until maturity, and therefore having the chance to spawn at least once before a bass is removed from the population (Bradford *et al*., 2012). The current retention size limit is the latest of many BoF DU regulation changes since 1978, which have become increasingly more restrictive through closures of direct commercial fisheries, reduced bycatch allocations, and reduced retention, size limits, and possession limits within the recreational fishery (Table 1).

Fisheries Management

In fisheries management, protective measures such as total allowable catch, management plans, and fishing seasons are typically species and location specific (DFO, 2016e). These plans and quotas are created through the integrated process of gathering

information on a population and fishery location, coupled with planning, consultation, and collaborative decision-making (FAO, 1997). Lack of enough information about population dynamics and/or potential negative effects to a population creates uncertainty when making decisions on setting quotas, regulations, or determining fish population health and the effects of fishing pressure. Typically in these situations, a management framework called the precautionary approach (precautionary principle) is implemented. This framework attempts to manage commercial, recreational, and aboriginal fisheries in a conservative manner considering uncertainty and risk. One management method implements reference points on stock biomass and harvest rates to satisfy both biological and socio-economic interests (DFO, 2009b). Without a well-defined management approach, a fish population can reach critically low levels or even collapse.

Within the SGoSL DU, the precautionary approach was used with reference points to measure the effectiveness of conservation measures and indicate when the population was stable enough to support recreational, aboriginal, and commercial fisheries. The reference points were used to estimate recovery of the population, considering a recovery limit of at least 21,600 total spawners in five of six consecutive years (Douglas *et al*., 2001). Once that was achieved, then the proposed recovery target for considering fisheries access was ≥ 31,200 spawners in three of six consecutive years (Douglas *et al*., 2001). This estimate was completed by measuring spawner abundance, catch per unit effort (CPUE), and biological characteristics in the Miramichi River through CMR of bass in commercial gaspereau trap nets in the spring, and analysed using Bayesian hierarchal models (DFO, 2017). YOY abundance indices are also calculated through bycatch in commercial American Eel fyke nets, and bag nets of Rainbow Smelt (DFO, 2017). Mortality estimates

obtained from acoustic tagging data are also used to adjust the population abundance estimates (DFO, 2017). Analysis is simplified in this DU compared to other populations as there is no known mixing between this SGoSL DU and other DUs, and there is only one spawning river.

Within the BoF DU, Striped Bass population abundance is unknown and thus reference points cannot be established. Because the coastal recreational fishery is unlicensed, and identified risks include unreported fishing, harvest rates are unknown. The precautionary approach has been applied since 1978 through systematic reductions in harvest, first by preventing directed commercial fisheries, followed with reducing bycatch harvest limits, and restricting the number and size of recreational angling retention. Filling existing information gaps can assist governing agencies such as the DFO and help conservation decision-making.

Typical Fisheries Analysis

In fisheries management, not only is it important to determine population size, but it is also essential to integrate multiple biological characteristics and population demographics to have a robust understanding of population dynamics. Size structure is one of the most used fisheries assessment tools. The size structure of a fish population at any point in time can be considered a snapshot that reflects the interactions of the dynamic rates of recruitment, growth, and mortality. Thus length-frequency data provides valuable insight into the dynamics of a population and can help identify problems such as poor recruitment or excessive mortality of a size class. As retention of bass in the fishery is based on a minimum length of 68 cm TL, it is important to understand and predict the future availability of larger size classes to the fishery.

The relationship between weight and length can provide insight into the status of a population. The relationship is used to estimate weights from lengths, or *vice versa*, when only one of the characteristics is provided, assess biomass of a population given length data, estimate condition factors, and characterize important life history characteristics.

Another important characteristic for fisheries management is growth. Growth affects vulnerability to fishing pressure and can be used as a metric to show availability of prey for an individual fish. Growth is typically calculated using age and length data for individual growth of an average individual in the population and can also be determined using length measurements taken from individual fish at different times. Typically, the latter require measuring fish during mark-recapture studies between 'times-at-liberty'. Growth is influenced by the mean maximum length, L_∞, which is calculated as the asymptotic mean length from a growth model through length observations, and the time required to reach L_∞. (Ogle, 2018).

Growth models in fisheries typically use a von Bertalanffy length-at-age model, but this is not the only growth model (Ortiz, 2017; Ogle, 2018). This model makes several assumptions that fit most fisheries such as reaching an asymptote with increased age. It also makes assumptions that all fish have the same growth curve and does not vary between individuals (Ogle, 2018). Since this model requires age, it ranges from more invasive to destructive sampling and requires more time and effort to obtain and age scales (invasive sampling) and/or otoliths (destructive sampling). Variations of the von Bertalanffy growth model utilize tagging data to look at difference in length over a difference in time (Ortiz, 2017).

Capture Methods

The use of commercial bycatch for Striped Bass research has been extensive (Boreman and Lewis, 1987; Rulifson and Dadswell, 1995; Rulifson *et al*., 2008; DFO, 2016b). Commercial bycatch allows for easy access and capture because the target fisheries are directed at bass prey species. Commercial fishing weirs tend to capture smaller bass whereas gill nets, trawls, and trap nets tend to catch larger bass depending on gear type. Recreational anglers catch a variety of sizes based on gear but most target larger bass as 'trophy fish' or to retain for FSC purposes to provide more food for the community (Clifford Paul, UNIR, pers. comm.; Dennys *et al*., 2013). However, access to landings data by commercial fishers, FSC, and recreational angler catches is limited. Commercial bycatch is required to be reported to DFO, but numbers are not always accurate, and are not available to the public. Due to the unlicensed recreational tidal fishery, recreational catches of bass are generally not reported.

Knowledge Gaps

Existing gaps in the BoF DU include identifying the presence and area of occupancy of bass, demographic information on size-class recruitment, and population abundance. It is clearly stated in the BoF DU recovery potential assessment that sex ratios, size/age structures, adult abundance, recruitment, mortality, and how marine overwintering contingents affect demographics are sources of uncertainty to population abundance estimation. Other than the 1994 estimate by Rulifson and Tull (2009), the 2002 DFO Shubenacadie River spawner abundance estimate, and the Broome (2014) localized Grand Pré abundance estimate, there have been no other abundance estimates thus no consideration of abundances at larger scales such as the Minas Basin where recreational angling pressure

is high, and none that represent the entire BoF DU population. Therefore, there is little information from which to infer how the population is changing inter-annually.

The Minas Basin is where much of the recreational fishery occurs for the Shubenacadie River population; anecdotally, this fishery is increasing. The number of recreational anglers in this fishery is estimated every five years through the DFO survey of recreational fishing in Canada and the Nova Scotia sportfish survey, both of which estimate anglers in NS from recreational license sales. As of 2010 NS had 57,756 licensed recreational anglers, of which 7,248 anglers reported catching 94,700 bass. In 2015 the number of licensed anglers decreased to 57,613; however, these are only anglers who have purchased licenses and does not consider the high number of saltwater anglers without a recreational license (NS DFA, 2011; DFO, 2016f; DFO, 2019a). Confounding the abundance estimates is the mixing rate of U.S.A. bass in the BoF DU, which contributes to abundance estimate uncertainty. Relatedly, the extent of immigration, spawning contributions, and timing and occupancy of habitats remain unanswered for bass from other populations (e.g., U.S.A., Saint John River, etc.). Exploring these sources of uncertainty on a long-term basis is required to make informative decisions on conservation measures and management of this DU. This thesis aims to answer some of these information gaps, specifically provide an estimate of growth rate, weight-length relationships, and length frequencies for Minas Basin. The presence and mixing of other bass populations are investigated in Chapter 3.

Objectives

1) Describe population characteristics of immature juvenile (25–32 cm TL) and mature adult (>32 cm) Striped Bass occupying the Minas Basin.

2) Explore the use of growth models using CMR data compared to traditional length-at-age growth.

Methods

Most of the Striped Bass data used for this thesis was conducted by the Striped Bass Research Team (SBRT) within the Minas Basin, including the Southern Bight and Cobequid Bay (Figure 5), and was collected with collaborators Clean Annapolis River Project (CARP) in the Annapolis River, Fort Folly Habitat Recovery (FFHR) and Petitcodiac Watershed Alliance (PWA) in the Petitcodiac River and Chignecto Bay, Marine Institute of Natural and Academic Science (MINAS) in the Minas Basin, and DFO population ecology division and Mikmaw Conservation Group (MCG) in the Shubenacadie River. The associated rivers of the inner BoF are also included as part of the study, as recreational anglers have reported tag recaptures within these rivers (Figure 4).

Biological Sampling

Striped Bass were measured for total length (TL), occasionally for fork length (FL), tagged externally if larger than 35 cm and in good condition. Condition was assessed as a healthy looking and responsive bass with no bleeding, no deep-set hooks or high entanglement, and no extended air exposure. Length was measured to the nearest mm (occasionally to 5 mm depending on bass length) using either a 1.5-m measuring board or a flexible vinyl measuring tape. Sex was recorded opportunistically during spawning months by presence of milt or eggs or upon dissection of carcasses donated by anglers. Bass selected for marking were tagged using a plastic yellow external dart tag labelled with "Acadia Biology" and an alpha numeric tag identification number starting with "BASS" followed by 4 digits. The other side of the tag read "www.trackmyfish.ca" where anglers could find our contact information to report the tag. Dart tags were used as they can be quickly and easily inserted. They are inexpensive, have high tag retention, and allow

recreational and commercial anglers to participate in the study (Boreman and Lewis, 1987; Rulifson *et al.*, 2008). The tags have a harpoon-shaped nylon head and last many years. Tags are deployed using a canula inserted between the lateral line and the base of the first dorsal fin and angled at 45 degrees to create a streamlined shape with the body of the fish. Once inserted, the tag is hooked onto the pterygiophores below 3rd or 4th spine of the dorsal fin as adapted by Chadwick (1963). The location and date were recorded for all bass tagged. Tag-induced mortality is estimated to be low (0% Goshorn et. al. 1998; 1.3% Rugolo and Lange 1993; 1.7% Dunning *et al.*, 1987) and no adjustment was made in the analysis for this. Weights were recorded opportunistically through angler reports and during fishing tournaments. Three to five scales were collected laterally between the first dorsal fin and the lateral line for molecular analysis and archived for ageing. Effort was made to avoid removing scales from one location to minimize potential for an open wound. Once removed, scales were placed in a Rite-in-the-Rain waterproof paper envelope, where all biological characteristics were also recorded. In all years, the sampling methods were reviewed and approved by the Canadian Council for Animal Care through Acadia University's Animal Care Committee (Permit # 04-15A1R1) and DFO under Scientific License # 326696.

Fishing methods

Recreational anglers can catch a variety of sizes of bass depending on gear used; however, anglers tend to target larger trophy or retention sized bass. Thus, it is important to include these bass in analyses in addition to bass caught in commercial herring weirs, which select smaller bass. The inclusion of multiple fishing methods not only provides wider distribution of sizes but also covers a larger geographic distribution. Anglers

catching fish reported tag data including when and where the fish was caught, tag

information, TL, or FL, whether the fish was released or kept, and the total number of bass

caught and time spent fishing during that fishing trip. Since most tag returns depend on

participation of recreational and commercial anglers, outreach, and awareness of the

tagging program at fishing derbies/tournaments and other events, and citizen science

programs were undertaken to engage with stakeholders and exchange information.

An important outreach avenue was through Striped Bass angling tournaments

(Table 2). During these events the SBRT assisted organizers with event activities including

recording catches, measuring, and collecting biological characteristic data on bass. Efforts

were also made at these events to speak with anglers and spread word of our research and

citizen science programs. All tournaments attended were in NS except for the Miramichi

Striper Cup, which occurs in the Miramichi River, NB. As this was a more popular

tournament, outreach was the main purpose of attending but length and weight data were

also collected to compare weight-length relationships of the two DUs. Individual fishing

trips were made with recreational anglers to discuss the project while collecting

morphometric data and tagging bass as they were caught. Bass morphometric data and

tagging were also completed with commercial fishers. At all interactions, our citizen

science program called the "STRIPED amBASSadors" was encouraged. Various levels of

participation were included in this program such as providing historical catches (e.g., past

records of fishing), tag reporting (reporting tagged fish when caught), and catch reporting

(participating in a fishing logbook program).

Similar datum were gathered through working alongside commercial fishers at their

operations. These operations include herring weirs, drift nets, and bottom trawls. The

herring weir was located approximately 1 km offshore Bramber, NS, in the southern bight

eco-region, and sampling occurred at low tide. Drift netting occurred in the Avon River

Estuary, primarily near the causeway in Windsor, NS, and in the Stewiacke River during

incoming, high, and outgoing tides. Otter trawls were always completed overnight in either

Scots Bay, NS located west of the Minas Passage, or in Kingsport, NS. At these operations,

the captured were measured for TL, tagged if in good condition and larger than 35 cm TL,

and scales were collected. The weir is a fixed structure that utilizes a passive capture

technique of fish based on their natural behaviour and movement. As the weir was located

on the mudflats, close to shore, it tends to catch smaller cohorts of bass with occasionally

larger bass. Drift net stretched nylon and monofilament mesh sizes ranged 1.5–5.5 inches,

which targeted a variety of fish species of various sizes. Bottom trawling gear consisted of

a large dragger net with a horizontal width of approximately 40 m, a vertical width of 5.5 m

and a stretched mesh size of 2 inches. This gear tended to capture larger bass as it was

towed in deeper waters further from shore. In addition to biological data, the amount of

time nets were set for both the drift nets and trawls were recorded. Working directly with

the fishers helped build relationships with other commercial fishers that resulted in more

tag returns.

Analysis

Data shared from other organizations, and historical data on Striped Bass in the

Bay of Fundy, were merged with the data from this study. Data were analyzed at various

resolutions for each data set, depending on the objective of analysis. All analyses for this

study were completed using the statistical software R (R Core Development Team, 2016).

Data Sources

Data were collected annually from the Miramichi Striper Cup tournament in Miramichi, NB from 2015–2019. These data were only used in the analysis for comparison of weight-length relationships. Data provided from the Fort Folly Habitat Recovery (Petitcodiac River; 2016) and historical data provided by Mike Dadswell (Annapolis River; 1981–1982) were used for length frequency, length-length and weight-length relationships, and describing biological characteristics of the BoF population. Historical data from 1984–1993 bass within the Minas Basin provided by Roger Rulifson and SBRT tag recaptures reported from DFO's research trap net in Enfield, NS were used for length frequency, weight-length relationships, describing biological characteristics of the BoF population, and fitting growth curves to CMR data. Data provided from recreational anglers in the St. Lawrence River DU, SGoSL DU, and in Cape Breton, NS, were not used in any analysis due to minimal records.

Standardization of Data

The data submitted by anglers, fishers, and partner organizations varied in units and detail. Data standardization was conducted to allow for comparison. Any fish length provided in inches was converted to cm and any weights provided in lbs were converted to Kg. Only weights for whole fish were used in analysis and any dressed weights were excluded from analysis. Where possible, measurement data were recorded either as an estimate or as actually measured. Angler-provided data, other than those recorded in logbooks, were assumed to be estimated unless stated otherwise. Those records having both FL and TL measurements were used to plot the relationship of FL to TL using a linear regression model (LM) so any measurements recorded in fork length could be

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converted to TL for analysis. Any records where FL was recorded as greater than TL were excluded from the model. Various resolutions were given for catch location. For this reason, any reported catches and recaptures were broken into the following categories: Country, Province, DU, Region (Cobequid Bay, Minas Basin-including both Central Minas Basin and Southern Bight, Chignecto Bay, Cabot Strait, Gulf of St. Lawrence, Northumberland Strait, Bay of Fundy) and location, which was usually identified by river or name of the shore fished.

Biological

Biological characteristics for the Bay of Fundy population were summarised each year for means and ranges of length and weight, as well as length frequencies. Variability in the data is presented as ± standard deviation (SD) unless otherwise stated. These characteristics were compared to capture method to assess gear selectivity. Length was also used in CMR analysis for mean TL at both mark and recapture to assess changes in size cohorts tagged over time.

Weight-Length Relationships

The weight-length relationship of Striped Bass in the BoF was calculated using a LM of the $\log_{10}$ length and $\log_{10}$ weight of individuals. To visualise this relationship, predicted values were back transformed utilizing a correction factor from the R package 'FSA' to reduce bias (Ogle *et al*., 2021; Sprugel, 1983). This dataset was compared to the SGoSL population with data gathered from the Miramichi Striper Cup tournament using the same LM model. Interactions between DUs were assessed using a multiple LM. Only data from the same month (May) were used for comparison to minimize potential

seasonal changes. The influence of season on weight-length relationships were also explored using a multiple LM.

Capture Mark Recapture

CMR analysis was conducted only on those tags marked by this study. Results from tag data analyses were used to describe movement, time-at-liberty, and growth. The general trends of movement were determined by looking at the percent recapture by location and region from where they were originally tagged. The number of bass tagged, and number of bass recaptured were summarised by both location and year. The number of total recaptures was divided by the total number of applied tags and multiplied by 100 to determine overall recapture rate. Recapture rate per year was calculated by dividing the total number of recaptured individuals each year, which may include bass that were tagged in previous years over the total number of individuals tagged to date and multiplied by 100 for percentage. Time-at-liberty and the maximum number of recaptures for individual bass were calculated.

Growth

The typical model for observing growth is the von Bertalanffy growth model (von Bertalanffy, 1938). This model uses the formula:

$$E(L_t) = L_\infty\left(1 - e^{-K(t-t_0)}\right) \qquad \text{Eq. 1}$$

where $E(L_t)$ is the expected or average length or weight at time (or age) t , L_∞ is the asymptotic average length or weight, K is the exponential rate of approach to the asymptotic average length or weight in years, and t_0 is a non biological parameter that is used to correct the model for the time or age when the average length was zero, so that the model passes through the origin (von Bertalanffy, 1938; Ogle, 2018)

The von Bertalanffy model makes several assumptions that fit most fisheries, such as fish reaching an asymptotic length with increased age. It also assumes that individual fish of the same species have the same growth curve. Values of L_∞ and K in von Bertalanffy models are typically calculated using length and age. Two methods are used to age fishes: scales and otoliths. Otoliths require destructive sampling (killing fish) but generally provide more accurate ages. Scales are also used, but for striped bass, scales are not as accurate as otoliths especially for larger individuals (Secor *et al.*, 1995); in addition, aging fish is a time-consuming activity. An alternative to using age is to use change in length and change in time; CMR analysis provides both of those variables.

Individual bass selected for analysis had been recaptured at least once and had TL measured (not estimated) for both the initial marking and recapture. If an individual was recaptured more than once, TL and time between each recapture was used. Time-at-liberty was estimated in days, thus individuals recaptured within 24 hours of tagging were excluded. Instances of negative growth were removed from the analysis as they were likely caused by measurement error (e.g., precision to 5 mm on one measurement and 1 mm on another) or recording error. Using the CMR changes in TL and changes in time both L_∞ and K values were calculated using three growth models: Fabens, Wang, and Francis.

The Fabens model (Fabens, 1965) estimates the difference in length between tagging and recapture and using the formula:

$$E(L_r - L_m) = (L_\infty - L_m)(1 - e^{-k\Delta t}) \qquad \textit{Eq. 2}$$

where L_r is the length at recapture, L_m is the length at marking, and Δt is change in time. This model makes the following assumptions: the hypothetical age in which the species

has 0 length is 0, assumes growth curves can be fitted to a collection of individuals, ignores individual growth variation, as change in length declines with a larger L_m, the variability of residuals decreases, and shows the growth of individuals rather than average length given a certain period (Fabens, 1965).

The Wang model (Wang, 1998) modifies Eq. 2 to account for variability in individual growth:

$$E(L_r - L_m) = \lim + \beta(L_t - L_t) - L_m(1 - e^{-k\Delta t}) \qquad \text{\textit{Eq. 3}}$$

where β is a parameter describing the variability in individuals. With this new parameter, the Wang model improves the Fabens model because it allows the average maximum length and growth rate to vary among individuals. The Wang model also assumes that parameter t_0 is 0 because it cannot be estimated from tagging data when age is unknown, it assumes there is both model and measurement error, and it ignores measurement error as it is considered negligible when compared with individual variability (Wang, 1998).

Finally, the Francis model (Francis, 1988) also includes individual variability, but is derived using a medial length set between two arbitrary lengths. The Francis model uses the equation:

$$E(L_t) = L_1 + (L_3 - L_1) \frac{1 - r^2 \frac{t - t_1}{t_3 - t_1}}{1 - r^2}$$

$$where \; r = \frac{L_3 - L_2}{L_{2 - L_1}}$$

Eq. 4

L_1, L_2, and L_3 are the mean lengths at ages t_1, t_2, and t_3, respectively. The t_1 and t_3 are arbitrary reference ages (and t_2 is half-way between each) but are generally a relatively

young (i.e., t_1) and old (i.e., t_3) age. This model makes the following assumptions: for short times at liberty, the residuals are caused mostly by errors in the measurement of length at tagging and recapture, and as the time-at-liberty increases so does the contribution from growth variability, the growth of a fish of length at marking (L_m) over a time increment is normally distributed, the greater the expected growth, the greater the scope for variation in growth, and any outliers are distributed uniformly over some range is quite arbitrary and not supposed to represent reality.

All parameters for Fabens, Wang, and Francis models were calculated using the R packages 'FSA' (Ogle *et al*., 2021), and 'nlstools' (Baty *et al*., 2015). Once calculated, parameters were used in a typical von Bertalanffy equation and plotted as size-at-age for comparing with historical Striped Bass studies. Model fit to the data was analyzed by observing the spread of residual vs fitted values, and models were evaluated using Akaike's Information Criterion (AIC). Growth parameters from this study were compared to historical growth data in the Minas Basin, NS (Broome, 2014; Rulifson unpublished data), in Kouchibouguac Park, NB (Melvin, 1979), Annapolis River, NS (Harris, 1988), as well as historical growth data from Chesapeake Bay, U.S.A. (Vladykov and Wallace, 1952). L_∞ values from Broome (2014), Melvin (1979), and Harris (1988) were provided as FL, thus, to allow for comparison, values were converted to TL using the FL to TL relationship calculated in this thesis. Growth parameters from all studies were plotted onto a von Bertalanffy growth curve for a visual comparison.

Results

Data Sources

Angler Participation

Angler participation provided much information to this study. In eight annual tournaments between 2010–2019, 885 Striped Bass were collected from angling in the BoF; for the 2015–2019. A total of 2,186 entries were recorded from the Miramichi Striper Cup in the SGoSL (Table 2.2). In addition to tournament participation, angler logbooks and sporadic fishing reports through reporting recaptured tags, outreach activities, and social media were collected from 2002–2019, resulting in 1,992 fishing effort records. A total of 1,970 bass were caught and 22 records where bass were targeted but not caught. Of the caught bass, 130 were reports of tag recaptures for a recapture rate of 29.7% by recreational anglers.

Partner organizations and historical data

A total of 2,018 bass records were provided by partner organizations and other researchers. Rulifson provided 1,758 records of bass from Minas Basin and associated rivers during the 1984–1993 period. Fort Folly Habitat Recovery provided 133 records of bass caught in the Petitcodiac River in 2016, and Dadswell provided 68 records of bass caught in Annapolis River system in 1981–1982. A total of 59 records of recaptured bass from this study were provided by DFO via their trap net in Enfield, NS during the 2008–2017 period.

This study

The gathering of data on Striped Bass outside of tournaments and angler records for this project occurred between 2008–2019 primarily alongside commercial fishing

operations. A total of 5,527 fishing effort records were recorded for this study, of which 5,468 bass were caught and 59 effort records where bass were not caught.

Population Characteristics

Length-Length

The FL-TL relationship of Striped Bass in the Bay of Fundy was calculated from 2,453 fish from 1982–2020 using a LM. FL ranged 4.8–105.4 cm (mean = 38 cm) and in TL from 7.9–107.9 cm (mean = 41 cm) (Figure 6).

The functional relationship for predicting FL from TL was

$$TL = 0.84 + 1.06 \times FL$$

<div align="right">*Eq. 5*</div>

Standard error was ± 0.001 (slope) and ± 0.058 (intercept) with a strong linear relationship ($r^2 = 0.99$).

Biological Characteristics

A total of 7,728 Striped Bass captured from the Bay of Fundy during the 1981-2019 period were measured for length, weight, or both. Individual TL ranged 2.4–123 cm with average TL of 43.7 ± 18.1 cm (Figure 7). Individual weights ranged 0.00009–22.7 kg with an average weight of 2.6 ± 2.9 kg (Table 3). Length-frequency was also compared for changes in size cohorts over time in relation to regulation changes in retention size (Figure 8). Commercial herring weirs in the Minas Basin provided the greatest number of records, providing data for 6,477 bass. Bass caught in weirs were 7.9–123 cm with an average of 38.3 ±12.5 cm. Recreational angler-caught fish were 6.3–115 cm with an average of 62.3 ±21 cm. Trawls targeting larger bass ranged 68.4–89.5 cm and an average of 80 ±7 cm. Gill net captures ranged 9.5–117.4 with an average of 60.5 ±21.9 cm. Trap net captures were only provided for recaptured bass. The TL ranged 33–

61.3 with an average of 45.6 ±6.1 cm. Fyke nets used by Fort Folly Habitat Recovery and

SBRT were used to target smaller bass with TL ranging 2.4–70.5 with an average 10.8

±14.2 cm (Figure 9). During this study 153 females and 176 males were identified.

Weight-Length

The weight-length relationship of Striped Bass in the Bay of Fundy (n=911) from

years 1985–2018 using a LM (Figure 10) was

$$Log(W) = 3.12 * Log(L) - 11.93 \qquad \textit{Eq. 6}$$

Standard error was ± 0.01 (slope) and ± 0.05 (intercept) with a strong linear relationship

($r^2 = 0.98$). The weight-length relationship of bass in the SGoSL (n=655) from 2015–

2019 using a LM (Figure 11) was

$$Log(W) = 2.68 * Log(L) - 10.16 \qquad \textit{Eq. 7}$$

Standard error was ± 0.04 (slope) and ± 0.18 (intercept) with an $r^2 = 0.85$. To compare

these two DUs a multiple linear regression model was used on data from 1992–2019

(n=817). The Bay of Fundy had a higher weight-length curve than the SGoSL population

but also had wider confidence intervals (Figure 12). The functional relationship for

weight-length between these management units was

$$BoF \ Log(W) = 2.82 * Log(L) - 10.67 \qquad \textit{Eq. 8}$$
$$SGoSL \ Log(W) = 2.82 * Log(L) - 10.67 + (-0.06) \qquad \textit{Eq. 9}$$

This model had an $r^2 = 0.88$. The weight-length of seasonality was compared using a

multiple linear regression model on Bay of Fundy bass (n=911) for the period 1985-2018.

No weights were recorded in winter months so only spring (n=192), summer (n=400),

and fall (n=186) seasons were compared (Figure 13). The functional relationship had a

linear relationship of $r^2 = 0.91$; the relationship between those seasons was

$$Fall\ Log(W) = 2.91 * Log(L) - 11.4 \qquad \text{Eq. 10}$$

$$Spring\ Log(W) = 2.91 * Log(L) - 11.74 \qquad \text{Eq. 11}$$

$$Summer\ Log(W) = 2.91 * Log(L) - 11.78 \qquad \text{Eq. 12}$$

Capture Mark Recapture

A total of 1,702 Striped Bass were tagged during my study for years 2013–2019; 89.5%

were tagged in the Minas Basin and the remaining 10.5% tagged in Cobequid Bay. As of

26 July 2019, a total of 437 recaptures were reported: 387 belonged to this study with the

remaining 50 recaptures belonging to Jeremy Broome (Broome, 2014; n=27), DFO

Dartmouth (Bedford Institute of Oceanography; n=7), DFO Moncton (n=4), Mike

Dadswell (n=3), Sam Andrews (Andrews *et al*., 2018; n=1), Roger Rulifson (n=1), and

source undetermined (n=5). Of the 387 recaptures belonging to this study, 322 unique

bass were recaptured with individuals recaptured as many as four times (Figure 14; Table

4). Across all years an overall recapture rate of 22.7% was achieved. Yearly recapture

rate varied from 1–9.2% (Table 5). The highest recapture rate locations in each region

were Bramber, NS (Minas Basin) and the Shubenacadie-Stewiacke River System

(Cobequid Bay) (Table 6). Recaptured bass were at liberty on average 473 ± 462 days

(range 0–2,093 days) post tagging. Average TL of marked individuals was 46.2 ± 13.1

cm and average TL of recaptured individuals was 51.4 ± 12.7 cm. Average TL of marked

individuals increased annually starting in 2015, and average TL of recaptured individuals

increased annually except for in 2016 and 2019 (Table 7). A size cohort of 30–39? cm

was tagged the most and a cohort of 40–50 cm was recaptured in the highest abundance

(Table 8). Recaptures reflected tagging location with the greatest number of recaptures

occurring in the Minas Basin (n=275), followed by Cobequid Bay (n=85), and other regions in the BoF (Chignecto Bay; n=2). Across the region, bass were recaptured in 38 rivers and shorelines (Table 9). Many recaptures occurred within the vicinity of where individuals were initially marked. All bass tagged herein occurred over a period of 7 years in the Minas Basin-Cobequid Bay, and to date only two bass were recaptured outside of this region (recaptured in Chignecto Bay). These two bass were tagged within two weeks of each other in Bramber, NS and were large adults (>80 cm TL), recaptured more than one year at liberty. Two additional tag recaptures provided by anglers for tags applied by Broome (2014) were reported in Chignecto Bay, and all four bass were recaptured in the fall (August and September).

Growth

Growth was calculated using recapture data from 2014–2019. L_m range was 23–82 cm TL, and the L_r range was 33.5–88.9 cm TL. Difference in time-at-liberty ranged 0–5.7 years and difference in TL ranged 0–36.1 cm. The Francis growth model estimated the lowest L_∞ (89.9 cm) followed by Fabens (107.5 cm) and Wang (131.3 cm). Fabens yielded the highest K (1.44) followed by Francis then Wang at 0.15 and 0.07, respectively (Table 10; Figure 15). The same models were also calculated using recapture data from 1985–1993 for 56 Striped Bass provided by Rulifson in the Minas Basin. L_m ranged 22.4–50.7 cm TL, and L_r ranged 24.2–80.3 (Figure 16). Difference in time-at-liberty ranged 0–7.6 years and difference in TL ranged 0.3–46.2 cm. Upon applying the same models to the data provided by Rulifson, the models did not follow the same trend. Across all models applied to Rulifson data, L_∞ and K values were less variable. Wang and Francis growth models estimated very similar, lower, L_∞ and K values with the

46

highest values being produced by the Fabens growth model (**Error! Reference source not found.**). These are visualised to historical growth data on the von Bertalanffy growth curve (**Error! Reference source not found.**).

Discussion

There remain several information gaps on the BoF Striped Bass DU pertaining to population demographics. However, combinations of large datasets that use catches and effort from multiple gear types and size ranges over many decades can be very informative for fisheries management. Information sharing through partnerships and collaborations as well as outreach and angler participation have been very impactful to these results and we hope will continue to provide additional information to address further knowledge gaps into the future.

In many instances biological characteristics of Striped Bass described in this chapter are comparable to values determined by other researchers (Melvin, 1979; Harris, 1988; Broome, 2014). Length-length linear regression for FL-TL was described to have a y-intercept of 0.84 and a slope of 1.06, which is comparable to Cook (2003) ($TL = 1.04 * FL + 0.1$) completed on hatchery raised juveniles collected from the Shubenacadie River, and that of Mansueti (1961) on bass caught in Chesapeake Bay (slope = 1.07, intercept not reported). Given that current and historical regulations require retention by TL and many historical studies used FL, periodic validation of this relationship can be helpful for comparing data from past studies and to convert data collected by anglers using FL.

Striped Bass were caught across multiple size cohorts because of multiple gear types. Commercial herring weirs provided the highest abundance of bass records, but the location was where the most effort was spent due to its ease of access, beneficial relations with the fishers, and good bass recovery rates post-handling. Angling records of bass were beneficial for increased effort across multiple locations within the Minas Basin and

targeting multiple size classes. Most angler reports came from the southern bight eco-region largely because the SBRT was present; it is suspected that if more effort were placed in northern shore of Minas Basin or other areas in BoF that catch reports would be higher. Gill nets are also beneficial for catching specific size ranges using targeted mesh size and is commonly used capture method for bass monitoring and research (Friedmann, 1991; Jessop, 1991; Rulifson and Dadswell, 1995). This gear type makes up most captures in the vicinity of the Avon River, NS. This method would be advantageous to explore presence in other rivers. Most of the gillnet catches were not actually by the opercula but rather just tangled and easily removed, allowing for minimal mortalities when paired with short set times. Trap nets can be useful for juvenile to adult catches and standardized monitoring; however, it requires regular checks, typically requires boat access, and only provides a snapshot of bass at that location. In this study we only received data from recaptured SBRT bass from trap nets. Fyke nets target smaller size classes; however, can prove difficult to set given site conditions (excess mud or flow, limited anchoring options. I recommended to use this gear on a continuing basis in additional locations or to combine with YOY beach seines collected by DFO. Trawl effort was minimal and thus provided a small sample size but provided records for larger bass. Exploring the use of trawls and/or joining recreational anglers by boat would allow for exploration of occurrence in the middle of the basin, in deeper waters, and larger size cohorts. Across all gear types, most records were successful in a minimum having a date, location, tag number (if applicable) and length. Other information on time fished, weight, sex, and angler gear and fish health was not always recorded and could be improved in the future.

Weight-length relationships were all statistically significant. Rulifson and

Dadswell (1995) completed an Atlantic-wide comparison of weight-length studies for

Striped Bass. The slope of the BoF regression was comparable to studies listed in the

Dadswell and Rulifson summary; however, the intercept was higher than most reported

studies except a study completed by Dadswell (1976) in the Saint John River, NB. The

weight-length relationship completed for Miramichi River bass recorded during the

Miramichi Striper Cup had a lower slope and intercept indicating that bass in the BoF DU

grew heavier than SGoSL bass per unit length. Since the Miramichi Striper Cup

tournament occurs in the spring, factors such as sex, gonad development, and feeding

behaviour could affect these values. Comparing the two populations, BoF had a higher

slope and wider confidence intervals suggesting that this population is growing heavier

per unit length than the SGoSL population during the month of May and can be an

indication of increased availability of prey, or perhaps reaching maturity faster. However

wide, overlapping confidence intervals suggest that further study is needed. Comparing

weight-length by season was significant. Model predictions showed that bass caught in

the summer had the highest increase in weight, followed by spring and fall, respectively.

Tag application was greatest at the Bramber, NS weir followed by fishing

tournaments hosted by the Sipekne'katik First Nations (LSK Kids tournament and

Sipekne'katik Shubenacadie Striped Bass Derby). Both these venues allowed for ease of

capture and release, were highly collaborative for this research, and held high

stewardship for the health of the fish. All bass tagged herein occurred over a 7-year

period in the Minas Basin-Cobequid Bay, and to date have had only two bass recaptured

outside of this region (recaptured in Chignecto Bay). These two bass were tagged within

two weeks of each other in Bramber, NS and were large adults (>80 cm TL) recaptured more than one year at liberty. Two tag additional recaptures reported by anglers from tags applied by Broome (2014) were reported in Chignecto Bay as well, and all four bass were recaptured in the fall (August and September). However, Broome (2014) initial tag application data could not be retrieved to identify further similarities among these individuals and no further recaptures of these individuals have been reported to identify further movement trends. Multiple recaptures of the same individuals occurred with some individuals recaptured as many as four times (Figure 14). Other CMR studies on bass found movement in and out of the Minas Basin; however, these are minimal in comparison to the total bass tagged in the BoF (Nichols and Miller, 1967; Rulifson *et al*., 1987; Rulifson and Dadswell, 1995; Broome, 2014; Keyser, 2015; Andrews *et al*., 2017). With the number of bass tagged during this study and over many years, it is likely that most bass in Minas Basin stay within the Minas Basin; see Chapter 3.

Modelling of Striped Bass growth using tag-recapture models found differences likely driven by changes in biological patterns of bass over time, model parameters, model assumptions, and primary residency or genetic origin of bass. Tagged bass used in the model were caught in the Minas Basin; however, it does not necessarily mean they are BoF origin. Indeed, some bass used in modeling may have been from any of the three historical spawning rivers in the BoF or migrants from the U.S.A., which may have different growth rates adding to model uncertainty. However, this uncertainty would be true of most growth studies completed on BoF bass.

Models were comparable in some respects to other growth described for bass using traditional age-at-length methods. The rate of growth to reach the asymptote, *K*,

produced similar predictions as traditional age-at-length except for the Fabens model, which trended higher. The predicted L_∞ from the Wang model in 2013–2018 recaptures were high but are comparable to L_∞ predictions in the SGoSL (Melvin, 1979) and Annapolis River (Harris, 1988). The lower model estimation of L_∞ predicted by the Francis model is like predictions described for Chesapeake Bay (Vladykov and Wallace, 1952) and Minas Basin (Broome, 2014) (**Error! Reference source not found.**). In using the Francis model, comparison of growth parameters is not valid when estimated from direct ageing versus tag recapture data (Francis 1988). Upon comparing Fabens, Francis, and Wang models on data from 2013–2018, the Wang model estimated the highest L_∞ and the Fabens model estimated the highest K. On the Rulifson data from 1985–1993 the Fabens model estimated both the highest L_∞ and K. These values indicate that in the 2013–2018 data the Wang model predicts that a fish (or an average fish in the population) would be larger, and the Fabens model predicts that a fish (or an average fish in the population) will grow faster than the other models. With the Rulifson data the Fabens model predicted the largest and fastest growth, suggesting that historically bass in the basin had an increased growth rate. All models were heteroscedastic likely caused by greater variability in difference in length at a greater difference in time and minimal records of longer time-at-liberty. Using AIC, the Francis, Wang, then Fabens performed best on the 2013–2018 data, respectively and the Wang, Francis, then Fabens performed the best on the Rulifson data. Ortiz (2017) utilized mark-recapture data to observe growth of Atlantic Yellowfin Tuna *Thunnes albacares* (Bonnaterre, 1788), using models described by Francis and Wang. The recapture data used by Ortiz is like Striped Bass herein as it spanned a wide range of lengths (11–190 cm) and across multiple years for

time-at-liberty (max= 7.15 years at liberty). Analogous to the predictions of our model outputs, Ortiz observed a higher L_∞ and lower K in the Wang model in comparison to the predictions of the Francis model.

Predicting L_∞ and K can assist with management decisions as informs when fish will reach retention size, or how quickly maturity is reached and fish begin contributing to the population. Using CMR is less time consuming than age-at-length data provided that a tagging program has already being implemented. Further exploration of using this approach should be considered given increased tag returns and more quality tag recapture data as it should improve the analysis. It is also recommended since there is a large geographic distribution of bass across the Atlantic coast, prey availability and length of feeding season vary and could be tested to explore changes in growth by location. With these data we described Bay of Fundy Striped Bass with mostly opportunistic non-standardized sampling in the Minas Basin. We have provided an estimate of growth rate, weight-length relationships by season, and compared neighbouring populations for differences in length frequency. It is recommended that further analysis be completed on these data such as fishing effort, angling pressure, mortality, population estimates, site fidelity, and occupancy-presence within the basin. It is also recommended to expand the tagging program to target specific sizes and locations to address growth gaps, and movements by size class and location. Some of these recommendations could be implemented by expanding angler participation in the tagging process as is done by the American Littoral Society (ALS). Although bass in the Minas Basin were described, it is possible that a proportion of the bass caught and described within this chapter are

migrants from the U.S.A., thus the question of genetic origin and influence on migration still remains. This information gap is explored in Chapter 3.

Table 1. Summary of commercial, recreational, and aboriginal regulation changes for Striped Bass *Morone saxatilis* in the Bay of Fundy Designatable Unit (summarized in Bradford et al., 2012).

Year	Management Action
1978	Commercial: Licensed fishery ceased, no targeted harvest permitted.
1994	Recreational: Reduced bag limit from 5 to 1 fish per day.
	Recreational: Retention Size Limit Increased: ≥48cm TL.
1995	Recreational: Retention Size Limit Increased: ≥58cm TL.
1996	Bycatch: Federal regulations amended to prevent retention and sale of incidentally captured Striped Bass in any other licensed fishery.
	Recreational: Retention Size Limit Increased: ≥68cm TL.
1997	Bycatch: Minas Basin weir fishers permitted retention of one fish ≥68cm TL per day.
	Bycatch: Shubenacadie drift net fishers permitted to retain: 3 fish (>3.6kg) per day.
	Bycatch: Shubenacadie River Gaspereau dip net fishers to release all Striped Bass.
	Bycatch: Saint John River drift net and trap fishers permitted to retain one fish ≥68cm TL.
	Bycatch: Stewiacke River upstream of Stewiacke Landing closed to drift netting, and shad
	season shortened by 2 weeks (May 31st closure).
2003	Bycatch: Shubenacadie River Gaspereau fishery not permitted at night during peak Striped Bass migration from Grand Lake.
2008	Aboriginal: Agreement reached on retention restrictions for subsistence and ceremonial harvest.
	Recreational: Hook and release only of Striped Bass from about mid-May to mid-June for the following waters: the inland and tidal waters of Grand Lake and the Shubenacadie River downstream to its confluence with the Stewiacke River, and the inland and tidal waters of the Stewiacke River downstream from the highway bridge (Pollock Bridge) in Stewiacke East to its confluence with the Shubenacadie River.
	Recreational: Artificial fly and single hook, or un-baited lures only, regardless of the species being fished, from about mid-May to mid-June for: tidal waters of the Shubenacadie River downstream from the CN Railway Bridge at East Milford to its confluence with the Stewiacke River, and the inland and tidal waters of the Stewiacke River downstream from the highway bridge (Pollock Bridge) in Stewiacke East to its confluence with the Minas Basin.
	Bycatch: Weir fishers limited to a maximum seasonal catch of between 10 and 40 Striped Bass ≥68 cm TL. The allocation is based on site and personal use requirements and is intended to cap retention across a 3-4-month season.
2009	Bycatch: Shubenacadie shad drift net fishers reduced from 3 Striped Bass < 8 lbs (3.6 kg) per day to 1 Striped Bass per day, >68 cm TL.
	The transition with time to a common retention limit of one Striped Bass >68 cm TL per day, in all fisheries, and seasons where retention is authorized, is intended to allow for Striped Bass surviving to maturity to have the chance to spawn at least once before their potential removal from the population.

Table 2. Summary of Striped Bass *Morone saxatilis* tournaments attended within the Bay of Fundy and Southern Gulf of St. Lawrence Designable Units from 2010–2019.

Year	Tournament name	Tournament Type	Location	No. bass entries
2010	Bear River Bass Derby	Catch and Release	Bear River, NS	0
2011	Bear River Bass Derby	Catch and Release	Bear River, NS	1
2012	Bear River Bass Derby	Catch and Release	Bear River, NS	6
2013	Bear River Bass Derby	Catch and Release	Bear River, NS	0
2013	Bramber Bass Bonanza	Keeper	Bramber, NS	10
2013	Grand Pre Tournament	Catch and Release	Grand Pre, NS	23
2013	Kids Action Program Walton Striped Bass Derby	Catch and Release	Stewiacke River, NS	22
2014	Kids Action Program Walton Striped Bass Derby	Catch and Release	Stewiacke River, NS	17
2015	Kids Action Program Walton Striped Bass Derby	Catch and Release	Stewiacke River, NS	17
2016	Kids Action Program Walton Striped Bass Derby	Catch and Release	Stewiacke River, NS	58
2017	Kids Action Program Walton Striped Bass Derby	Catch and Release	Stewiacke River, NS	65
2018	LSK School Tournament	Catch and Release	Stewiacke River, NS	49
2019	LSK School Tournament	Catch and Release	Stewiacke River, NS	41
2017	LunkerTrunk Striper Run	Catch and Release	Stewiacke River, NS	4
2015	Miramichi Striper Cup	Catch and Release	Miramichi River, NB	19
2016	Miramichi Striper Cup	Catch and Release	Miramichi River, NB	375
2017	Miramichi Striper Cup	Catch and Release	Miramichi River, NB	634
2018	Miramichi Striper Cup	Catch and Release	Miramichi River, NB	555
2019	Miramichi Striper Cup	Catch and Release	Miramichi River, NB	603
2012	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	83
2013	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	121
2014	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	29
2015	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	101
2016	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	2
2017	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	94
2018	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	68
2019	Sipekne'katik Shubenacadie Striped Bass Derby	Catch and Release	Stewiacke River, NS	74

Table 3. Summary of total length (TL, cm) and weight (kg) data of Striped Bass *Morone saxatilis* in the Bay of Fundy from 1981 – 2019. SD = standard deviation; NA = not available.

Year	Min TL (cm)	Max TL (cm)	Mean TL (cm) ± SD	No of Bass (TL)	Min Weight (kg)	Max Weight (kg)	Mean Weight (kg)	No of Bass (weight)
1981	58.7	117.4	84 ± 17.4	38	NA	NA	NA	NA
1982	56	107.2	86.2 ± 12.6	26	NA	NA	NA	NA
1984	33.5	46.7	36.8 ± 4.9	6	NA	NA	NA	NA
1985	14.6	67.8	30.8 ± 9.4	1062	0.09	2.8	0.7 ± 0.5	231
1986	22.3	67.5	35.5 ± 6.2	304	0.1	1.9	1.2 ± 0.5	18
1987	23.1	75	38.4 ± 17.3	16	NA	NA	NA	NA
1988	34.9	65.5	49.4 ± 9.7	6	NA	NA	NA	NA
1989	49.3	76.2	65.8 ± 12.6	4	NA	NA	NA	NA
1990	79	79	NA	1	NA	NA	NA	NA
1991	69.7	69.7	NA	1	NA	NA	NA	NA
1992	27.3	100.5	65.5 ± 19.8	41	0.11	12.5	4.1 ± 3.9	41
1993	80.3	80.3	NA	1	NA	NA	NA	NA
2002	72.4	72.4	NA	1	NA	NA	NA	NA
2008	33	33	NA	1	NA	NA	NA	NA
2010	27.1	107.9	56.5 ± 18.8	87	0.25	16.28	4.1 ± 2.8	50
2011	30.5	104.1	50.4 ± 18.1	89	1.816	8.61	4.1 ± 1.9	17
2012	15.5	107	48.7 ± 20	512	0.4	14.75	3.5 ± 2.6	132
2013	11.4	105	45.6 ± 15.7	1368	0.11	12.06	4.3 ± 2.7	101
2014	10	123	45.5 ± 18.6	607	2.27	9.52	5.6 ± 1.8	56
2015	10	96.5	46 ± 14.7	851	2.72	7.53	5.9 ± 1.5	16
2016	2.4	102	34.3 ± 25.8	406	0.00009	11.08	1 ± 2.2	202
2017	7.9	104	44.7 ± 17.4	1886	0.004	10.43	2.8 ± 2.8	264
2018	9.5	104.1	56.6 ± 16.4	269	1.57	13.15	5.6 ± 3.4	20
2019	19.2	115	53.3 ± 11.8	138	0.91	22.68	7.3 ± 10.3	4

Table 4. Cumulative multiple recaptures for individual Striped Bass *Morone saxatilis* tagged in the Minas Basin, Nova Scotia, Canada, from 2013–2019.

No of recaptures	No of bass
1	265
2	100
3	18
4	4

Table 5. Percent recapture of tags by year of Striped Bass *Morone saxatilis* in the Bay of Fundy, Canada, from 2013–2019.

Year	Number applied	Number recaptured	Percent recapture of total tagged per cumulative years
2013	555	51	9.2
2014	347	41	4.5
2015	314	98	8.1
2016	45	87	6.9
2017	217	70	4.7
2018	143	22	1.3
2019	81	18	1.0

Table 6. Summary of tags applied and recaptured of Striped Bass *Morone saxatilis* from 2013–2019 by region in Canada.

Region	No of Tags applied	Tags recaptured	% Recaptured of total applied
Bay of Fundy	0	0	0
Chignecto Bay	0	2	0.12
Cobequid Bay	179	96	5.34
Minas Basin	1523	288	17.35
Unknown	0	1	0.06
Total	**1702**	**387**	**22.7**

Table 7. Mean total length (cm) of Striped Bass *Morone saxatilis* by year of marked and recaptured individuals in the Minas Basin, Nova Scotia, Canada, from 2013–2019.

Year	Mean TL at marking	Mean TL at recapture
2013	45.7	NA
2014	42.4	46.4
2015	44.3	48.2
2016	44.6	47.6
2017	50.6	56.8
2018	52.6	67.7
2019	52.1	56.9

Table 8. Total lengths of Striped Bass *Morone saxatilis* tagged and recaptured from 2013–2019 in the Bay of Fundy, Canada.

Size range (cm)	Number of tags applied	Number of tags recaptured
10–20	2	0
20–30	75	2
30–40	623	47
40–50	478	100
50–60	282	69
60–70	115	37
70–80	82	18
>80	38	8
Unknown (no length recorded)	7	103

Table 9. Summary of dart tags applied and recaptured of Striped Bass *Morone saxatilis* from 2013–2019 by location within the Minas Basin, Nova Scotia, Canada.

Location	No of tags applied	No of tags recaptured	% Recapture per location
Avon Estuary	0	2	0.019
Avon River	68	7	0.067
Avonport	0	4	0.038
Bass River	2	3	0.029
Blue Beach	0	1	0.010
Bramber	1340	214	2.060
Cheverie	0	4	0.038
Cogmagun River	8	1	0.010
Dorchester Wharf	0	1	0.010
Economy	0	8	0.077
Gaspereau River	12	11	0.106
Gays River	0	1	0.010
Grand Lake	0	1	0.010
Grand Pre	25	7	0.067
Highland Village	0	1	0.010
Horton Landing	2	0	0.000
Houstons Beach	1	0	0.000
Kempt Shore	0	1	0.010
Kingsport	6	2	0.019
Level	0	1	0.010
Little Bass River	0	1	0.010
Newport Corner	0	1	0.010
Noel	0	1	0.010
Noel Shore	0	1	0.010
Parrsboro	0	2	0.019
Portapique	6	0	0.000
Porters Point	59	4	0.038
Rockport	0	1	0.010
Shubenacadie River	27	71	0.683
St Andrews River	0	2	0.019
Stewiacke River	144	16	0.154
Summerville	0	1	0.010
Walton River	0	11	0.106
Wolfville Harbour	0	2	0.019
NA	2	3	0.029
35 Locations	**1,702 tagged**	**387 Recaptures**	

Table 10. Summary of growth model parameters for Striped Bass *Morone saxatilis* in the Minas Basin and Chesapeake Bay.

Study	Years	Location	Data Type	Growth Model	L_∞ (cm)	K	t_0
Vladykov & Wallace, 1952	1936 - 1937	Chesapeake Bay, U.S.A.	Age-at-length	von Bertalanffy	98.7	0.158	-2.96
Melvin, 1979	1978	Kouchibouguac, NB	Age-at-length **	von Bertalanffy	148.1*	0.059	1.18
Harris, 1988	1987	Annapolis River	Age-at-length **	von Bertalanffy	134.4*	0.11	-0.96
Broome, 2014	2008 - 2010	Minas Basin, NS	Age-at-length	von Bertalanffy	91.4*	0.13	-1.07
Rulifson–This study	1985 - 1993	Minas Basin, NS	CMR	Fabens	113.2	0.78	0
Rulifson–This study	1985 - 1993	Minas Basin, NS	CMR	Wang	110.1	0.14	0
Rulifson–This study	1985 - 1993	Minas Basin, NS	CMR	Francis	110	0.13	0
This study	2013 - 2018	Minas Basin, NS	CMR	Fabens	107.5	1.44	0
This study	2013 - 2018	Minas Basin, NS	CMR	Wang	131.3	0.07	0
This study	2013 - 2018	Minas Basin, NS	CMR	Francis	89.9	0.15	0

* Value recorded as FL for this study, it was converted to TL using a conversion of TL=1.06*FL+ 0.84.

** Lengths are back-calculated from scale annuli
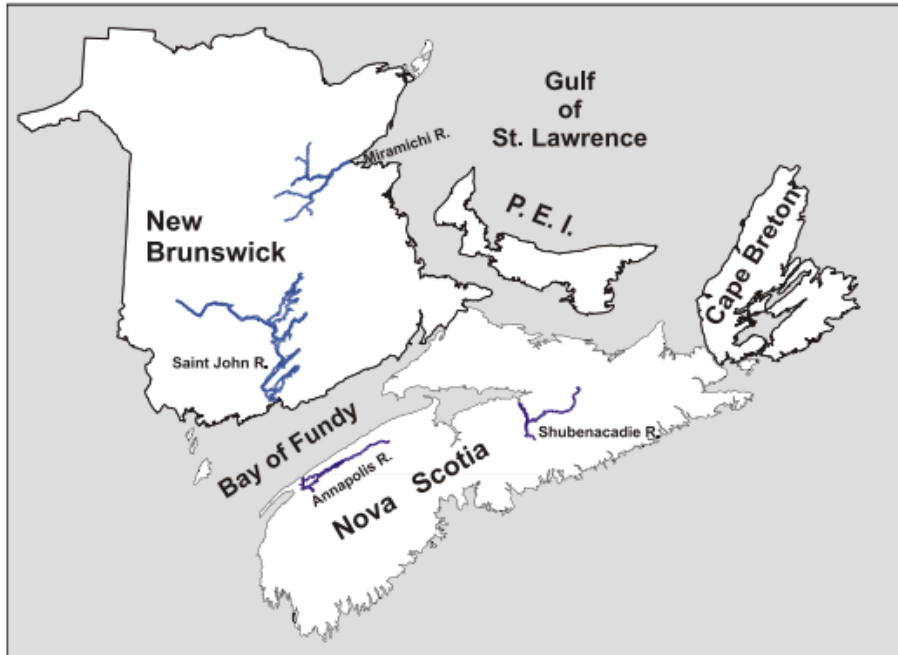
Figure 3. The Bay of Fundy and Southern Gulf of St. Lawrence Striped Bass *Morone saxatilis* Designatable Units and association spawning rivers (DFO, 2012).
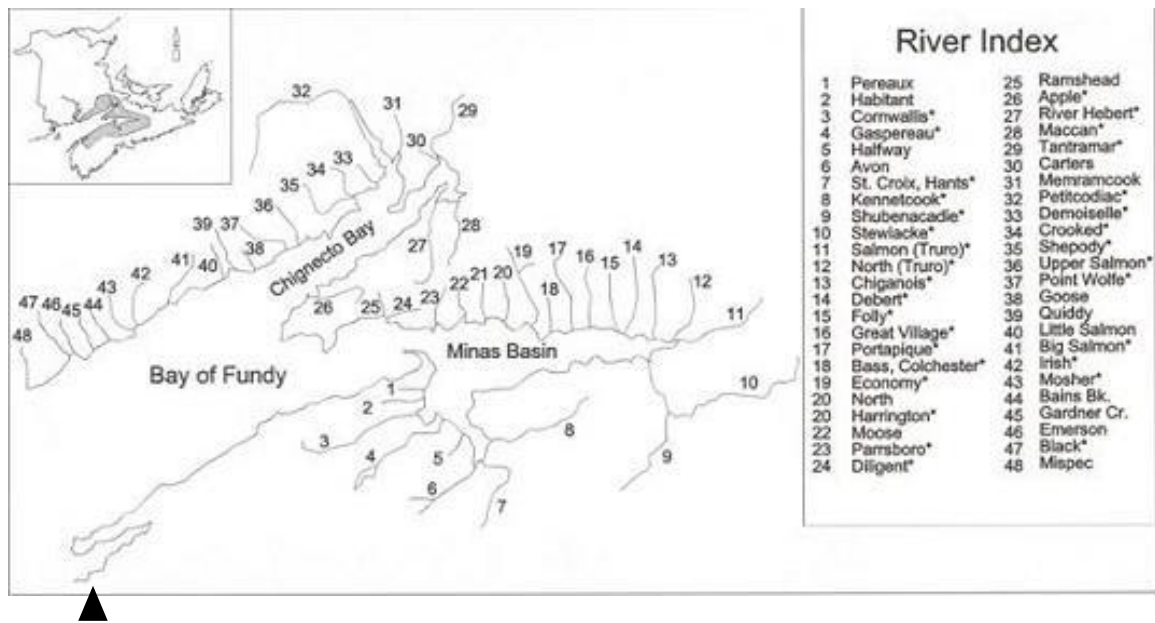
Figure 4. Inner Bay of Fundy and associated drainage rivers. Partner collaborators located on Shubenacadie River (9), Petitcodiac River (32), and the Annapolis River (triangle) (adapted from COSEWIC, 2006).
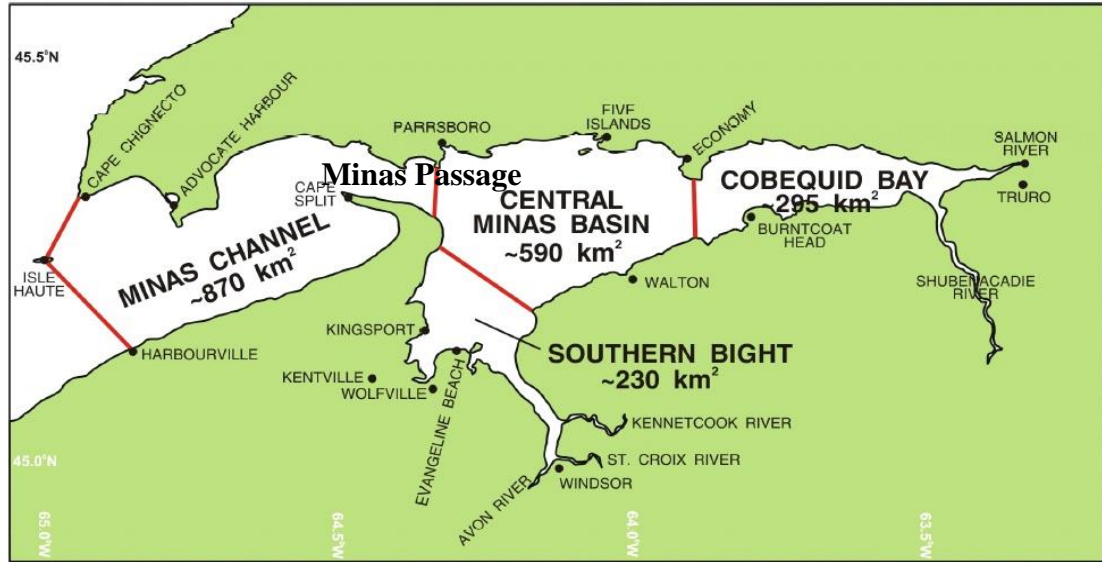
Figure 5. The Minas Basin showing the location and approximate size of the four eco-regions, major rivers, and coastal communities (adapted from Percy, 2001).

TL= 0.84 +1.06 *FL

R^2=0.99
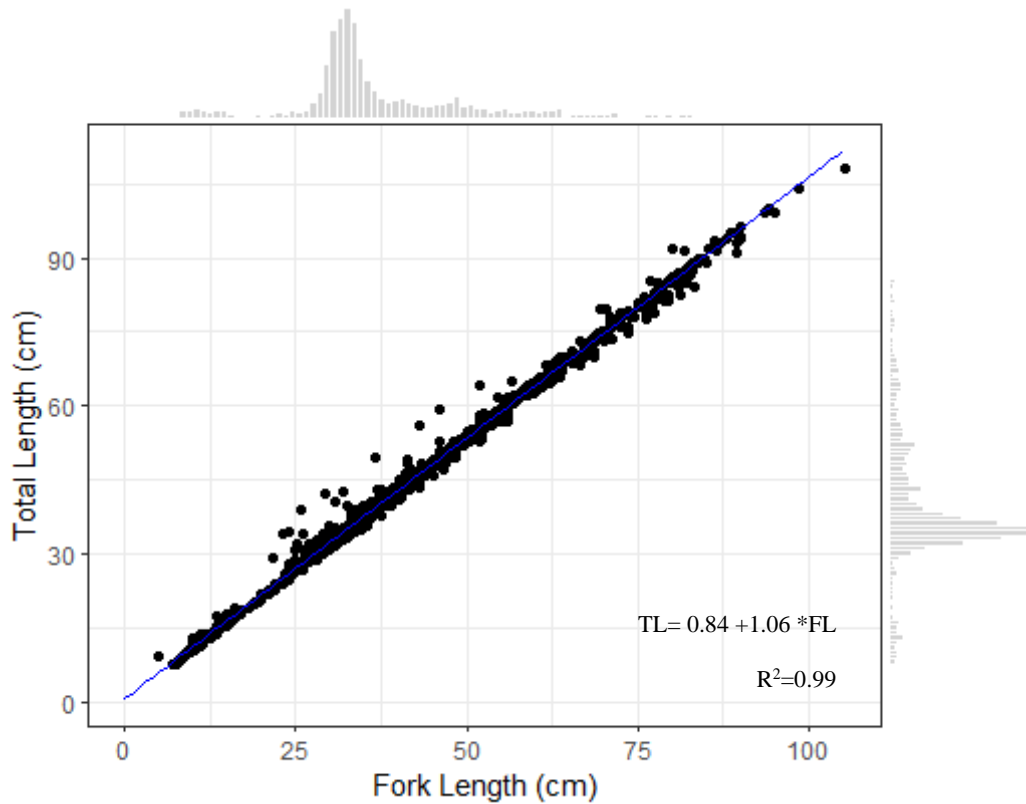
Figure 6. Linear regression model of Fork Length (cm) and Total Length (cm) of Striped Bass *Morone saxatilis* in the Bay of Fundy from 1982–2020 (n=2,453). The histograms of fork length (top of graph) and predicted total length (right-hand side of graph) represent length-frequency.
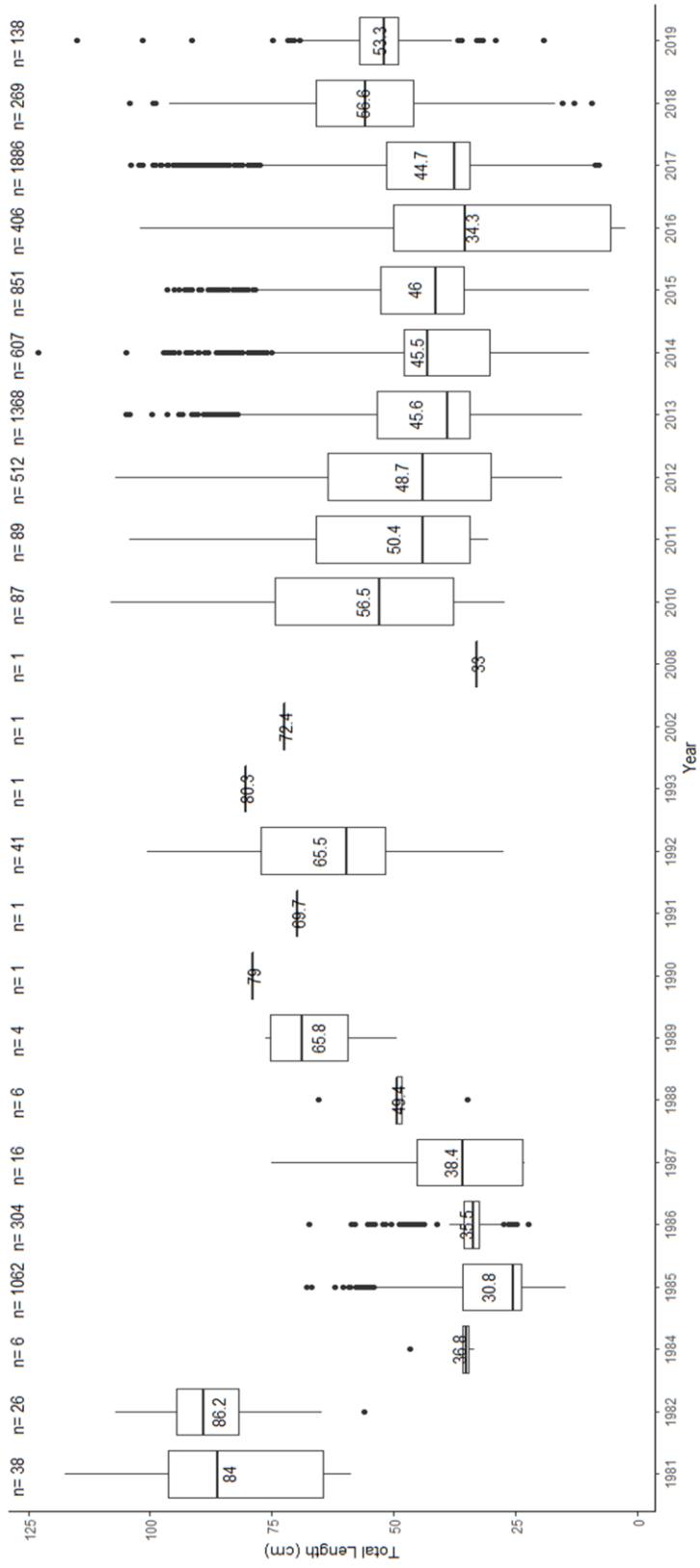
Figure 7. Mean total length of Striped Bass *Morone saxatilis* in the Bay of Fundy from 1981–2019. n indicates number of bass, and numbers inside of boxplots indicate mean. n = number of Striped Bass.

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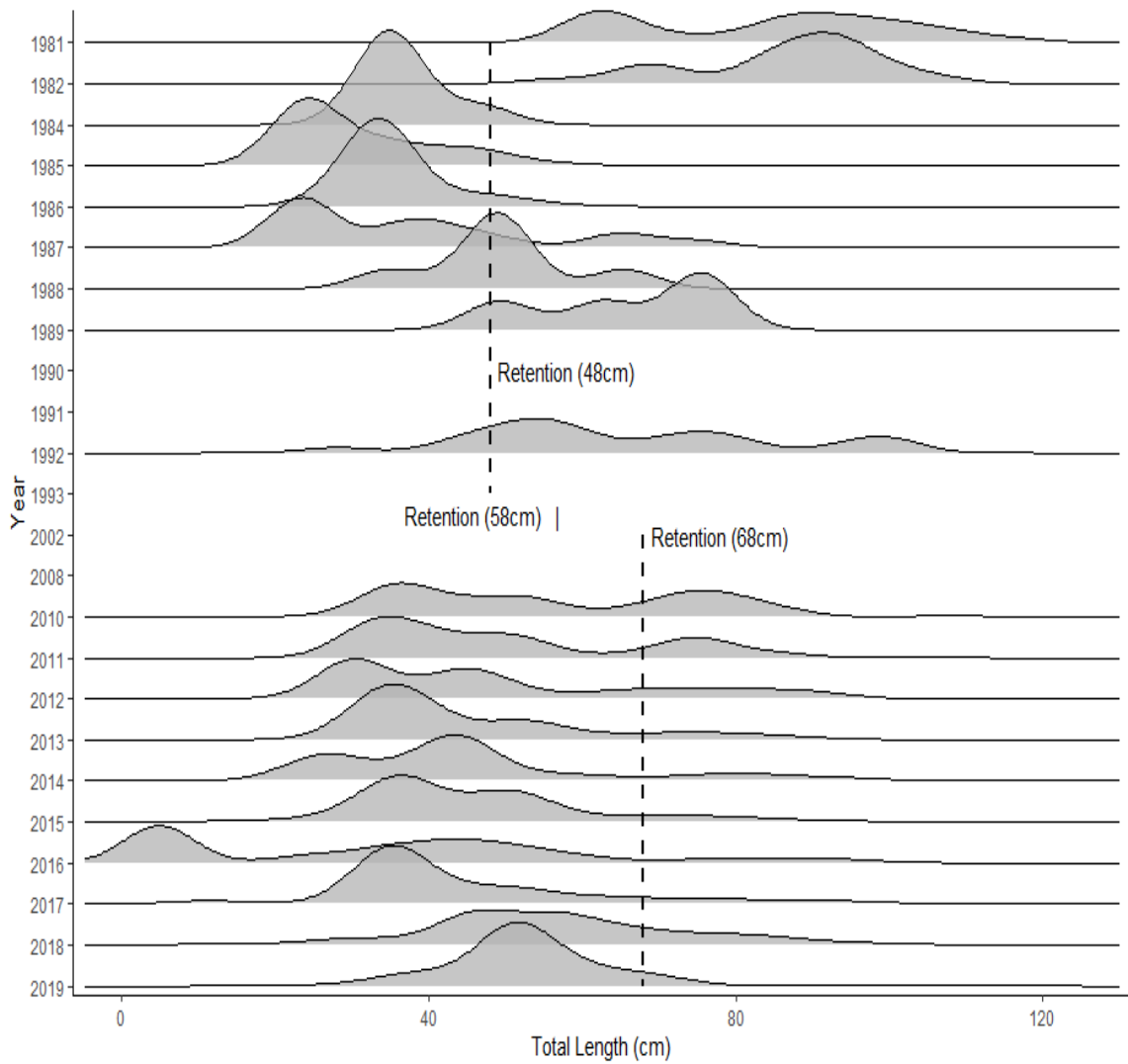
Figure 8. Length frequency of Striped Bass *Morone saxatilis* in the Bay of Fundy, Canada from 1981–2019. Dotted line indicates maximum size of retention.
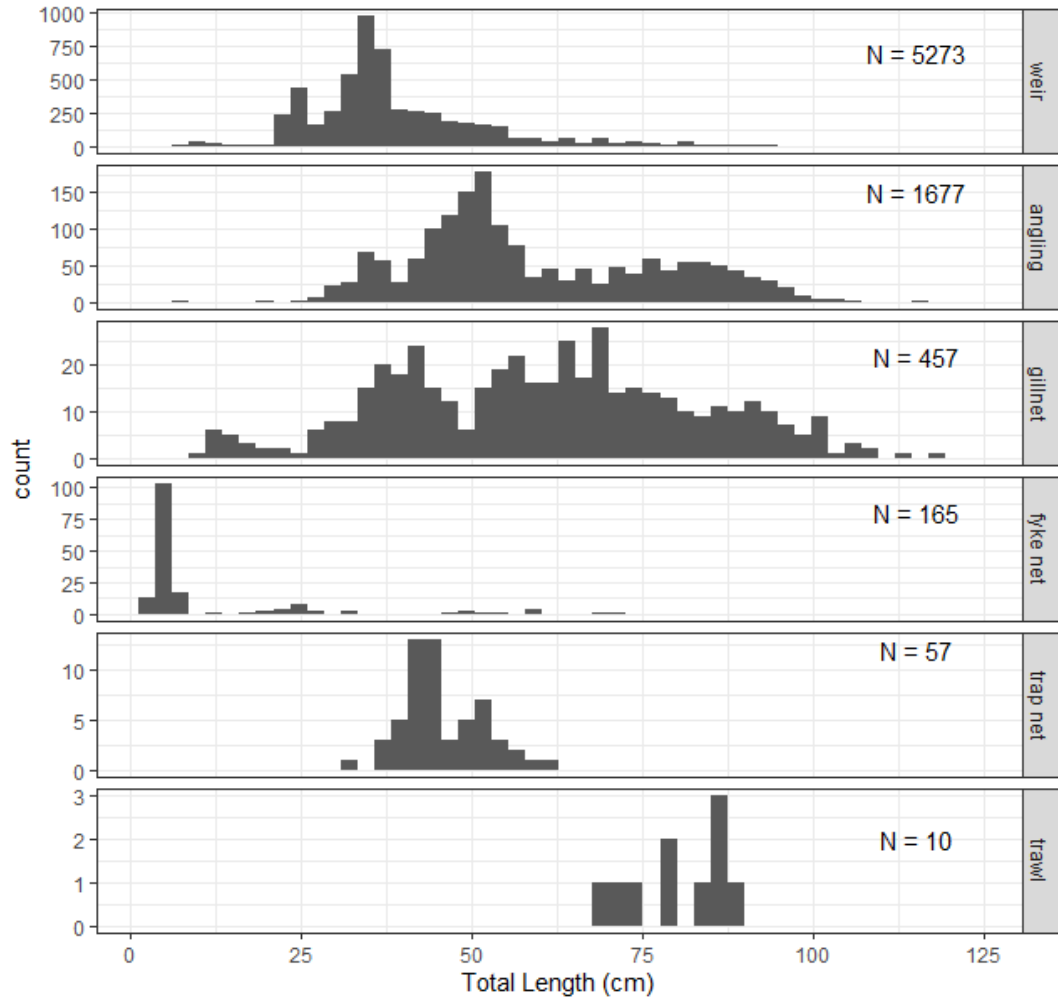
Figure 9. Length Frequency of Striped Bass *Morone saxatilis* caught by 6 different fishing gear in the Bay of Fundy from 1984–2019. N = number of Striped Bass.
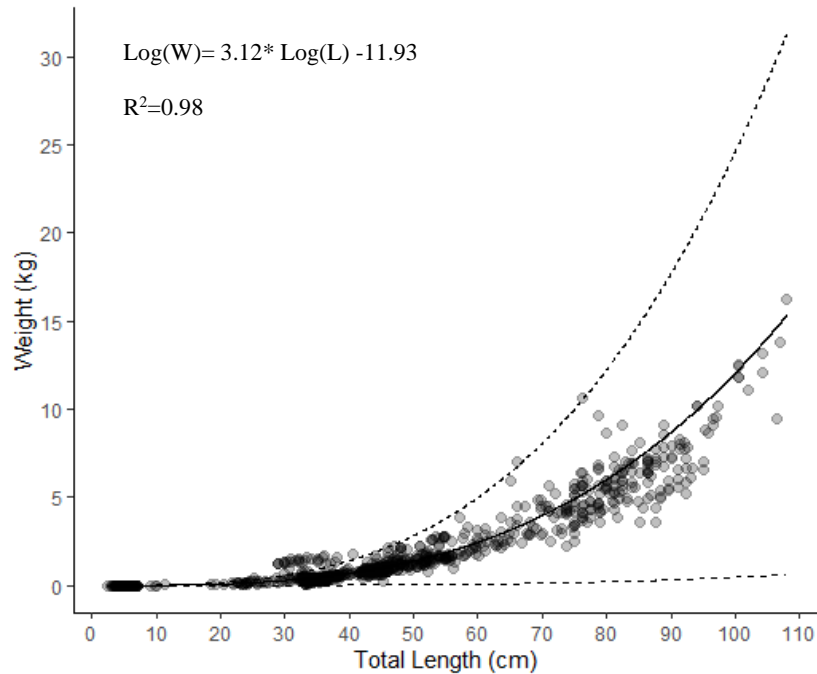
Figure 10. Weight-length relationship of Striped Bass *Morone saxatilis* in the Bay of Fundy, Canada, from 1985–2018 from measured values. Dotted lines represent confidence intervals of model predicted values.
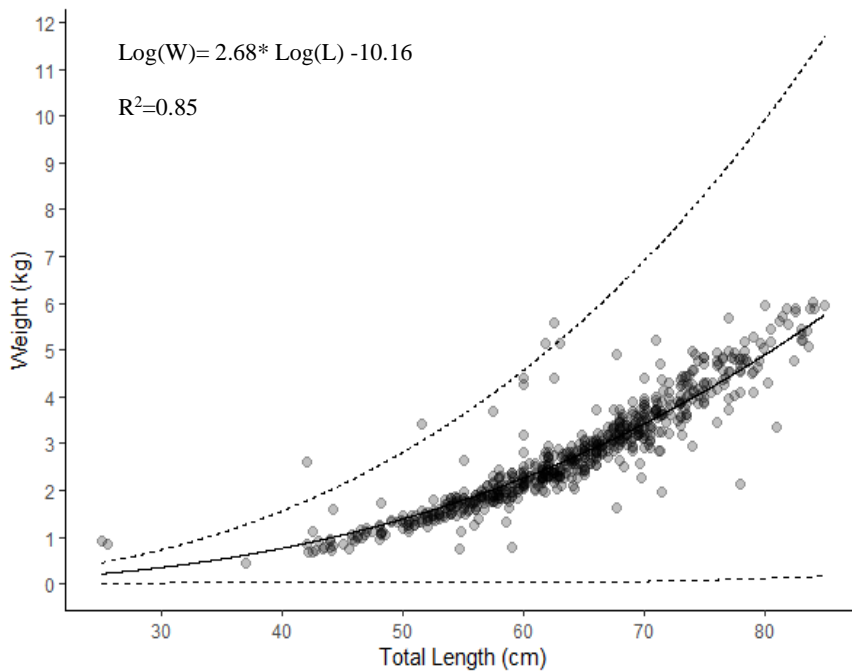
Figure 11. Weight-length relationship of Striped Bass *Morone saxatilis* in the Miramichi River, NB, from 2015–2019 during the Miramichi Striper Cup tournament in the month of May from measured values. Dotted lines represent confidence intervals of model predicted values.

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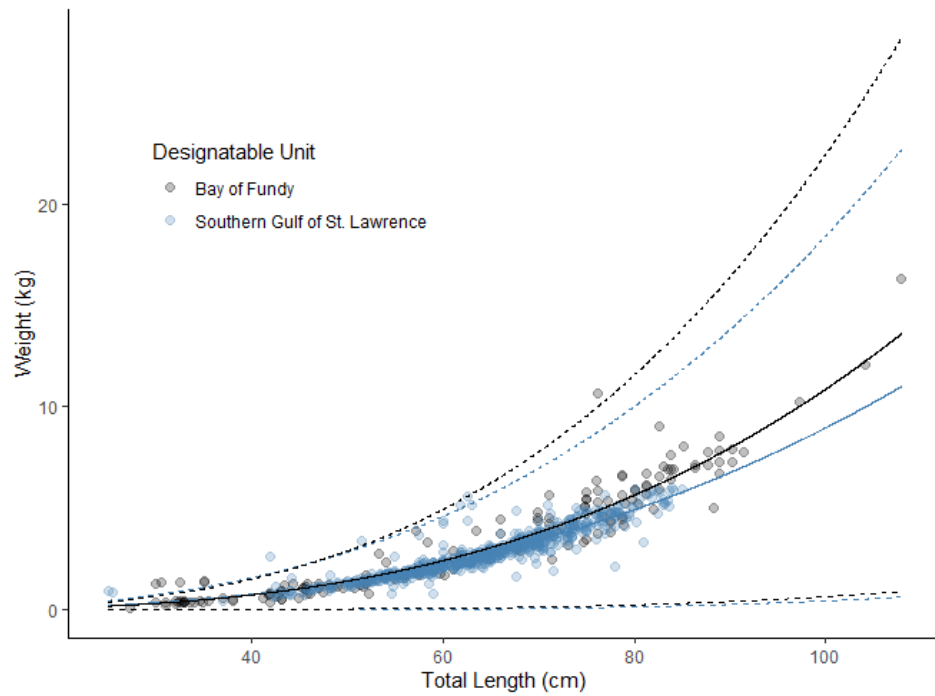
Figure 12. Weight - length relationship of Striped Bass *Morone saxatilis* in the Miramichi River, New Brunswick, Canada, from 2016–2018 during the Miramichi Striper Cup tournament compared to Bay of Fundy, Canada from measured values in the month of May. Dotted lines represent confidence intervals of model predicted values.
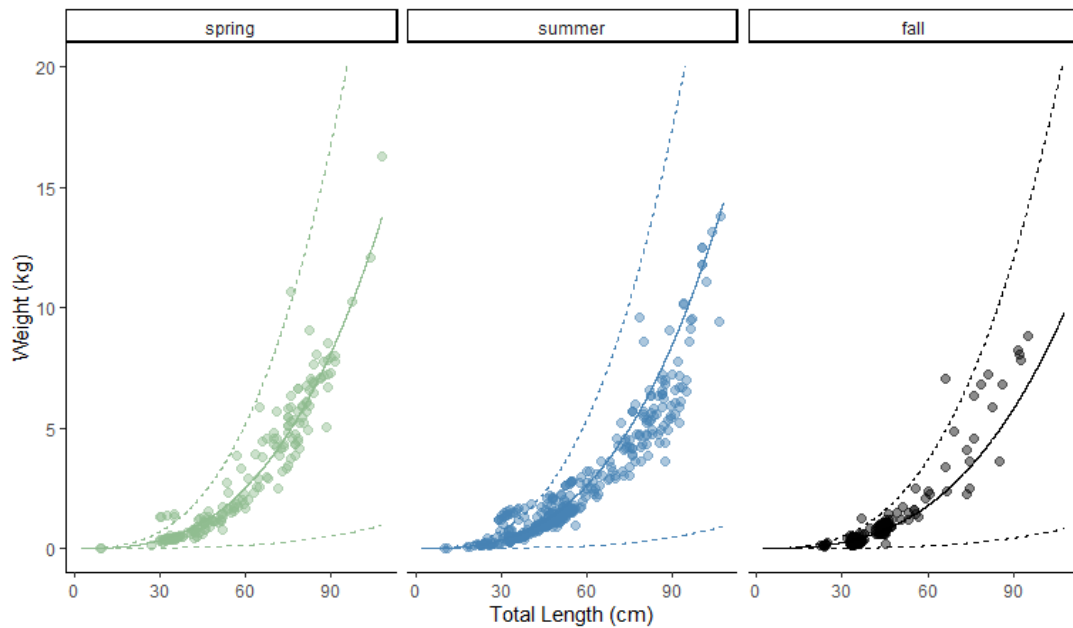
Figure 13. Weight-length relationship by season captured of Striped Bass *Morone saxatilis* in the Bay of Fundy, Canada, from 1984–2018 from measured values. Dotted lines represent confidence intervals of model predicted values.
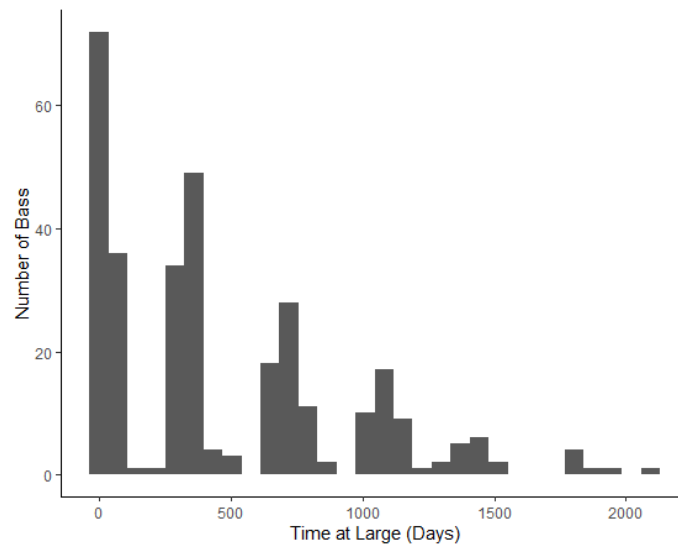
Figure 14. Time-at-liberty for Striped Bass *Morone saxatilis* tagged in the Minas Basin, Nova Scotia, Canada, from 2013–2019.
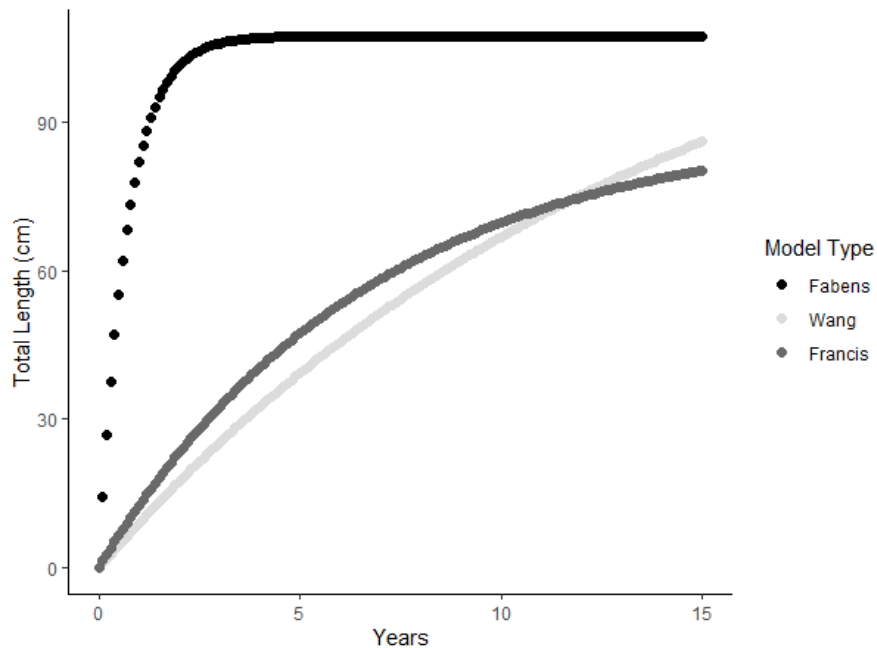
Figure 15. Comparison of growth rate parameters (L∞ and K) estimated from capture-mark-recapture data and three different growth models (Fabens, Wang, Francis) plotted on a Typical von Bertalanffy growth curve from Striped Bass *Morone saxatilis* captured in the Bay of Fundy, Canada during 2014–2018.
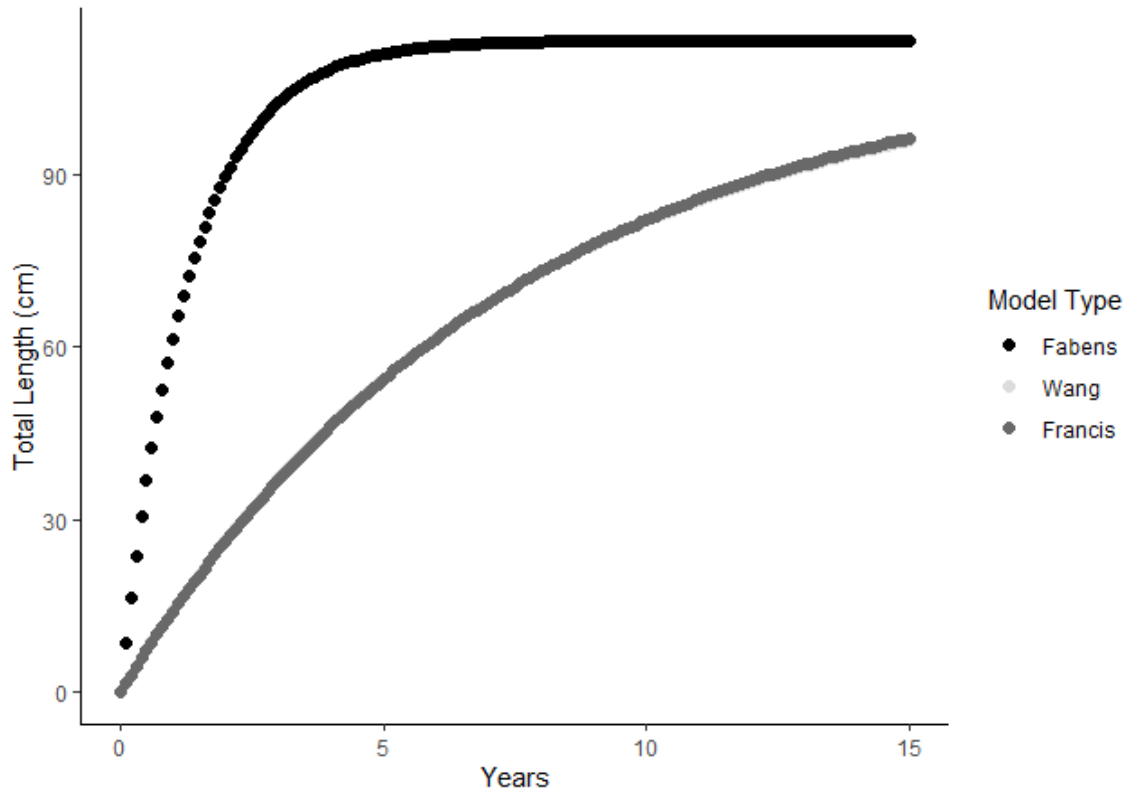
Figure 16. Comparison of growth rate parameters (L∞ and K) estimated from capture-mark-recapture data and three different growth models (Fabens, Wang, Francis) plotted on a Typical von Bertalanffy growth curve from Striped Bass *Morone saxatilis* captured in the Bay of Fundy, Canada, during 1985 - 1993. Note overlapping growth curves for Wang and Francis models.
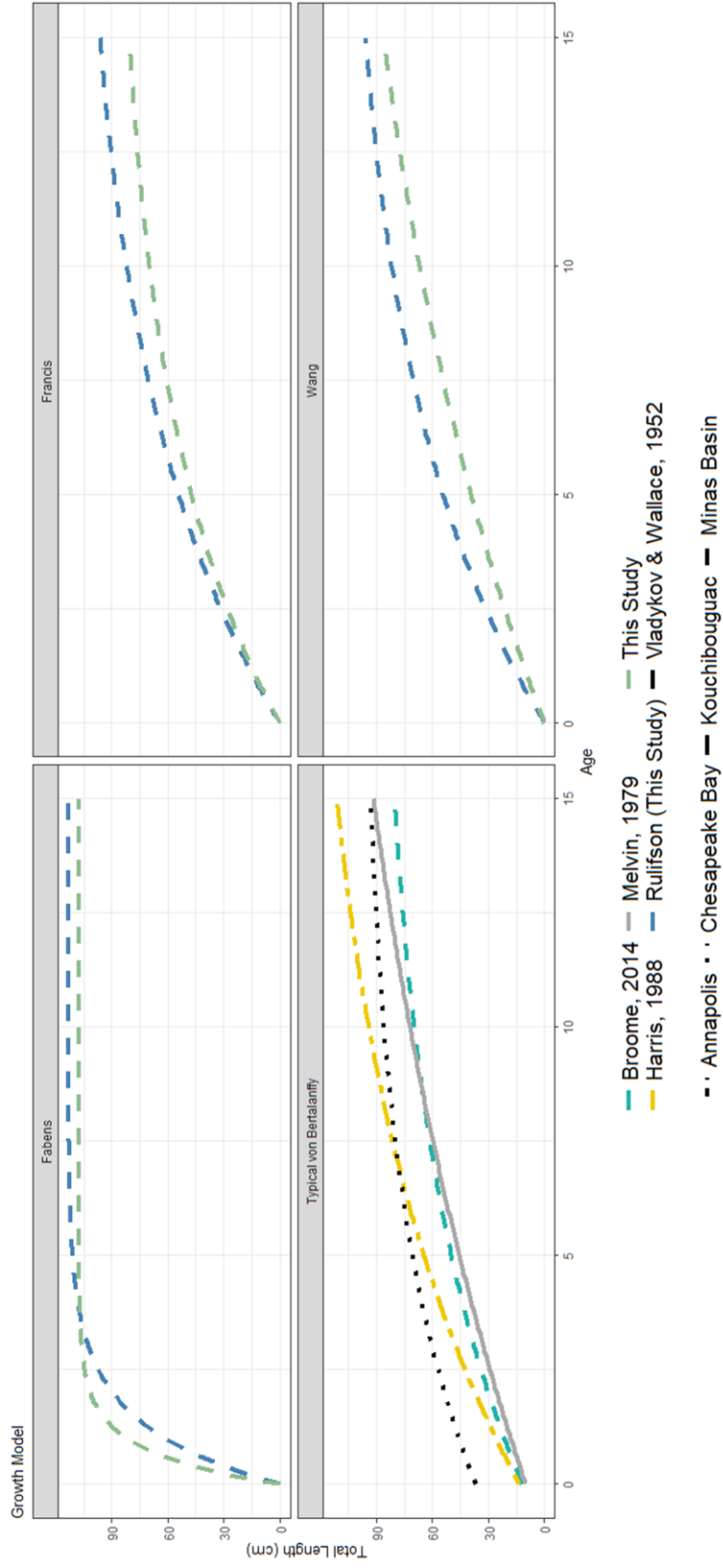
Figure 17. Comparison of capture-mark-recapture growth models used in comparison to historical Striped Bass *Morone saxatilis* growth curves in Minas Basin, NS, Annapolis River, NS, Kouchibouguac, NB, and Chesapeake Bay, USA from age-length data. Models Fabens, Francis, and Wang are plotted on a Typical von Bertalanffy curve for comparison.

Chapter 3

Mixing of Striped Bass in the Minas Basin

Periodically U.S.A. Striped Bass migrate into the BoF and some Saint John River bass migrate to the Shubenacadie River during spawning season (Dadswell *et al*., 1986; Andrews *et al*., 2017). Tagging studies and molecular analysis are the two primary methods used to determine migration patterns and rivers of origin. Tagging studies include external tags such as dart or t-bar tags and internal acoustic tagging. Within the BoF, molecular studies have focused on estimating the proportion of U.S.A. bass in the Saint John River and the Shubenacadie River, and differentiating Canadian spawning populations (Wirgin *et al*., 1993; Wirgin *et al*., 1995; Diaz *et al*., 1997; Bentzen and Paterson, 2008; Bradford *et al*., 2012; LeBlanc *et al*., 2018, 2020; Wirgin *et al.,* 2020).

U.S.A. Striped Bass start migrating northward to the BoF in June or July (Nichols and Miller, 1967) with larger bass (>50 cm) migrating further distances (Waldman *et al*., 1990). Larger female bass migrate longer distances and in greater proportion than males (Westin and Roger 1978; Boreman and Lewis 1987). In October or November, bass return to the U.S.A (Nichols and Miller, 1967). There is evidence of U.S.A. bass overwintering in the Saint John River system (Andrews *et al*., 2020) and anecdotal evidence that some U.S.A. bass may overwinter in the Grand Lake, NS (Rulifson *et al*., 2008). Overwintering may be caused by sharp temperature declines preventing bass from return migrations; however, Andrews *et al.* (2020) found some of the U.S.A. origin bass remained in the Saint John River system for >3 years and found evidence of bass with mixed Saint John River and U.S.A ancestry and U.S.A. origin. It is unknown whether U.S.A. bass spawn with Shubenacadie River origin bass in the spring. No molecular

evidence is published to confirm mixing and overwintering with bass in the Shubenacadie River.

Regionally, recent evidence suggests the persistence of local Saint John River population where it was previously believed to be extirpated (LeBlanc *et al*., 2018, 2020). Furthermore, Andrews *et al.* (2020) showed four bass acoustically tagged in the Saint John River migrating to the Shubenacadie River during spawning season and shortly after spawning ended returning to the Saint John River whereas the remaining 59 acoustically tagged bass remained in the Saint John River for the duration of the study. Although molecular analysis was completed on many of these bass, molecular analysis could only be completed on three of the four bass that migrated to the Shubenacadie River. One individual was determined to be of Shubenacadie River origin, a second individual in this group is reported as being of U.S.A. origin (Andrews *et al*., 2020; Andrews *et al*., 2020a) but this was a misprint (Andrews, S. Pers. Comm), thus the remaining three exhibiting this behaviour have not been determined molecularly for origin. Bass of the Saint John River genotype were tagged in the Saint John River and recaptured in the Minas Basin, but details of this study are not available because the analysis is unpublished (Bradford *et al*., 2012). Andrews *et al.* (2017) also reported that bass tagged with dart tags in the Saint John River were recaptured in the Minas Basin, but no molecular evidence was completed to determine population origin, but it was assumed these were of Shubenacadie River origin based on this movement behaviour. Saint John River Striped Bass may stray to the Minas Basin, but other than occasional acoustic and tag recaptures, when and for how long mixing occurs is unresolved.

Implications of Population Differentiation for Management

If a mixed stock is managed as a single unit, like it is in the BoF, there is potential

for underrepresented populations such as the Saint John River to become overexploited,

thus putting more stress on recovery potential (Casey and Meyers, 1998). Conversely,

more productive populations may be able to withstand greater harvesting rates.

Therefore, information on the relative contribution of the populations that contribute to

the BoF DU is vital for sustainable management; this includes populations that are part of

the DU and migrant populations from the U.S.A. If the presence of U.S.A. bass in the

Minas Basin is minimal, then population abundance and structure of BoF bass can be

used within the Minas Basin to set management goals or adapt management to target or

avoid populations during peak mixing periods. The first step is to determine seasonal

presence of different populations of bass within the BoF DU, and particularly within

Minas Basin where the Shubenacadie River population is assumed to predominate.

Molecular vs. Morphometric Population Identification

Both phenotypic and genotypic traits have been used to differentiate Striped Bass

populations. Morphology and meristics have been used in early stock differentiation of

bass, but many overlapping traits between populations decreases the accuracy of this

method as a population discriminatory tool (Rulifson and Dadswell, 1995). Morphology

has been used to successfully differentiate between overwintering cohorts where bass

overwintering in marine waters have greener colouration along the dorsal area, whereas

black dorsal colouration indicates overwintering in fresh water (Paramore and Rulifson,

2001). Otolith microchemistry, fatty tissue analysis, and diet support these findings, but

so far, no molecular differences related to these traits have been investigated, thus, the

utility of colouration for population discrimination is molecularly unresolved (Paramore and Rulifson, 2001). Additionally, otolith microchemistry and fatty tissue analysis are destructive methods.

Stripe patterns, either full or broken stripes, is thought by many anglers to discriminate between Canadian and U.S.A. Striped Bass. The broken stripe pattern has been shown to differentiate hybrid Striped Bass and White Bass (*M. saxatilis* x *M. chrysops*) and cultured Striped Bass from "wild" bass using significantly different meristic counts with minimal overlap (Fullner *et al*., 2007; Waldman and Vecchio, 2011). Yet, broken stripes are common in wild Striped Bass in Minas Basin. Of 1,305 Striped Bass observed in Shubenacadie and Stewiacke Rivers from 1984–1987, 96% (1,255) had broken stripes (Rulifson, unpublished data). In these rivers there has been no stocking of cultured Striped Bass, and no confirmation of hybrids in Atlantic Canada. Broken stripes may well be entirely environmental (Waldman and Vecchio, 2011). Overlap in morphometric and meristic characteristics in population and the potential for subjective group assignment decreases confidence in these methods for population discrimination. Molecular analysis is a great alternative to morphometric and/or meristic discrimination especially when the latter two can be affected by environmental factors such as temperature, salinity, and oxygen levels (Coyle, 1998).

Molecular Methods

Molecular analysis uses three methods as a way of discriminating groups, 1) by identifying variations in alleles frequencies at distinct loci (the location of a given gene on a chromosome), 2) through comparing the lengths of DNA fragments and, 3) comparing substitutions of single nucleotides in a DNA sequence (single nucleotide

polymorphisms or SNPs) (Wirgin *et al*., 2020). Discriminating populations within Canada have used both mitochondrial DNA (mtDNA) and nuclear DNA (nDNA). Mitochondrial DNA is only inherited maternally, which causes genetic drift to occur faster, and mutation rates to be slower. Because it has slow mutation rates, mtDNA it is more efficiently used to differentiate populations that have not recently diverged and is commonly used on populations greater than 100,000 years old. Additionally, polymorphisms in mtDNA are not good indicators of the overall genetic differentiation within or between populations because the relatively small contribution that mtDNA makes to the overall gene pool in a population and biased distribution of length fragments caused by breakage (Stellwag and Rulifson, 1995; Wirigin *et al*., 2020). Mitochondrial DNA has been a main option in the past before polymerase chain reaction (PCR) technologies were available because it was relatively easy to isolate high amounts of purified mtDNA.

Nuclear DNA is relatively new in fisheries genetics. Nuclear DNA has more possibilities than mtDNA as a source of genetic markers due to its bigger size and its biparental inheritance (Robinson and Courtenay, 1999). It uses non-coding genes that are highly polymorphic and have high mutation rates. Nuclear DNA can also be amplified using PCR, and therefore less genetic material is required whereas mtDNA requires larger samples of fresh or frozen material (Carvalho and Pitcher, 2012).

To compare the differences of genes within either mtDNA or nDNA, restriction fragment length polymorphisms (RFLP), microsatellites and next-generation sequencing (NGS) are used. RFLPs use restriction endonucleases to cut or digest DNA at specific recognition sites. Once the DNA has been cut, several fragments remain which are

separated using electrophoresis (Robinson and Courtenay, 1999). The frequencies of the fragment lengths are used to infer genetic differences between populations. RFLPs requires substantial amounts of sample DNA and the procedures are tedious (Robinson and Courtenay, 1999). However, RFLPs are less useful for differentiating Striped Bass (Stellwag and Rulifson, 1995; Wirgin *et* al., 2020). Microsatellites use differences in lengths of repetitive non-coding genes at loci to differentiate populations. Unlike RFLPs, they require small quantities of genetic material (Ashley and Dow, 1994). Microsatellites have high genotyping error rates and relatively low density throughout the genome (Evans and Cardon, 2004). NGS involves extracting sequences and comparing markers based on the substitution of one nucleotide in a specific position of the DNA (i.e., SNPs), allowing genotyping of hundreds of markers at the same time with low scoring errors.

NGS and SNPs of nDNA are used herein because this method can detect fine scale polymorphisms, can sequence multiple samples at once, and has the maximum amount of redundancy in sequencing of the genome-providing more reads with less error (Evans and Cardon, 2004; Baxevanis and Oulette, 2005).

Population Discrimination of Bay of Fundy Striped Bass

Genetic work has been conducted in the BoF since 1991 and has been used to determine presence and differentiation of Striped Bass populations (Table 11). Early genetic work by Wirgin *et al*. (1993, 1995) used mtDNA and RFLPs to determine genetic relatedness of populations in Canada and mixing of U.S.A. bass in the BoF. Wirgin *et al.* (1993) compared samples from Shubenacadie River, Miramichi River, Tabusintac River, and used samples from Hudson River and Chesapeake Bay samples to represent U.S.A. contingents. Differences were detected between all Canadian populations and U.S.A.

populations, differences were also detected between SGoSL rivers (Miramichi River and Tabusintac River) and Shubenacadie River, but no differences were found between Miramichi River and Tabusintac River individuals (Wirgin *et al*., 1993). Wirgin *et al*. (1995) compared the Saint John River and Shubenacadie River, to samples collected from Long Island, NY which was believed to contain migratory Hudson River and Chesapeake Bay populations. Adult bass were used in this study except for the Shubenacadie River, which consisted of both juvenile and adult bass. Distinctions between Saint John River origin bass and other populations were not attempted as it was believed there was no spawning population present. They concluded that the proportion of bass with U.S.A. ancestry within the Saint John River was 63% in 1992 and 97% in 1993, and the proportion of Shubenacadie River bass in the Saint John River was therefore 37% in 1992 and 3% in 1993 (Wirigin *et al*., 1995). The proportion of U.S.A. bass in the Shubenacadie River in the same years was 1.2% and 6.8%, respectively, however these results should be used with caution due to limitations of RFLP techniques (Wirgin *et al*., 1995; Stellwag and Rulifson, 1995; Wirgin *et al*., 2020).

Diaz *et al*. (1997) compared similar Striped Bass populations as Wirgin *et al*. (1993) with additional U.S.A. Atlantic and Gulf of Mexico populations, but used nDNA instead of mtDNA. Canadian bass were genetically different from the U.S.A. bass, and variances existed among the U.S.A. bass. The highest contributors to the observed genetic heterogeneity were from geographically extreme population in the Apalachicola, Tabusintac, and Shubenacadie Rivers. They concluded that population subdivision had occurred between the U.S.A. populations, and that migration levels were sufficiently low

to prevent genetic homogenization. Nuclear DNA also discriminated the same populations as mtDNA (Diaz *et al*., 1997).

Robinson (2000) used microsatellites on four loci with nDNA to determine origin of YOY Striped Bass found in the Richibucto River in the SGoSL. Microsatellites were used with nDNA because prior studies using RFLPs were unable to discriminate SGoSL populations. YOY bass from the Stewiacke River were used as an outgroup for comparison, and it was determined that Richibucto River bass belonged to the Miramichi River population and this population was genetically distinct from the Stewiacke River individuals. This study was the first to indicate Canadian YOY bass are migratory and its presence in a river does not necessarily indicate spawning is occurring in the system within which they were found.

Bentzen and Paterson (2008) attempted to identify whether a local aggregate of bass in the Saint John River persisted using adult bass collected near the Mactaquac Dam, NB, during summer months of 1999–2006. Bass were compared to three U.S.A. populations: Chesapeake Bay (Maryland), Hudson River (New York), and Kennebec River (Maine), and two Canadian populations (Shubenacadie and Miramichi Rivers). The study used 11 microsatellite loci and discriminated between U.S.A. origin, Shubenacadie River origin, and a genetically distinct population different than all source samples, which was believed to be the native Saint John River population. The study found that the presence of this native population was exclusive to only two year classes (1999: 40-57 cm; 2006: 66-93 cm) and were indicative of an erratically spawning, precarious population. The proportion of this population ranged from 69–85% in the years 1999–

2001, to 9–22% in the years 2002–2006. This study was the first study to genetically discriminate Saint John River origin bass from other Canadian populations.

Bentzen *et al*. (2009) built on previous work also utilizing 11 microsatellite loci but with additional historical samples from Annapolis River (1972, 1975, 1976, 1978, and 1981) as well as additional samples in the Saint John River system. However, the results of this study have not been published.

Bradford *et al*. (2012) and DFO (2011) further explored Striped Bass within the Saint John River using 11 microsatellite loci with the aim to identify a putative local population as well as bass from the Atlantic coast of NS. Information concerning this study is not published (conference abstract in: Haro *et al*., 2009; result summary in: Bradford *et al*., 2012; Douglas *et al*., 2011) so it is unclear whether mtDNA or nDNA was used, when the samples were collected, how many and what month or year reference samples of other populations were used, or where samples were collected from the U.S.A.. It is also unknown whether the samples used in this study were the same samples used in the study by Bentzen and Paterson (2008), or Bentzen *et al*. (2009). It is known that 810 juvenile and adult samples were collected from the Saint John River for analysis and a genetic population was present that was not an admixture (hybrid) of multiple populations, or of distinct U.S.A., Shubenacadie River, or Miramichi River origin. It was also suggested that the identified population appeared to describe isolation rather than adaptation (DFO, 2011). Results of samples from the Atlantic coast of NS were not provided.

Molecular analysis was also undertaken to evaluate the origins of juvenile Striped Bass in the Petiticodiac River, BoF, NB. The Petitcodiac River has had increasing

presence and size of bass since allowing free-flowing water through a causeway-gate system in 2010. A total of 200 samples were analyzed using 11 microsatellites and were compared with Striped Bass from Miramichi River, Shubenacadie River, Saint John River, Kennebec River, Hudson River, and Chesapeake River. Adult samples from Annapolis River, SGoSL, and mixed-origin Saint John River bass were used for comparison as well. As the work was contracted out to Bentzen, it is likely these reference samples are the same as what was used in Bentzen *et al*. (2008; 2009). There were 32 unusable samples due to DNA degradation. Of the remaining 168 samples, greater than 92% were of distinct Shubenacadie River origin, five Shubenacadie River origin individuals with slight mixed ancestry, and two juveniles that were of mixed Shubenacadie-Miramichi River origin (Mazerolle, 2014).

Bentzen and Paterson (2016) used 8 microsatellite loci with the same reference samples as Bentzen and Paterson (2008) to identify the presence of U.S.A. migrants within the Minas Basin. Samples were used from both acoustic and external tag studies completed by Broome (2014) and Keyser (2015) from 2008–2012. Out of 294 samples analyzed, 279 were from the Shubenacadie River, 12 were Shubenacadie River origin, but with some possibility of mixed ancestry, two were Shubenacadie River origin, but showed a greater possibility of mixed ancestry, and only one was a U.S.A. migrant. This study was the first to explore the presence of U.S.A. origin bass in the inner Bay of Fundy.

Leblanc *et al*. (2018) used more advanced methods including NGS and SNPs with the aim to identify a putative Saint John River Striped Bass population using samples from YOY and juvenile bass. NGS with SNPs has advanced the field of population

mixing in bass because it can detect diverging populations with low error. The samples were compared to two U.S.A. populations (Chesapeake Bay and Hudson River) and one Canadian population (Shubenacadie River). Their results aligned with the findings of Bradford *et al*. (2012) and Bentzen and Paterson (2008) identifying a genetically distinct population of Saint John River bass. It also discovered one juvenile bass of mixed Saint John River and Shubenacadie River origin, and five bass of mixed Saint John River and U.S.A origin. This study was the first study to identify hybridization between Canadian populations and between Canadian-U.S.A. populations in the BoF DU.

Continued effort has been placed on identifying mixed stocks in the Saint John River system. Andrews *et al*. 2020 worked alongside Leblanc utilizing NGS and SNPs in the Saint John River and genotyped 110 samples, of which 23 were juveniles (ages 1–3) that were also used in Leblanc *et al.* 2018, as well as an additional 87 fish (aged 3–7). These were compared against the reference samples described in Leblanc *et al.* (2018). Upon removing samples without enough data, 101 were genotyped. These showed similar trends as Leblanc *et al.* 2018 in that there was presence of Saint John River origin Striped Bass (78%), Striped Bass with mixed ancestry (23 %; 16 individuals of U.S.A.-Saint John River origin, 5 individuals of Saint John-Shubenacadie River origin, and one individual with ancestry of Saint John River, U.S.A., and Shubenacadie River origin), and one bass of Shubenacadie Origin. Interestingly some of these individuals were acoustically tagged and their genetic origin is also mentioned in Andrews *et al*. (2020a) and Andrews *et al*. (2020b).

Wirgin *et al*. (2020) completed a molecular range-wide study of Striped Bass. Using 12 microsatellites they genotyped individuals from all three historic spawning

rivers in the BoF DU. In the Saint John River samples from 42 individuals were analyzed to determine 11 bass were of Shubenacadie River origin, 26 were of U.S.A. ancestry, and the remaining five were of mixed ancestry. This method failed to detect individuals of a genetically distinct Saint John River origin as seen by use of SNP (Leblanc *et al*., 2020; Andrews *et al*., 2020). Samples used in analyses were from 2014, and no seasonal timing of samples were provided. Relatedly, Wirgin *et al*. (2020) examined 95 samples from the Annapolis River prior to extirpation including September 1994 (n=25) and May–June 1995–1996 (n=69), failing to detect a genetically distinct population, but found a higher proportion of U.S.A. origin bass. Of the 95 analyzed, four were of Shubenacadie River origin, one of Shubenacadie River-U.S.A. origin, and the remainder of U.S.A. origin; thus, <5% Shubenacadie River origin. Wirgin *et al*. (2020) did not find any presence of U.S.A. origin bass in the Shubenacadie River, nor Shubenacadie River origin bass in the U.S.A.

Leblanc *et al*. (2020) built upon past 2018 research by assessing presence of additional samples in the Saint John River as well as samples from the Mira River and Bras d'Or Lakes in Cape Breton. This study was also a range wide comparison like that of Wirgin *et al*. (2020), but the samples were more recent (2014–2017). Leblanc *et al.* (2020) continued to find admixed Striped Bass in the Saint John River of Saint John River and either U.S.A. or Shubenacadie River origin. Three individuals from Mira River were determined to be of U.S.A. origin; however, no individuals in the Shubenacadie River displayed any admixture or presence of any other individuals from neighbouring Canadian or U.S.A. populations and no presence of Shubenacadie River origin bass were detected in the U.S.A.

Knowledge Gaps

Molecular analysis has been extensively used to identify the river, management unit, or population of origin of Striped Bass throughout its range with discrimination between populations within the BoF, which was the main consideration for this thesis. However, many information gaps still exist. A summary and critique of population discrimination is presented (Table 11). The Miramichi River remains the only identified spawning river in the SGoSL and the genetic population is indiscriminate from the St. Lawrence River because the St. Lawrence River population was stocked with Miramichi River bass from 2002–2019 (Robitaille *et al*., 2011). The BoF and SGoSL are genetically distinct and both Canadian DUs are genetically distinct from U.S.A. bass. There is a genetically distinct population in the Saint John River, but because there is no historical genetic signature available to compare current samples against, the origin of this population remains unresolved. The simplest explanation is the population has always been present. The study completed by Wirgin *et al*. (1995) suggests that the presence of U.S.A. in the Saint John River was very high, yet minimal in the Shubenacadie River. One potential reason for this outcome could be the samples collected in the Saint John River were collected during the feeding season when U.S.A. bass are moving through, whereas the samples from the Shubenacadie River were collected during the spawning season. A second reason is RFLPs are not as good at discriminating populations of Striped Bass as other molecular methods (Wirgin *et al*., 2020). Specific sample collection timing was not always provided but is necessary to untangle movement patterns from specific migrations, and to estimate population mixing accurately.

Although molecular studies have been used to describe the proportion of U.S.A. Striped Bass in the Saint John River, all samples were collected post spawning and thus it is unknown how many U.S.A. bass were present within the Saint John River during that spawning season. LeBlanc *et al*. (2018, 2020) detected bass that appeared to be mixed Saint John River-U.S.A. indicating that U.S.A. bass are present in the Saint John River during spawning season and likely contributing to the population. Wirgin *et al.* (2020) results were similar; however, with microsatellite methods no genetically distinct Saint John River population was found, rather presence of migrants from multiple U.S.A. stocks and evidence of hybridization of U.S.A. and Shubenacadie River bass.

Although Wirgin *et al*. (1995) showed that U.S.A. Striped Bass presence is low in the Shubenacadie River during spawning season, and LeBlanc *et al*. (2018) found mixed Saint John River-Shubenacadie River bass within the Saint John River, but no studies have identified mixed bass within the Shubenacadie River. Bass acoustically tagged by Andrews *et al*. (2017) in the Saint John River migrated to the Shubenacadie River during the spawning season and promptly return to the Saint John River for the remainder of the year. This behaviour raises uncertainty in the origin of these tagged individuals, which could not be molecularly confirmed for origin and whether they were spawning in the Shubenacadie River. Petitcodiac River, north of the Saint John River, showed no evidence of U.S.A. origin bass. Bentzen and Paterson (2016) showed potential mixed Shubenacadie River-U.S.A. bass but did not include Saint John River bass in the analysis. Consequently, some of the putative hybrids could be Saint John River bass. Bentzen and Paterson (2016) results only indicated one U.S.A. migrant within the Minas Basin out of

294 samples, which suggests a much lower proportion of U.S.A. bass reside in Minas Basin than suggested by Wirgin *et al.* (1995).

There are information gaps on the proportion of U.S.A. Striped Bass present in the Shubenacadie River during spawning, whether U.S.A. bass spawn with bass in the Shubenacadie River successfully, and the presence of U.S.A. or bass from other populations in the Minas Basin and other watersheds during peak migration or feeding periods. CMR studies have been completed on bass throughout the Atlantic coast since the 1930s (Pearson, 1933). Bass tagged in Canada have been reported recaptured in the U.S.A. and *vice versa* (Rulifson *et al.*, 2008, Boreman and Lewis, 1987). Summaries of cross-border recaptures have been completed by many, but most have focused on one-way travel (just Canada to U.S.A. or just U.S.A. to Canada) or have not included CMR studies that did not have any cross-border recaptures. With bass that were cross-border recaptures, none have been genotyped to determine if they were a Canadian bass migrating to the U.S.A. or a U.S.A. bass that happened to be captured and marked in Canada; the opposite proposition is also possible.

Objectives

Information gaps on the presence of Striped Bass from other populations other than the Shubenacadie River in the Minas Basin will be addressed using two analyses: 1) an analysis of historical CMR studies, and 2) NGS, a more sensitive genetic analysis method, to identify potential migrants from other populations, and, secondarily, mixed origin Striped Bass.

Methods

Tagging Studies

Data from prior tagging studies were compiled through an extensive literature review by selecting papers known to include tag data or reference tag data and/or studies. Any papers that referenced other research regarding movement, migration, tag returns, CMR, or U.S.A.-Canada presence were reviewed to capture as many CMR studies as possible. Because there were many studies, focus was placed on externally tagged bass, as transboundary recaptures cited are primarily of this type. Years tagged, locations, number of Striped Bass tagged, cross-border recaptures with their associated year, location, and abundance, within region and within country recaptures were summarised. If a study did not discuss recaptures in opposing countries, it was assumed that there were none. When possible, data from original published studies were used. However, in the event the original study was not available, or the information comes from an unpublished data source, the study from which the citation/information originated from was noted. In cases where CMR studies are on-going, or results are published multiple times (e.g., mentioned in multiple studies) attempts were made to compile the data to accurately reflect the totals tagged and recaptured meanwhile noting any potential inconsistencies. The presence of U.S.A. bass was quantified by the sum of all Canadian recaptures over total tagged in U.S.A. To quantify the presence within the BoF, these proportions were also calculated by region. As bass tagged in Canada could potentially be U.S.A. migrants that happened to be tagged in Canada, we also calculated these proportions for sum of all U.S.A. recaptures over total tagged in Canada.

Tissue Sampling

Since 2008, Striped Bass scale samples were collected by the SBRT, through commercial fishers and recreational angler collections under outreach programs managed by the SBRT, and through historical samples compiled from donations obtained from past researchers. Many anglers, commercial fishers, and community members have been engaged for this research through outreach at fishing tournaments, fishery meetings, citizen science programs, presentations, social media, and fishing trips. From 2002–2019, data was collected on 10,730 Striped Bass throughout the SGoSL and BoF DU. Scales were collected from 3,738 fish. Predominantly, samples were from the BoF DU with 8,467 Striped Bass records and 3,294 scale samples. In some instances, tissue samples in the form of fin clips or other tissues from angler-donated carcasses were taken instead of scale samples (n=57). Replicate tissues samples were taken in addition to scales for 229 fish; thus 3,580 genetic samples from 3,287 different fish were collected.

Tissue samples used for molecular analysis came primarily from scales, but four samples were from freeze-dried muscle and liver tissues. Collecting scales is an inexpensive and low effort way to collect DNA tissue (Li *et al*., 2013). Extracting scales has low invasiveness and provides minimal skin exposure for disease compared with fin clipping, anglers and commercial fishers can easily remove scales, and dried scales preserve DNA well making them ideal for molecular sampling (Li *et al*., 2013). Scales were also collected for aging fish although aging bass by scales is only effective up to about age 12 (Secor *et al*., 1995; Paramore and Rulifson, 2001).

DNA on scales is contained in epithelial cells, therefore multiple scales are required to acquire enough DNA for NGS. Generally, 5–6 scales were collected dorsally

between the first dorsal fin and the lateral line. Scales were not taken from the same spot,
because an open wound can increase the possibility of infection. Scales were stored in
Rite-in-the-Rain paper envelopes and each scale envelope was given a unique
identification code referred hereafter as a 'genetic ID' that contained information on the
year, capture method, scale collector, tag identifier (if applicable) and sample number.
Genetic IDs were recorded in a database so that all associated meta information such as fish
TL and capture location can be linked to genetic information.

Carcasses donated by anglers were stored in a -20° C freezer to preserve specimens
until they were ready to be processed. Most carcasses were filleted of the lateral muscle.
After carcasses were thawed, 5–10 pieces of 1 cm^3 liver tissues were taken from the central
part of the liver with sterile extraction tools. Muscle tissues were taken as one larger section
of 1 x 1 x 5 cm just posterior to the head. Each liver and muscle tissue sample were placed
into a separate autoclaved glass vial and re-frozen. Once frozen, vials containing samples
were placed into a SP Scientific© Virtis Benchtop Freeze Dryer for 24 hours at a
temperature of -40° C and a pressure of 200 millitorr. Once dry, samples were ground using
a sterilized mortar and pestle and placed in a labelled 1.5-mL centrifuge tube and stored at
room temperature or frozen at -20° C.

Sample Selection

Based on past tagging studies, movement and size of Striped Bass tracked by
Nicholas and Miller (1967) and Waldman *et al*., (1999) bass $\geq$50 cm TL and caught
between July and November were presumed more likely to be migratory and thus were
selected for molecular analysis. All samples were from bass caught in the Minas Basin
except for samples from vagrant fish caught in Labrador in 2017. Samples from bass

caught in the Shubenacadie River or Stewiacke River (except for two samples) caught

during the spawning season were excluded as there is a higher probability that they

originated from those rivers. Samples were selected from bass ≥50 cm TL caught from 7

July to 25 November from 2012–2017. Since scales were occasionally taken from tagged

bass both at time of marking and recapture, size was determined at time of initial tagging

for recaptured bass. Larger scales from each sample were used because they contain more

epithelial cells, and misshapen scales were selected over intact scales because they were

likely re-generated and not useful for aging (Zale *et al*., 2012). DNA was extracted from

all samples, with a goal of having 192 samples with enough DNA for NGS analysis.

Next-Generation Sequencing

DNA extraction

Extraction of DNA was required to separate nuclear DNA from other cellular

components and make it available for sequencing. For each fish sample, 3–4 scales were

cut up into smaller pieces to fit into the bottom of a 1.5-mL microcentrifuge tube.

Remaining scales were stored for future projects and aging. DNA was extracted using the

Omega Biotek© E.Z.N.A. Blood and Tissue DNA extraction protocol with the following

changes: 25 mg/µL of RNase A was used instead of 100 mg/µL, 200 µL of BL buffer and

ethanol instead of 220 µL, and a second elution using elution buffer was not completed as

a higher concentration of DNA was desired rather than a larger volume. Microcentrifuge

tubes were individually labelled with the genetic ID to track samples throughout the

extraction process. Laboratory bench surfaces were cleaned with both bleach and 70%

EtOH before beginning any procedure, extraction tools (tweezers and scissors) were

sterilized with 70% EtOH between each sample, and care was taken to prevent cross

contamination of samples. Samples were analysed for total concentration of DNA using a Thermo Scientific© Nanodrop 2000 spectrophotometer. Any samples with less than 20 mg/µL of nucleic acid were re-extracted using remaining scales.

Normalization

Normalization is a process of diluting samples with a high concentration of total DNA to create a working stock of samples for measuring double stranded DNA. Total concentration of DNA from a sample includes single-stranded DNA and small fragments of DNA, thus it overestimates the concentration of useable DNA (double-stranded DNA). Once reliable measurements of double-stranded DNA from the working stock were acquired, the values were calculated for dilution to 20 ng/µL for enzymatic digestion for all samples (see protocol in Appendix 1). Samples with a total DNA concentration greater than 75 mg/µL total DNA were diluted to 75 mg/µL using elution buffer. Double-stranded DNA concentrations were found using PicoGreen reagents. PicoGreen reagents used to measure the concentration of double-stranded DNA become saturated when using DNA concentrations >1ng/µL. Thus, it is necessary to obtain a rough estimate of DNA concentration in samples using a NanoDrop. Once the concentrations of double-stranded DNA are determined using PicoGreen reagents, samples with less than 20 ng/µL were excluded and the remaining samples with higher concentrations were diluted to 20 ng/µL to reduce sample variability in starting material and allow even amplification across all samples for comparisons.

Library Preparation

A DNA library is a collection of total genomic DNA from an individual. Libraries were prepared using a modified double-digest restriction-site associated DNA sequencing

(ddRAD-seq or ddRAD) protocol using restriction enzymes *PstI* and *MspI* developed by Poland *et al.* (2012). DNA was selected for fragment size (377–523bp) before PCR amplification using a Sage Pippin Prep © platform. All individuals were processed on the same lane using paired-end sequencing of 125bp with an Illumina® HiSeq™ 2500 (San Diego, U.S.A.) at Génome Québec Innovation Centre.

Data processing

NGS data consist of billions of sequences and thus requires data validation, processing, and analysis. Bioinformatics is a scientific field that marries biological data, computer science, mathematics, and statistics. Molecular data must be processed using bioinformatics. Nathalie LeBlanc (Canadian Rivers Institute, University of Saint John, New Brunswick) completed all bioinformatics for this research. Bioinformatics was used to piece together sequence fragments from individuals by mapping individual reads to a reference genome. Each of the billions of bases in the genome was sequenced multiple times, providing high depth to deliver accurate data and an insight into DNA variation.

The first processing step involved checking samples for missing data and excluding samples that have either too much or not enough data. Too much or not enough data can occur when samples fail to amplify well and therefore very few DNA fragments would be sequenced, or when amplified DNA was not of sufficient quality to make it past filtering. Using NGS, millions of short sequences-referred to as 'reads' are produced. Including data with too many or too few reads can make sequencing less efficient during reaction runs. A good indicator of whether too little or too much data were present in a sample was the sequence data text files size; a small file size indicates a small number of reads.

The second step involved trimming and sorting sequences. Adaptors were trimmed from the resulting DNA sequence libraries using Cutadapt v. 1.13 (Martin, 2011), and quality before and after trimming was assessed by eye with FastQC v.0.11.5 (Andrews, 2010). Data files were then sorted by sequence barcodes and short sequences were aligned to the Striped Bass genome (BioProject accession no. PRJNA266827) using BWA v. 0.7.15 (Li and Durbin 2010). Sequences that matched closely enough to a location on the genome were given a position and became official loci. Sequences that did not align were discarded. Alignments were output as Binary Alignment Map (BAM) files, a binary text file format designed to efficiently store substantial amounts of nucleotide information (Li *et al*., 2009).

The third step involved checking loci quality. A catalogue of loci was created based on genomic position to compare with individual samples. Since reads are amplified randomly, replicate reads can be produced for some samples that occur at one loci, whereas some samples will have no reads at the same location. To organize reads, they were arranged into 'stacks' of loci. A loci 'stack' was all the replicate reads that one sample had at a single locus. The more replicates present, the higher the 'stack depth', which indicates a lower rate of sequencing error. Stacks were compared using stack depth as an indicator for quality. Modules of the R Studio program Stacks 1.46 were executed using Stacks workflow scripts from (Normandeau, 2016), which makes use of the module 'rxstacks' to remove confounded and poor-quality loci and make corrections to SNP calls. The 'snp' model type and an alpha of 0.1 was used for this purpose. Loci with a log-likelihood of less than -40 and stacks with a depth of less than 5 were excluded. Furthermore, sequences were excluded using FIS values (FIS -0.3 or lower) that were

calculated in the Stacks module called 'populations' to eliminate highly heterozygous loci as possible paralogues. The remaining loci were then filtered once more using VCFtools v. 0.1.13 (Danecek *et al*., 2011) to eliminate all loci with a minor allele frequency less than 0.01 over all individuals. At this point another quality check was completed by removing samples that were missing data for all but a couple of loci. Samples that passed the quality control checks were compared against previously sequenced reference panels from Miramichi River, Shubenacadie River, Saint John River (local population described by Leblanc *et al*., 2018), Hudson River, Chesapeake Bay, and Cape Fear River, NC. Seven models were run 10 times to determine the number of ancestral populations, and entropy values were used to determine that five ancestral populations were the most informative (Figure 19). Entropy measures the uncertainty of the genotype of a population, with the lower entropy being the most probable as the true number of ancestral populations (Wang *et al*., 2002; Leblanc *et al*., 2020). Admixture coefficients of each sample and reference panels were graphed to show the origin of each fish (Figure 20).

Other analyses

Metadata gathered from genotyped Striped Bass were mapped according to location caught to show distribution and abundance of samples throughout the Minas Basin. Mapping was completed with open-source software QGIS (Version 2.14.11).

In addition to NGS and SNP molecular work, 41 samples collected from anglers participating in the SBRT angler logbook program in Annapolis River (n=10) and Bear River (n=31) were sent to Dr. Paul Bentzen at Dalhousie University for microsatellite

analysis. These samples were collected in spring and fall of 2010 (n=9), 2011 (n=6), 2018 (n=1), and 2019 (n=25).

Results

Tagging Studies

Historical tagging study data of U.S.A. Striped Bass show recaptures within the BoF, but many were recaptured in the outer BoF and recaptures in the BoF in general were extremely low in comparison to the number of individuals marked (Table 12). In total, 2,074,482 bass were tagged in 40 studies from 1931–2015. Of these, only 23 were caught in Canadian waters and only one in the inner BoF (Table 12; Nicholas and Miller, 1967). The proportion of bass reported as migrating to Canada was 0.001% and this proportion decreased to 0.000048% after excluding captures from the outer BoF. Both the Saint John River, NB and Annapolis River, NS had the same proportion (0.00024%) of U.S.A. recaptures, which was higher than any other Canadian area. However, it is likely the recaptures reported as just NB were Saint John River recaptures.

Conversely, significantly fewer bass were tagged in the BoF. 20 studies tagged 8,623 bass from 1964–2020, of which there were 25 recaptures (0.28%) in the U.S.A (Table 13). Bass also were recaptured moving between the Minas Basin into the BoF or *vice versa*. 11 bass (0.15%) tagged in the Minas Basin were recaptured past the Minas Channel in the Cumberland Basin, Scots Bay, Fundy National Park, Saint John River, and Annapolis River. Similarly, two bass (0.15%) tagged in either Saint John River or Annapolis River were recaptured in the Shubenacadie River. These combined 13 bass reflect 0.15% proportion of bass moving through the Minas Channel (Table 13). Across the entire Atlantic coast into the BoF 48 (0.002%) transboundary recaptures have occurred from published studies using external tags.

Sample Selection and Quality control

To satisfy the selection criteria of using only fish that were ≥50 cm TL, caught in late summer to autumn, and not caught in the Shubenacadie River system (including the Stewiacke River) or Estuary during spawning season, a suite of samples from individual Striped Bass spanning several years and across the Southern Bight and Cobequid Bay area of Minas Basin were used ranging 2012–2017. Initial selection criteria identified 336 samples, with the addition of 8 samples from Labrador, the total selection pool was 344. All samples had DNA extracted; however, only 294 samples had enough extracted DNA to be sequenced. Of 294 extracted samples, only 143 samples had enough high-quality DNA to be analyzed as determined through bioinformatics. Of the 143, 8 samples came from Labrador, the remaining 135 came from the Minas Basin (see Figure 18). Two bass with TL below 50 cm were included; this was due a clerical error in using the length at recapture rather than length at marking when organizing samples. Final set of tissue samples represents bass ranging 37–107 cm TL (Table 14). Most samples were collected in 2017 and July yielded the most samples across years (Table 14).

Population Discrimination and Associated Movement

Samples collected from Annapolis River (n=10) and Bear River (n=31) were determined to be of Shubenacadie (n=39; 95.2%), Saint John River (n=1; 2.4%), and U.S.A. origin (n=1; 2.4%) using microsatellites. The U.S.A. origin bass was captured 22 May 2019 at 119 cm TL, and the Saint John River origin bass was caught in 2019 but no length measurements or specific date information were provided.

Of the 135 Striped Bass from the Minas Basin only one was determined to be of U.S.A. origin. It was caught in a commercial fish weir in Bramber, NS in August 2014

and measured 97 cm TL, a specimen quite large for this region. Thus, 0.74% of bass sampled in the Minas Basin were from the U.S.A.. During this same fishing event, 24 other bass were caught, all of which either had a tag applied or was recaptured with lengths ranging 35–97 cm TL. Five of these were genotyped and were all determined to be of Shubenacadie River origin. Upon reviewing movement through tag recaptures of these 24 individuals, many were recaptured in the Bramber weir in subsequent years, except for one individual (not genotyped), which was recaptured in the Shubenacadie River two years later. Three of these individuals were large (>70 cm), a result interesting in that it shows large bass of different genetic origin, potentially schooling together within the Minas Basin (Figure 21).

The remaining 134 Striped Bass (99.26%) were of Shubenacadie River origin and no hybrids were identified. Of these Shubenacadie River origin bass, 133 were tagged along the southern shore of the Minas Basin. A total of 21 of these individuals were recaptured, all of which occurred along the southern shore of the Minas Basin except for one, which was recaptured in along the northern shore in Parrsborro, NS. Eight samples from Labrador ranging 49–70.5 cm TL were of Miramichi River origin.

Discussion

The presence of U.S.A. Striped Bass in the BoF contributes to the difficulty in producing population estimates of the BoF DU (Bradford *et al.*, 2012; COSEWIC, 2012). The variability in migratory behaviour of bass within and between populations creates challenges for management of local stocks, especially when transboundary migrations extend into waters managed under the policies of a different country. Past evidence of potential and confirmed U.S.A. origin bass in Canadian waters has not explained whether presence is migratory or occasional vagrancy. If U.S.A. bass migrate to the BoF for spawning or feeding, then the proportion of U.S.A. bass present in the BoF would be dependent on population abundance in the U.S.A. as well as other factors such as forage fish stock sizes, and density dependent effects. However, if the presence is a factor of wandering, then mixing rates of U.S.A. bass within the BoF would fluctuate unpredictably yearly, seasonally, and spatially.

This study is the first to extensively summarise all external tagging studies across the range of both BoF and the Atlantic U.S.A. seaboard across all years. In total 57 studies conducted external tagging of Striped Bass. Sharing of tag data seems common and although attempts were made to group these studies, it is possible that the total bass tagged in each country may be inflated. This potential inflation could be under-estimating the proportion of bass migrating to the BoF; however, even upon removing the top four studies in the U.S.A. with the greatest numbers of bass tagged that may cause this inflation due to their coastwide collaborations or state involvement (ALS, Friedmann, 1991; Jiang *et al.*, 2007; ASMFC, 2013), the proportion is still less than 0.02%. It is unlikely that the recaptures were duplicated as given their rarity in comparison to total

tagged, the specific river location and year recaptured were given and none of these records appear to be duplicated. Citations of the transboundary recaptures have likely provided the impression of a higher proportion of bass demonstrating transboundary movement behaviour. In many cases these recaptures were summarized in publications and re-cited or summarized in later publications, also providing a false sense of recency. For example, transboundary recaptures in 1959–1961 originally outlined in Nichols and Miller (1967) were summarised by Dadswell *et al*. (1984) and subsequently Dadswell *et al*. (1984) was then summarised by Rulifson and Dadswell (1995) and again herein, persisting these records in literature for over 62 years.

Over two million bass were tagged in the U.S.A. from 1931–2015 and only 23 tagged bass were recaptured in the BoF; a proportion of 0.001%. Of the 23 tagged, six were recaptured in the Annapolis River watershed and Southern NS, 10 in Saint John River and Southern NB, and only one was recaptured in the inner BoF. No U.S.A. tagged bass were reported recaptured in Canada since 1996. In the BoF, bass tagging began 33 years after the first U.S.A. bass tagging study (first study in Canada = 1964). Difference in time as well as localized tagging efforts instead of range-wide tagging has resulted in significantly fewer bass tagged in BoF (n=8,623) than the U.S.A. Atlantic coast. Only 25 bass of these Canadian tagging studies were recaptured in U.S.A. waters, seven (0.08%) of which were tagged in the Minas Basin and associated watersheds; the most recent recapture in the U.S.A. occurred in 2006. These results are overwhelming in that the proportion of transboundary recaptures are <1% and no recaptures have occurred for 15 years according to current literature. Of all transboundary recaptures across all the Atlantic coast (n=48; 0.002%) none were reported to repeat their transboundary

movements. This lack of repeated recaptures across country lines suggests that these movements are more wandering than migratory; however, the sample size is small and the lack of repeated recaptures could be due to mortality, lack of tag reporting, or lack of publication of the movements of these individuals post transboundary recapture.

Of the Canadian literature, only four studies have had molecular analyses completed alongside tagging efforts: this study (external tags–Minas Basin), Bradford *et al.* (2015; tag type unknown–Saint John River), Bentzen and Paterson (2016; tag information provided in Keyser, 2015 and Broome, 2014; acoustic and external tags–Minas Basin and Shubenacadie River), and Andrews *et al.* (2017, 2020a; acoustic tags–Saint John River). Of these tagged individuals with known genetic origin (n= 474; one misprint in Andrews *et al.*, 2020a as U.S.A. origin not included Andrews, S. pers. comm.), three bass were reported to be of U.S.A. origin (0.6%), six were of mixed ancestry (1.3%), and the remaining were of Shubenacadie River origin (98.1%). Despite presence of U.S.A. origin bass in both the Saint John River (n=2) and the Minas Basin (n=1), only one of the 474 individuals were cited as being recaptured or acoustically detected outside of Canada. This individual was tagged at the Mactaquac Dam in the Saint John River, genetically determined to be of Shubenacadie River origin, and recaptured near Mt. Desert in Maine. Of the Canadian tag studies reviewed that did not have published genetic origin (n=8,196) it is unknown whether bass tagged were of BoF origin or a U.S.A. migrant that happened to be captured and tagged in Canada.

A higher proportion of bass were recaptured moving from Minas Basin into the BoF or *vice versa*. Twelve bass (0.14%) tagged in the Minas Basin were recaptured past the Minas Channel in the Cumberland Basin, Scots Bay, Fundy National Park, Saint John

River, and Annapolis River. Three bass (0.03%) tagged in either Saint John River or Annapolis River were recaptured in the Shubenacadie River. These combined 15 bass reflect a low 0.17% proportion of bass moving through the Minas Channel, a result also found in acoustic tag detections and molecular studies (Leblanc *et al*., 2018, 2020; Andrews *et al*., 2020a; Wirgin *et al*., 2020; this study – Annapolis River watershed samples). It is known that a proportion of these individuals were spawning (Andrews *et al*., 2020a; Leblanc *et al*., 2018, 2020), occupying other rivers (Mazerolle, 2014; Wirgin *et al*., 2020; Dadswell, unpublished), or found in coastal regions (this study; Broome, 2014; Keyser, 2015). It is not known if movement into other rivers or costal regions was for feeding, spawning, or other reasons.

The low proportion of U.S.A. origin Striped Bass found using molecular methods supports the tag recapture summary. Bass selected for analysis targeted a typical migratory pattern and size with the aim to increase the probability of finding U.S.A. bass in the Minas Basin. Only one U.S.A. bass was found. It was 97 cm TL and present during August; right in the middle of the expected U.S.A. feeding season and following the TL ranges for migration patterns of U.S.A. origin bass from the Chesapeake (Chapoton and Sykes, 1961; Secor *et al*., 2020). The 135 samples used herein did not cover all size ranges or the entire season and were collected over several years, so year-to-year comparisons were not possible. Further studies within a single season and year of substantial samples to verify seasonal and yearly variation in the estimated proportion would be beneficial. Additionally, size ranges and seasonality of samples selected for DNA extraction were primarily based on the findings from Nicholas and Miller (1967) and Waldman *et al*., (1999) for likely migrants. Further study could explore smaller size

classes to explore the potential of smaller bass completing this migration or investigate genetic mixing. Although there are gaps in sample coverage, the results herein are compelling in concert with Bentzen and Paterson (2016) and considering the interpretation of past tagging studies. The presence of U.S.A. migrants during the feeding season is much fewer than previously perceived and was supported by Bentzen and Paterson (2016), which found a small proportion (0.34%) of U.S.A. bass in the Minas Basin. Bentzen and Paterson (2016) and the results herein span over 10 years (Bentzen and Paterson (2016): 2008–2012; this thesis: 2012–2017) and when results are combined, only two U.S.A. bass of 429 (0.47%) samples were identified. Molecular evidence shows a higher proportion of U.S.A. origin bass and more recent evidence of presence in the Minas Basin than tagging studies.

Both lines of evidence show a low proportion of U.S.A. Striped Bass in Canadian waters within the BoF; lower still in the Minas Basin. Mixing of different populations has important implications for management because it confounds population estimates and may require transboundary management of stocks (Moss, 1971; Bradford *et al.*, 2012). It would be helpful to reliably estimate the proportion of U.S.A. bass present in the BoF. Population mixing was identified as an important limitation to estimating the population size within the Minas Basin (COSEWIC 2012; DFO, 2014). The Minas Basin is where much of the recreational angler pressure exists for the Shubenacadie River population. A better understanding of population mixing could be used to adjust DU-specific population estimates (Smith *et al.*, 2013). Given past tagging provided only 0.0003% from all transboundary recaptures between Minas Basin and U.S.A over all bass tagged and 0.0004% for recaptures over only Minas Basin and U.S.A. tagged bass. and recent

molecular evidence was 0.47%, the proportion is still conservatively <1% mixing for the Shubenacadie River population for a contemporary estimate; thus, adjustments in management actions would be minor.

No Striped Bass in the Minas Basin during feeding season were from Saint John River or were admixed Saint John River-Shubenacadie River. However, sampling was targeted well beyond the Shubenacadie River spawning period. Acoustic tracking of Saint John River bass showed bass exhibiting a year-round presence within the Saint John River, but a low proportion visited the Shubenacadie River during spawning season (Andrews *et al.*, 2017; 2020). Using genetics, one specimen was determined to be of Shubenacadie River origin and the second was erroneously reported as U.S.A. origin but in fact origin was not determined (Andrews, S. pers. comm.). Whether the remaining three bass were of Shubenacadie River or Saint John River origin is unknown. Regardless, this low proportion suggests Saint John River bass have minimal presence in the Minas Basin during the feeding season when bass are taken frequently in the recreational fishery. The difference in acoustic and molecular proportions was likely due to sampling timing or that these bass were of Shubenacadie River origin but behaviourally divergent — spending the rest of their time in the Saint John River system. Therefore, increased sampling during other periods, such as spawning season, might show a proportion of bass in the Minas Basin of Saint John River origin.

A higher proportion of confirmed Shubenacadie River origin Striped Bass left the Minas Basin. Two acoustically tagged bass from Keyser (2015) were observed leaving the Minas Basin and were detected near Fundy National Park, NB. Later, these bass were determined to be of Shubenacadie River origin and were not detected further in the Minas

Channel (Keyser, 2015; Bentzen and Paterson (2016). Genetically Shubenacadie River origin bass were found outside of the Minas Basin in the Saint John River, Annapolis River, and Petitcodiac River (This study; Mazerolle, 2014; Leblanc *et al*., 2020; Andrews *et al*., 2020; Wirgin *et al*., 2020). These genetic and tag records have spanned many years including Wirgin *et al*., (2020) Annapolis River samples from 1994–1996 and Rulifson *et al*., (2008) tagging from 1985–1986, suggesting Shubenacadie River origin bass have strayed from the Minas Basin for many decades and that this movement pattern is not recent. In the more recent samples (2010–2011, 2018–2019) from the Annapolis River watershed analysed in this study, only one bass (2.4%) was of U.S.A. origin and one (2.4%) was of Saint John River origin of the 41 samples analysed; the remaining 39 samples (95.2%) were of Shubenacadie River origin. Conversely the historical samples from Annapolis River in 1994–1996 analysed by Wirgin *et al*. (2020) showed a higher proportion of U.S.A. origin bass (94.7%), one Shubenacadie River-U.S.A. hybrid (1%), and four Shubenacadie River bass (4.3%). The years of historical samples used by Wirgin *et al*. (2020) also correspond with U.S.A. tagged recaptures in the outer BoF (Table 12). On the contrary, Bentzen and Paterson (2008) observed lower proportions (<20%) of U.S.A. origin bass in the Saint John River in subsequent years (1999–2003, 2005–2006). Seemingly, a decrease in U.S.A. tag recaptures in Canada by the 1990s and molecularly a shift from having high proportions of U.S.A. bass to more recently, higher proportions of Shubenacadie River bass in extirpated or at-risk BoF spawning rivers has occurred.

Efforts were made to genotype 192 samples, but 50 samples did not provide enough DNA fragments to be sequenced. This sequence failure was likely due to DNA degradation that occurred in these samples during sample collection, sample storage, or

the samples did not amplify well. Mazerolle (2014) experienced similar degradation with a loss of 32 fin clip samples out of 200 and microsatellites analysis. Some of the samples used herein consisted of freeze-dried muscle and liver tissues for DNA extraction. Although these likely contained higher amounts of DNA than scale samples, they were difficult to process. Fat present in tissues remained suspended in solution and could not be settled properly using centrifugation, which likely resulted in reduced DNA isolation as the fat may have clogged the filters used in the extraction kit. Although the material was problematic to separate, three of the four freeze-dried tissue samples were analyzed successfully.

Striped Bass is currently not a species with recreational or commercial regulations within DFO Newfoundland and Labrador (DFO, 2018). Bass collected from Labrador were of Miramichi River origin and this result holds significant importance for future management regulations. Discriminating Labrador bass as Miramichi River origin was not a surprise as one of the recaptured bass was tagged in Miramichi River by the DFO during its yearly CMR program (DFO, 2018; Andrews *et al*., 2019). It was also possible that Labrador bass are from the St. Lawrence River population. However, there is no molecular reference for St. Lawrence River bass because the St. Lawrence River population was stocked with Miramichi River bass (Robitaille *et al*., 2011); it is unlikely the bass in the St. Lawrence River are genetically distinct. Based on the precautionary approach, the initial reaction of DFO was to recommend against retention of bass in Labrador. Because the St. Lawrence River population is listed under the SARA, retention of individuals from this population is prohibited (DFO, 2009b). Yet, the St. Lawrence River spawning population, and thus genetic difference, has been purported to be

extirpated since the late 1960s so it is questionable that anything would be gained from restrictive regulations for Labrador retention. Given Labrador bass were of Miramichi River origin, there are implications for bass management in what is now the most northern extent bass have ever been recorded.

Many information gaps were left unanswered by previous molecular analyses, and the results herein only partially bridge these gaps. Mixed ancestry of Striped Bass was detected in the Saint John River; however, there is little evidence of mixed Shubenacadie River origin elsewhere. Five samples outside the Saint John River have shown mixed Shubenacadie River ancestry (Petitcodiac River, n=2, Mazerolle, 2014; Minas Basin, n=2, Bentzen and Paterson (2016); Annapolis River, n=1, Wirgin *et al*., 2020). The presence of Miramichi River origin bass in the BoF has not been supported by other molecular or tagging studies. Since Bentzen and Paterson (2016) did not include Saint John River samples, which were recently found distinct, it is uncertain whether these individuals would have been re-assigned as Shubenacadie-Saint John River ancestry. No confirmed mixed ancestry of Shubenacadie River or even presence of confirmed Shubenacadie River origin bass has been detected in the U.S.A. to date. The extent of hybridization and its implications for management needs to be explored further.

This marks the second molecular study completed in the Minas Basin, but both studies were focused on the Southern shore of the Minas Basin. To understand the full scope of presence of other populations within the BoF and specifically the Minas Basin, samples from the northern shore of Minas Basin and samples collected during other seasons should be analyzed. Genetic samples from the St. Lawrence River population should also be genotyped to confirm assumptions on genetic similarity to the SGoSL and

to provide historical genetic makeup for comparing current and future bass in the St.

Lawrence river as it recolonizes and Labrador migrants.

Table 11. Summary of genetic studies of Striped Bass, *Morone saxatilis*, within the Bay of Fundy, Canada (U, Unknown; YOY, Young-of-Year; J, Juvenile; A, Adults).

Sampling Year	DNA type & Method	Location (number samples)	Sample size & life stage	Author
1991-1992	mtDNA RFLP	Miramichi River Shubenacadie River Tabusintac River Hudson River Chesapeake Bay	U U U U U	Wirgin et al., 1993
1989, 1991-1993	mtDNA RFLP	Saint John River Shubenacadie River Long Island, NY	128 181 J/A 483	Wirgin et al., 1995
1992-1993, 1995	nDNA RFLP	Shubenacadie River Tabusintac River Apalachicola River, FL Hudson River Congaree River St. Johns River, FL Choptank River	32 U 26 U 59 U 41 U 125 A 61 A 85 A	Diaz et al., 1997
1997-1998	nDNA Microsatellites 4 loci	Richibucto River Miramichi River Stewiacke River	40 YOY 40 YOY 40 YOY	Robinson, 2000
1998-2008	DNA type - U Microsatellites 11 loci	Saint John River Shubenacadie River Miramichi River USA (locations unknown)	810 J/A U U U	Bradford, 2012
2008	DNA type - U Microsatellites 11 loci	Miramichi river Shubenacadie River Saint John River Kennebec River Hudson River Chesapeake Bay	81 J/A 81 J 720 A 48 J 94 A 93 J	Bentzen and Paterson, 2008
1972-2003; 2013	DNA type - U Microsatellites 11 loci	Petitcodiac river Miramichi River Southern Gulf of St. Lawrence Shubenacadie River Saint John River (local) Saint John River (hybrids) Annapolis River Kennebec River Chesapeake Bay Hudson River	168 YOY 81 A 81 YOY U A 111 A 48 YOY 93 YOY 94 YOY	Mazerolle, 2014
2008-2012	DNA type - U Microsatellites 8 loci	Minas Basin Shubenacadie River Miramichi River Chesapeake; Hudson; Kennebec Rivers	294 258 118 258	Bentzen and Paterson (2016)
2012-2016	nDNA NGS	Saint John River Shubenacadie River Chesapeake Bay Hudson River	40 YOY/J 22 23 A 23 A	LeBlanc et al., 2018

1990; 1997-1998		Miramichi River	64 YOY/J	
1991-1992		Shubenacadie River	54 YOY/J	
2014		Saint John River	42 J/A	
1994-1995		Kennebec River	49 YOY/J	
1994-1996		Annapolis River	94 A	
1989; 2007; 2015		Hudson River	167 A	
2010		Delaware River	77 A	
1989; 2011; 2016	Microsatellites 8 loci	Upper Chesapeake Bay	125 J/A	Wirgin et al., 2020
1989		Choptank River	41 J/A	
1989		Potomac River	51 J/A	
1979; 1989		Rappahannock River	65 J/A	
1979		York River	23 U	
1997		Patuxent River	41 YOY/J	
1997		Nanticoke River	54 YOY	
1997		Pocomoke River	19 YOY	
1989; 2010; 2014		Roanoke River	144 J/A	
1979; 1989; 1992		Santee Cooper Reservoir	101 J/A	
2011–2017	nDNA NGS	Bras d'Or/Miramichi River	19 A	LeBlanc et al., 2020
		Mira River	22 A	
		Shubenacadie River	33 A	
		Saint John River	32 J	
		Kennebec River	16 YOY/ J	
		Hudson River	55 A	
		Delaware River	57 A	
		Upper Chesapeake Bay	27 A	
		Potomac River	33 YOY/ J	
		Rappahannock River	32 A	
		James River	33 U	
		Choptank River	33 YOY/ J	
		Nanticoke River	33 YOY/ J	
		Roanoke River	30 A	
		Cape Fear	22 A	
2013-2019	nDNA NGS	Saint John River	87 A 23 J	Andrews et al., 2020

Table 12. Review of U.S.A. Striped Bass, *Morone saxatilis*, tagging studies completed in the U.S.A. and a summary of the number of tag recaptures in Canada.

Location	Year Tagged	No Tagged	Canadian Recapture Site	Year Recaptured	No Recaptured	Study	Data Source
Chesapeake Bay: MD	1931	305				Pearson, 1938	Boreman and Lewis 1987, Goodyear 1974
CT, NY, NC	1936-1937	2642				Merriman, 1937, Merriman, 1941	Boreman and Lewis 1987
Hudson River, NY	1940, 1942, 1954-1956	504				Neville, 1940	Alperin, 1966
Chesapeake Bay: MD and Virginia	1936-1937	3352				Vladykov and Wallace, 1952	Boreman and Lewis 1987, Goodyear 1974
Massachusetts to Chesapeake Bay	1949-1952	9320				Raney et al, 1954	Boreman and Lewis 1987
Chesapeake Bay	NA	457				Hollis and Davis, 1955	Goodyear, 1974
Chesapeake Bay	NA	31				Mansueti, 1956	Goodyear, 1974
NC and Chesapeake Bay	1955-1959	478				Chapoton and Sykes, 1961	Chapoton and Sykes, 1961
Chesapeake Bay: Virginia	1957-1958	2429				Massman and Pacheco, 1961	Boreman and Lewis 1987
Potomac River	1957-1958	1103				Mansueti, 1961	Boreman and Lewis 1987
Rock Hall, MD; Conowingo dam	1958 -1959	5376	Saint John River, NB	NA	1	Whitney, 1961	Whitney, 1961
Chesapeake Bay		104				Mansueti and Murphy, 1961	Goodyear, 1974
James River, York River, Rappahannock River, Potomac River, Delaware Canal	1957	4329				Lewis, 1961	Lewis, 1961
Canada to Carolina*	1963 -2015	42,000	Weymouth, NS	1992	1	American Littoral Society	Boreman and Lewis 1987; Underwater Naturlists publications, ALS publications
			Lepreau River, NB	1995	1		
			Reversing Falls, NB	1996	1		
			Canada		6		
Long Island, NY	1956-1961	1917				Alperin, 1966	Boreman and Lewis 1987

Location	Years	N	Location	Year	Count	Source	Source
			Walton, NS	1959	1		
Potomac River	1959-1961	8973	Bear River, NS	1960	1	Nichols and Miller, 1967	Boreman and Lewis 1987; Dadswell et al 1984; Melvin, 1978
			Annapolis Royal	1961	1		
			Saint John River, NB	1976	1		
Maine to Chesapeake Bay	1959-1963	6679	Saint John River, NB	NA	1	Clark, 1968	Clark, 1968
			NB	NA	4		
Long Island, NY	1961-1964	912				Schaefer, 1968	Boreman and Lewis 1987, Goodyear 1974
Chesapeake Bay: Virginia	1968-1969	8525				Grant et al, 1970	Grant et al, 1970
Maurice River, NJ	1961	88				Hammer, 1971	Goodyear, 1974
NJ	1955-1957	111				Hammer, 1971	Goodyear, 1974
Long Island, RI, Chesapeake Bay**	1968	500				Moss,1971	Moss,1971
NC	1968-1971	1752				Holland and Yelverton, 1973	Holland and Yelverton, 1973
Chesapeake Bay: MD	1971-1972	1818				Ritchie and Koo, 1973	Boreman and Lewis 1987
Chesapeake Bay: MD	1972-1973	1375	Reversing Falls, NB	1976	1	Florence, 1974	Florence, 1974; Boone MD fish and game
Chesapeake Bay: MD	1972	1726				Moore and Burton, 1975	Boreman and Lewis 1987
Long Island, NY	1976-1979	1701				Young, 1980	Boreman and Lewis 1987
Hudson River, NY	1977-1978	6114				Texas Instruments 1980, Texas instruments, 1981	Boreman and Lewis 1987
Roanoke River, NC	1956-1980	11141				Hassler et al, 1981	Boreman and Lewis 1987
Hudson River, NY	1976-1977	5219				McLaren et al, 1981	Boreman and Lewis 1987
Hudson River, NY	NA	1400000				Friedmann, 1991	Friedmann, 1991
Choptank river, MD	1991	3960				Henderson-Arzapalo et al. 1999	Henderson-Arzapalo et al. 1999
Chesapeake Bay	1991-2003	24533				Jiang et al. 2007b	Jiang et al. 2007b
Cape Hatteras to cape cod	NA	NA				Able et al., 2012	Able et al 2012
Atlantic US Coast	1985-2013	507097				ASMFC, 2013	ASMFC,2013
Neuse River, NC	2013-2015	50				Bradley et al, 2017	Bradley et al, 2017

Location	Year Tagged	No Tagged	USA Recapture Site	Year Recaptured	No recaptured	Study	Data Source
Western Albemarle Sound, Roanoke River-NC	2011-2012	3914				Harris and Hightower, 2017	Harris and Hightower, 2017
Conowingo Dam	1957	3947				Hollis, unpublished	Whitney, 1961
Hudson River, NY	NA	NA	Annapolis River	1987	3	Hudson River Foundation	Harris, 1988
Total Tagged	**2,074,482**		**Total Recapture in Canada**	**23**			

NA is 'Not Applicable'

*Data not provided on how many were tagged in Canada, total tagged likely contains bass tagged in Canada

Table 13. Review of Striped Bass, *Morone saxatilis*, tagging studies completed in Canada with summaries of the number of tag recaptures in the U.S.A. and recaptures involving movement through the Minas Channel

Location	Year Tagged	No Tagged	USA Recapture Site	Year Recaptured	No recaptured	Recapture past Minas Passage	Year of Recapture	No Recaptures	Study	Data Source
Tagged in Minas Basin										
Minas Basin, NS	2013-2020	1702				Cumberland Basin, NB	NA	4	*This study*	
Minas Basin, Shubenacadie River, NS	2011-2012	85				Fundy National Park, NB	2011	2	Keyser, 2015	Keyser, 2015
Minas Basin, NS	2008-2010	1126				Bear River, NS	NA	1	Broome, 2014	Broome, 2014
						Scots Bay, NS	NA	2		
Shubenacadie River, NS	1999-2002	2500							Bradford et al 2012	Douglas et al, 2003
Cobequid Bay, NS	1985-1986	1866	U.S.A.	NA	4	Annapolis River, NS	1986	1	Rulifson et al, 1987	Rulifson et al, 1987, 2008; Dadswell et al., 1986; Boreman and Lewis, 1987
			Newport, RI	1985	1	Cumberland Basin, NB	1986	1		
			Norwich, CT	1986	2					

Tagging location	Year	Number	Recapture location	Year	Number	Source	Reference
Gaspereau River, NS	1981	12				B. Sabean NS Dept of Lands and Forests	Jessop, 1990
Tagged in Annapolis or Saint John Region							
Saint John River, NB	2016	44				Andrews et al, 2018	Andrews et al, 2018
Saint John River, NB	2010-2011	51				Wallace, 2012	Andrews et al,2017
Saint John River, NB	1999-2002	595				Douglas et al, 2003	Douglas et al, 2003
Mactaquac Dam, NB	2005	NA	Mt Desert, ME	2006	1	*Unknown*	Bradford *et al.*, 2015
Saint John River, NB	1972-1975	70	Southhampton, NY	1973	1	Williamson, 1974; Dadswell,1976	Williamson, 1974; Dadswell,1976
			Blackstone River, RI	1972	1		
			MA	NA	1		
Saint John River, NB	1964	110	NJ	NA	1	NB Fish and Game Protective Association	Dadswell, 1976; Melvin, 1978, 1991
			DE	NA	1		
			MD	NA	1		
			NY	NA	1		
Saint John River, Darlings creek, NB	1968-1969	100	Montauk, NY	1969	1		
Annapolis Royal, NS	1966	NA	NC	NA	1		
Annapolis River, Cheboque River, NS	1966, 1969	200	Rockinghma, NC	1967	1	Moss, 1971	Moss, 1971
			Patcong Creek, NJ	1967	1		
			Indian River, DE	1967	1		
			Long Beach Island, NJ	1970	1		
			Sakonnet River, RI	1970	1		

Annapolis River, NS	1975	9							Jessop 1975	Melvin, 1991
Annapolis River, NS	1975	NA	Potomac River, VI	1976	1				ALS	Dadswell et al 1984
Annapolis River, NS	1976	44							Jessop and Vithayasai, 1976	Jessop and Vithayasai, 1976
Annapolis River, NS	1981-1982	37				Shubenacadie River, NS	1983, 1985	2	Dadswell unpublished	Dadswell et al 1984, Harris, 1988, Jessop 1990, Melvin 1991
Annapolis River, NS	1984	15							Melvin and Dadswell, unpublished	Melvin, 1991
Annapolis River, NS	1987	57	Connecticut River	1987	1				Harris, 1988	Harris, 1988
			Long Island Sound, NY	1988	1					
Total Tagged in Canada	**8,623**		**Total Recaptured in U.S.A.**		**25**	**Total Recaptures Past Minas Channel**		**13**		

NA is 'Not Applicable'

Table 14. Summary of Minas Basin, Nova Scotia, Canada, Striped Bass, *Morone saxatilis*, samples used for next-generation sequencing analysis

Year> Month∨	2012	2013	2014	2015	2016	2017	**Total**
May	0	0	0	0	1	0	**1**
July	2	13	7	29	2	16	**69**
August	1	11	0	1	2	18	**33**
September	0	0	0	0	1	2	**3**
October	0	2	0	0	3	18	**23**
November	0	0	0	0	0	6	**6**
Total	**3**	**26**	**7**	**30**	**9**	**60**	**135**

Figure 18. Geographic locations of Striped Bass, *Morone saxatilis*, DNA samples collected within the Minas Basin, NS, Canada, from 2012–2017 and analysed using next-generation sequencing methods. Brackets indicate the number of samples analyzed at each location (map created using QGIS. Version 2.14.11 software by Lita O'Halloran, 2018).
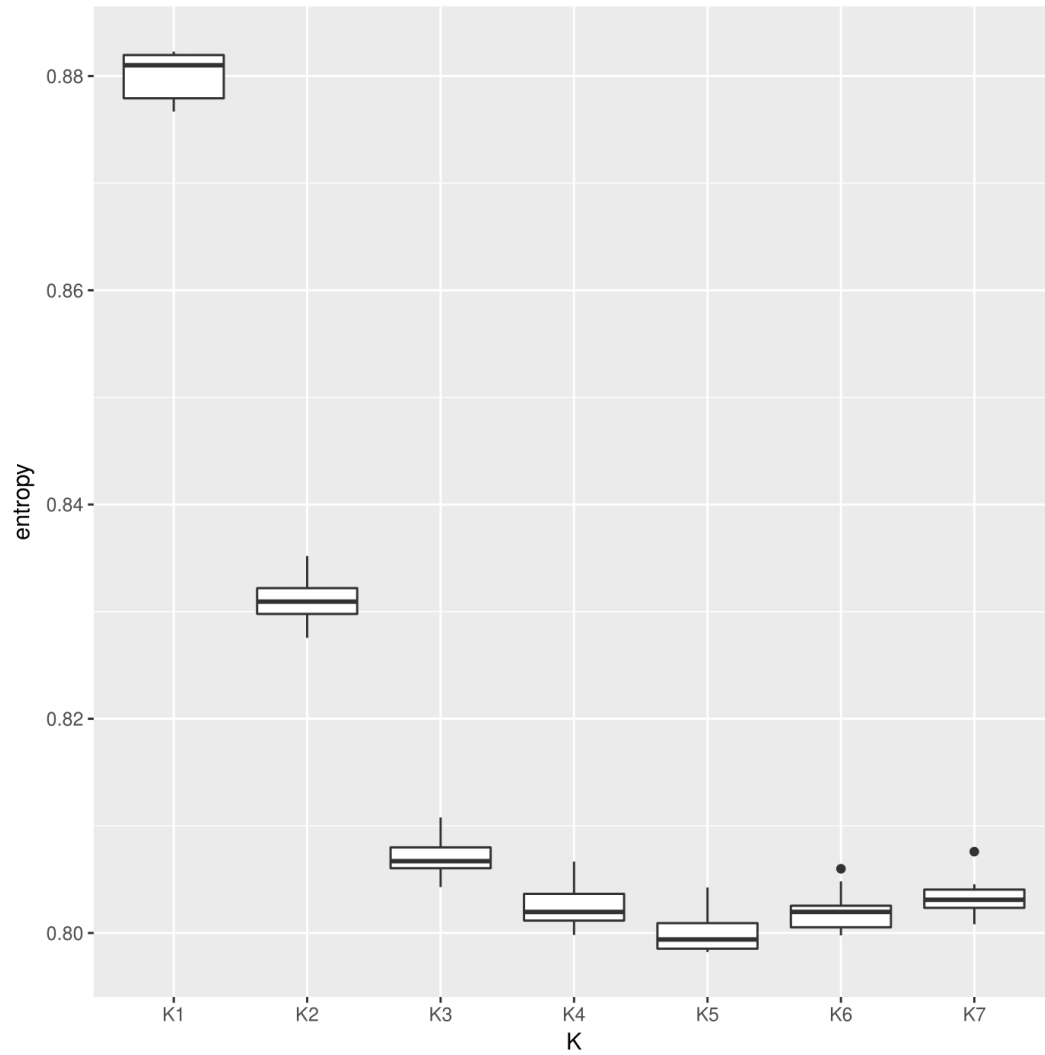
Figure 19. Entropy values for genetic samples of Striped Bass, *Morone saxatilis*. Seven ancestral populations identified with five (K3 – K7) considered most probable as the true number of ancestral populations.
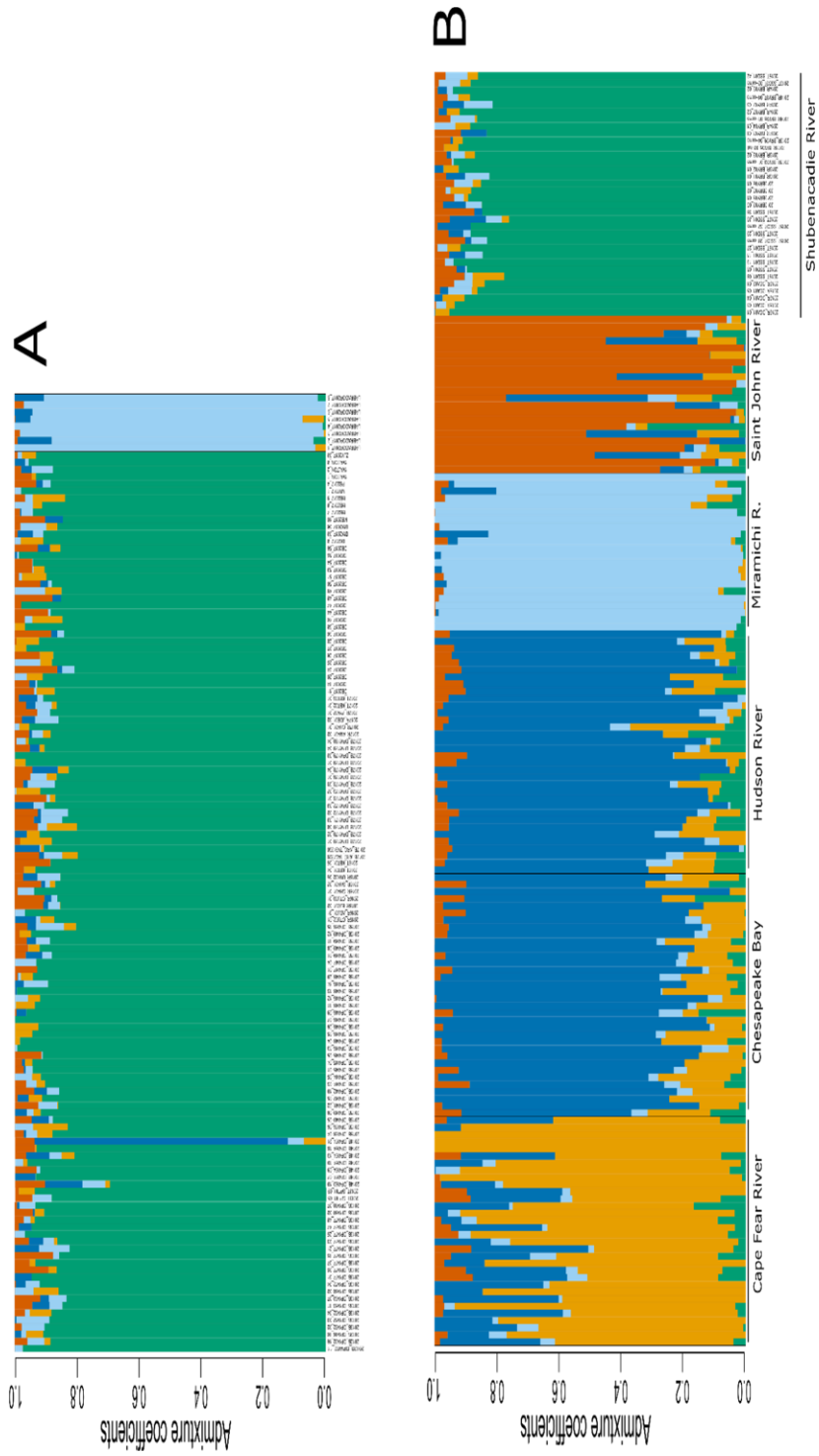
Figure 20. Stacked probability bar plot showing results of Striped Bass, *Morone saxatilis*, origin using next-generation sequencing. Colours represent the estimated proportional ancestry of each fish (orange, Saint John River; light blue, Miramichi River; navy, central Atlantic U.S.A.; yellow, southern Atlantic U.S.A.; green, Shubenacadie River). Panel A shows individuals from this study and panel B shows reference collections. Note sample 2014B_DPW64_21 indicates central Atlantic U.S.A. ancestry.
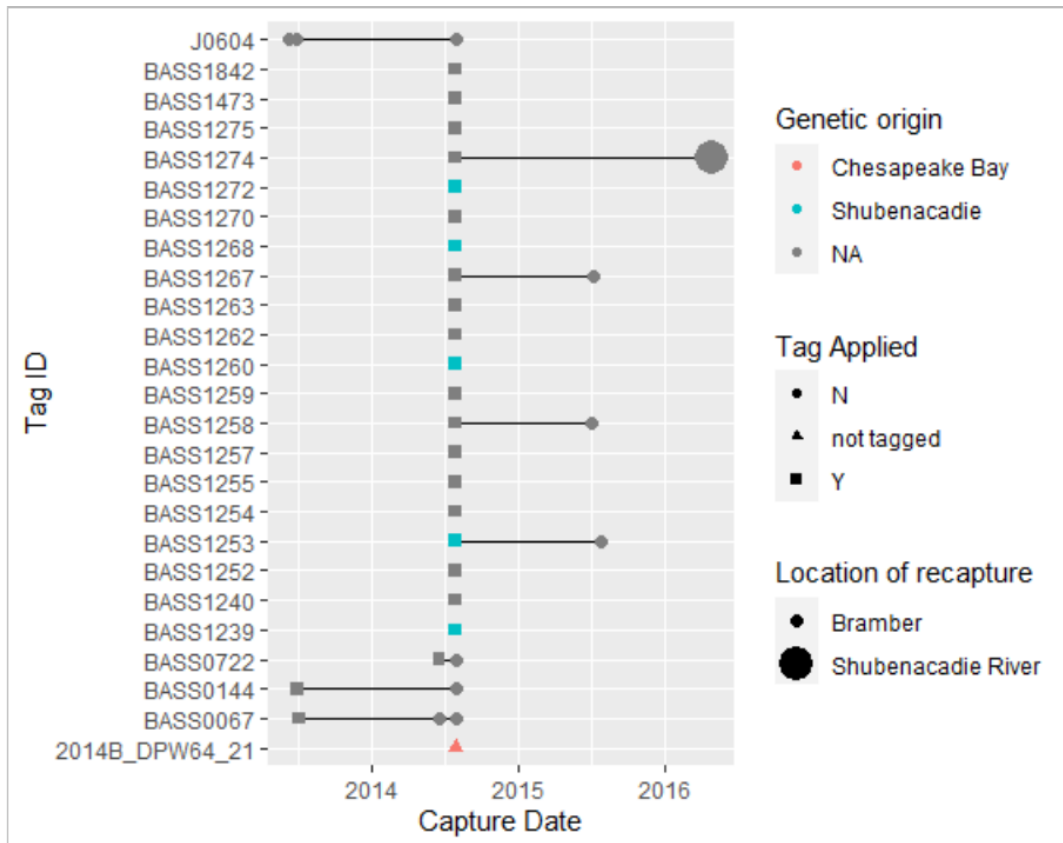
118

Figure 21. Genetic origin and movement of Striped Bass, *Morone saxatilis*, caught with a U.S.A. migrant at a commercial herring weir in Bramber, NS during the same tide. Note tag ID J0604 was not marked by this study and initial tagging location is within the Minas Basin, NS.

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Appendix 1

Normalization protocol

Normalization

Summary

PicoGreen reagents become saturated when using DNA concentrations ([DNA]) >1ng/µL. As such, it is necessary to obtain a rough estimate of [DNA] in your samples using NanoDrop. Since NanoDrop estimates the total concentration of nucleic acids (dNTPs, small fragments, ssDNA), one should assume that it over-estimates DNA concentrations by a factor of 2-3X. If DNA is highly concentrated (>100 ng/µL), it is a good idea to prepare tubes or plates of DNA that will serve as new working solutions (50-100 ng/µL), while the full strength DNA stock can be stored at -20C until after normalization is completed, at which point it can be moved to -80C storage. Small aliquots of the working solution will be used to create 100µL aliquots of diluted DNA (<2 ng/µL) for PicoGreen analysis. Once reliable measurements of [DNA] of diluted working solutions are acquired, these values can be used to calculate dilution factors necessary for the final 200 µL of 20 ng/µL.

NOTE: Elution Buffer (10mM Tris-HCl, pH 8.0-8.5) must be used for dilution of DNA moving forward to the next step in the pipeline (enzymatic digestion) **AND 1X TE** must be used for all dilutions used for dilution of aliquots to be used for PicoGreen measurements (i.e. 1X TE is used for measurements but should not be carried forward in any samples for following steps).

Dilutions
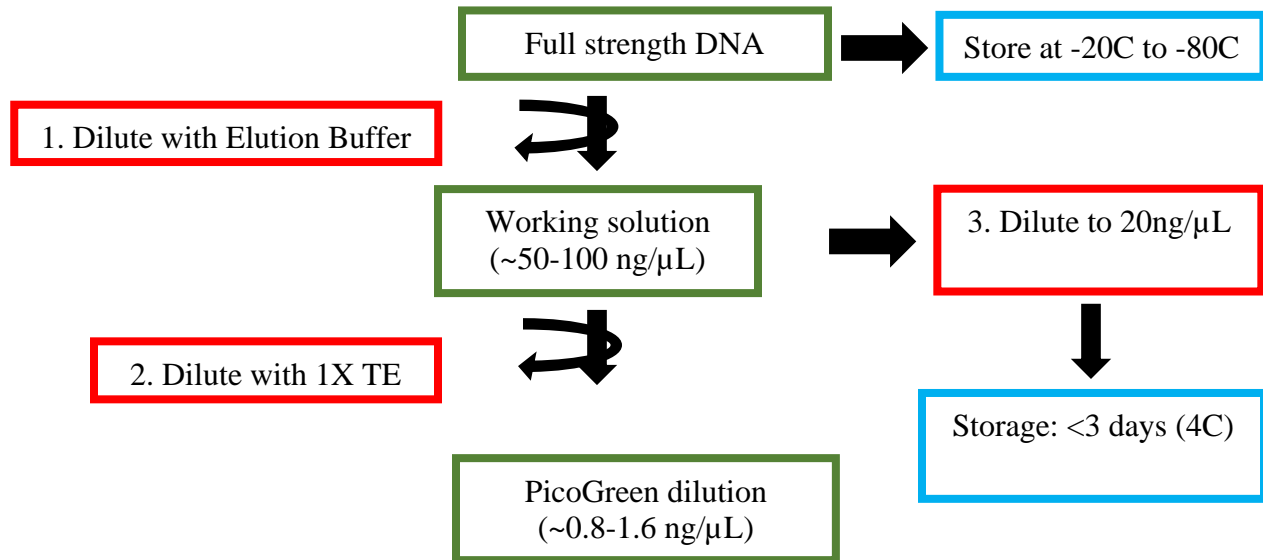
1) Measure all samples to be diluted with NanoDrop in order to have any understanding

of how much the samples should be diluted for a working solution of ~50-100 ng/µL.

2) Dilute samples with Elution Buffer (10mM Tris-HCl, pH 8.0-8.5).

3) Dilute a small aliquot of each sample with 1X TE, for a final concentration of 0.8 - 1.6

ng/µL and minimum volume of 100 µL. Avoid pipetting volumes of <2 µL. For

examples, 2 µL of samples of 100ng/µL should be combined with 198 µL of 1X TE for a

final concentration of 1 ng/µL and volume of 200 µL.

NOTE: For all dilutions requiring 1X TE, the 20X TE stock DNA will need to be diluted

1:19 with NanoPore autoclaved water.

4) Prepare standards by way of a serial dilution using 1X TE and a ratio of 1:4. Each point in the standard curve should have at 2 replicates. The DNA standard stock is 100 ng/µL and the highest concentration standard must be 2ng/µL (=2µg/mL).

Example of Standard Curve Serial Dilution

i.   Fill 6 x 1.5 mL microtubes with 375 µL 1X TE.

ii.   Prepare a microtube with 350 µL of 2ng/µL DNA standard (7 µL of 100 ng/µl DNA standard stock 343 µL 1X TE). This will be standard #1.

iii. Pipette 125µL from standard #1 into the first microtube containing 375µL of 1X TE. This will be standard #2. Do not discard tip.

iv.   Mix by pipetting up and down 10 times. Do not discard tip.

v.   Transfer 125µL from standard #2 into the second microtube containing 375µL of TE. This will be standard #3. Mix as before.

vi.   Repeat until standard #6.
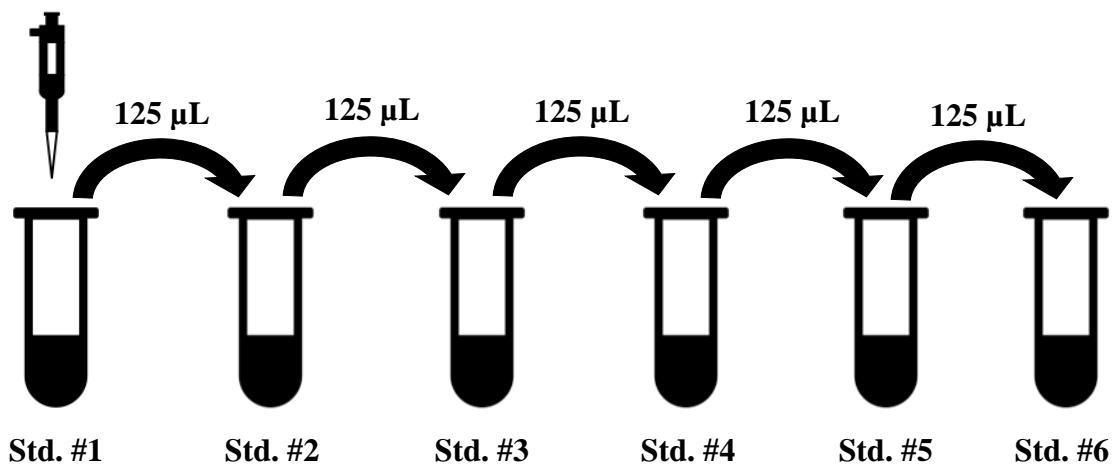
5) Prepare a master mix containing 100 µL of diluted Quant-iT PicoGreen dsDNA reagent for each sample and standard to be quantified. The reagent must be diluted 1: 199 with 1X TE before use.

NOTE: The Quant-iT PicoGreen dsDNA reagent is photo-reactive and should be protected from exposure to light as much as possible (i.e. wrap tube in aluminium foil and incubate plate in darkness).

NOTE: All reagents to be room temperature before analysis.

6) Turn on the Synergy HTX plate reader and then the accompanying computer.

NOTE: The plate reader door of the Synergy HTX will automatically open at various steps during the analysis. Please ensure that this door does not remain open, as extended exposure to the light can have negative impacts on the internal sensors.

7) Prepare/confirm protocol in Gen5 Data Analysis Software.

Gen 5 / Synergy HTX

Click on the Gen5 icon:

  i. A) Select the following protocol: L:Drive > Faculty-Student Share > Pavey Research > PicoGreen > PicoGreen Protocol Template
      B) If the template or L:Drive are unavailable, start a new template with the following Read Method: Fluorescence intensity, Endpoint, Filters (these options will not be displayed if an existing protocol is selected). Complete the template

with the settings outlined below.

Figure: Gen5 TaskBar

ii. Click on the "Procedure" icon and ensure that all settings are as follows:
Plate type: Costar 96 Black Opaque
Excitation: 485/20
Emission: 528/20
Optics position: Top
Gain: Automatic gain adjustment
        Scale to high wells (Note: these must be defined by the user as the wells
        containing the most concentrated standard)
Read speed: Normal
Read height: 1.0mm
Random: Click on this icon and select only the wells that contain DNA, standards
and blanks (unselected wells will be passed over; thereby saving time and bulb
lifespan).

iii. Plate layout must be defined for each new plate to be analyzed. Using the
mouse, define the positioning of all samples and be sure to number the samples in
a logical order. Define the positions of all standards and their concentrations:

1) 1000 pg/µL
2) 250 pg/µL
3) 62.5 pg/µL
4) 15.625 pg/µL
5) 3.906 pg/µL
6) 0.977 pg/µL

Define the position of at least two blanks.

iv. Ensure that the following settings have been selected and defined in Data

Reduction :
Blank transformation: Data in: 485/20, 528/20
                        Blank wells: BLK
Standard curve: Generate curve(s) from the current plate
                      Well ID: STD
                      X axis: <concentration / dilutions>

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Y axis: Blanked data

    v.   Save the new/adjust protocol (analyses can only be launched as experiments which are based in protocols) to your own personal folder.

    vi.   Select the Task Manager icon and "Create using an existing protocol". Browse for the appropriate protocol and select.

    vii.   Double check the procedure, plate layout and data reduction.

    ➢ *Gen 5 / Synergy HTX* instructions continued after plate preparation.

Plate preparation

8) Pipette 200 µL of water into all wells that have not been assigned with samples, standards or blanks. This is important for avoiding light scatter and absorbance.

9) Pipette 100 µL of samples, standards and blanks into their assigned wells.

10) Pipette 100 µL of 200X diluted Quant-iT PicoGreen dsDNA reagent into all assigned wells. While transferring samples, mix each assigned well by pipetting up and down several times.

11) Once pipetting has been completed, place the plate in a dark cupboard or drawer for 5 minutes before reading.

Gen 5 / Synergy HTX continued

    viii.   After the plate has been prepared and is incubating for 5 minutes at room temperature, click on the "Read New" icon . The bulb will require180 seconds to warm up.

    ix.   Once the tray has automatically opened after 180 seconds, place the plate in the tray and select "OK" in the dialogue box.

    x.   Wait for results.

    xi.   Once the read is completed, click on Graphs > Results> Std. curve fitting results. Points within the standard curve should fall along the curve and R2 should be >0.98. If this is not the case, attempt another read, problem solve, seek help or abandon the results. If the standard curve does not appear reliable, then the results from the samples will be misleading.

    xii.   Export an excel spreadsheet of the results.

12) Multiply all concentrations by 2 (this accounts for the 1:1 dilution using the PicoGreen reagent).

13) Multiply each of your samples by the amount by which they were diluted during the sample preparation steps of the protocol. These values can be used to extrapolate the concentration of DNA in the working solution.

14) Cover the plate and let sit on the benchtop close to the Synergy HTX for a couple of days until the toxicity of the photo-reactive components of the mix has been exhausted. Dispose of all liquids into the PicoGreen wastes container in the fume hood.

15) Dilute working solutions with Elution Buffer (10mM Tris-HCl, pH 8.0-8.5) for a final concentration of 20 ng/µL.

16) Store new "20 ng/µL DNA" in the 4C fridge if proceeding to digestion. If digestions won't take place for a few days, store plate/samples with sealed caps in the -20C freezer.