Spatiotemporal variability in northern shrimp (*Pandalus borealis*) life-history traits in Newfoundland and Labrador

by

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ABSTRACT

After the collapse of the groundfish stocks in the mid-90's, northern shrimp has become one of the most economically important fisheries in Newfoundland and Labrador. However, the biomass has drastically decline since 2006 to reach similar low biomass levels as before the mid-90's. Several reasons have been proposed for that decline including the recovery of predators, high fishing pressure, and changes in water temperature. Collapses and slow recoveries of fisheries have often been associated with life-history changes, but this has not yet been documented for northern shrimp in Newfoundland and Labrador. The goal of this thesis is to determine if there is variability in life-histories of northern shrimp and if it has contributed to the observed decline of the stock. I first used data from onboard observers and scientific surveys to estimate variation in size at sex transition from 1995 to 2016 and evaluate which factors are driving this variation. I found that trends in size at sex transition varied depending on the data source, but a general decline was observed. Fishing and temperature were identified as the main factors driving this decline, but the decline is more likely a consequence than a cause of reduction in abundance by fishing. I suggest that a compensatory response to reduced local abundance caused by fishing is the mechanism explaining observed variation in size at sex transition. In the second part of this thesis, I updated estimation of shrimp fecundity, which has not been done for 40 years. Then, I integrated new fecundity estimates with the size structure and size at sex transition information from the previous chapter to test if the variability in life history is affecting the estimation of indices of stock reproductive potential. I found that the number of eggs at size was 30% lower in 2018 than in 1978.

However, the variability in size at sex transition and fecundity had little effect on the estimation of stock reproductive potential and did not cause major changes in the categorization of the stock status within the currently precautionary approach. I suggest that for this stock, the spawning stock biomass can be considered a good, parsimonious index to represent the reproductive potential.

ACKNOWLEDGMENTS

Thanks to Arnaut LeBris, for the guidance in the thesis, the program, and the whole process of moving far from home to study here. Thanks for being always so accessible and supportive. Thanks to Eric Pedersen for the help with the data and the advice about the fishery and the statistics. I am also grateful to Noel Cadigan for his suggestions to improve the models. Thanks to Catherine Skanes and Frederic Cyr for their help accessing DFO’s data. I am very grateful to the summer interns Taylor Hughes, Elanor Dillabough, and Mechaella McDonald, who help me process my samples; it would have taken me an eternity without them. A lot of people gave feedback on my research during my oral presentations in different meetings and conferences; their comments helped to refine the ideas and improve this work. I could not have finished my degree and thesis without the help of my colleagues in the fisheries program at the Marine Institute. My mom and dad, my siblings and Jeancarlo made a lot of sacrifices to provide me essential emotional and financial support so I could continue with my studies, my eternal gratitude to them.

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Chapter 1. Introduction

1.1. Biology

Pandalus borealis Krøyer, 1838, commonly known as northern shrimp, deep-sea prawn, or pink shrimp, was considered a circumboreal species, present in the Artic and in both the North Atlantic and North Pacific (Garcia 2007). In 1992 the Pacific population was elevated to the status of a new species, *Pandalus eous*, leaving *P. borealis* in the Artic and the North Atlantic in both the American and the European side (Squires 1992).

The local distribution of northern shrimp depends on several variables such as substrate, temperature, and depth, among others. The species prefers soft bottoms with high content of organic matter and can live in temperatures ranging from -1.6 ºC to 12 ºC, preferring ranges between 0ºC and 5ºC. *P. borealis* has been reported at depths from 9m to 1450m, although they are more common from 50m to 500m (Shumway et al. 1985). Shrimp growth depends on food availability, but population density and temperature also affect growth rates (Garcia 2007). Males grow all year round; females only grow when they are not reproducing (Garcia 2007).

Pandalus borealis is an opportunistic omnivore; it can act as a predator as well as a scavenger. The species predominantly feeds on benthic organisms including small crustaceans, polychaetes, foraminifera, radiolarians, sand, etc. (Shumway et al. 1985). During their nocturnal diel migrations, they can also eat some pelagic organisms such as copepods. Northern shrimp plays an important role as a prey for several species of groundfish (Savenkoff et al. 2006). In the 1980's, predation by cod and redfish was the main cause of shrimp mortality and the collapse and recovery of ground fish species in the North Atlantic have been proposed as a possible driver of the abundance of northern shrimp in these waters (Savenkoff et al. 2006).

Northern shrimp is a protandrous hermaphrodite, hatching first as males and then transiting to females after sufficient growth. The age at which the sex change occurs is variable, but most individuals transition at ages between 4 and 6 years (Garcia 2007). The sex of an individual is easily distinguishable by the morphology of the endopodite of the first and second pleopod (Shumway et al. 1985). Females carry their fertilized eggs in their pleopods until the larvae are released to the water. Hence, fecundity is often related to the size of the mother. Spawning is annual, however some populations in Greenland have been reported to spawn every two years (Garcia 2007). There is a high mortality of eggs in the northernmost part of their distribution due to the cold waters. Also, in Maine and Newfoundland, the egg masses are affected by parasites that can produce a significant loss in eggs (Shumway et al. 1985).

The egg development time depends on local bottom temperatures, and the development time ranges from 6 months in warmer areas to 19 months in colder areas. The hatching time is synchronized with the phytoplankton bloom (Koeller et al. 2009). Larvae are pelagic and their spatial distribution is greatly affected by local currents. A study from Newfoundland and Labrador found that the larvae are carried southwards by the Labrador current, and as a result the recruitment of a given site is subsidized by larvae from northern areas (Le Corre et al. 2018, 2020).

1.2. Fishery

Pandalus borealis is an important commercial species fished using trawl nets in all its geographic distribution. The species is exploited in the continental shelf of Canada, Denmark, Greenland, Iceland, United States of America and Norway among others (Garcia 2007). In Newfoundland and Labrador, an exploratory fishery started in the early 1970's, conducted by international offshore vessels (Powles 2016). Following the extension of the national jurisdiction to the 200 miles Exclusive Economic Zone, Canada started to take control of the activity, substituting the fleet for national vessels. After the collapse of the predominant groundfish fisheries in the region, the shrimp fishery grew and became a major fishery (Powles 2016). Subsequently an inshore fleet was developed and fished part of the total allowable catch (TAC), primarily in the Shrimp Fishing Areas (SFA), SFA 5 and SFA 6 (Fig. 1.1). In 2009, when the catch was at its peak, the TAC was allocated equally among the offshore and inshore fleet. In the last years, as the stock started to decline, there has been a decrease in the exploitation rate of the southern areas, where the allocation is still balanced. In contrast, constant or even increasing exploitation rates are observed in northern fishing areas with the fishery being done almost exclusively by the offshore fleet (Anonymous 2016, DFO 2018).

The region of Newfoundland and Labrador is divided in shrimp fishing areas that are treated as separate management units or stocks (Figure 1.1). The areas of interest for this thesis are SFAs 5 and 6, which are the SFAs with the best available data, from both onboard observers and scientific surveys. Because of the high level of larval connectivity among SFA's, it is likely that they are not single independent stocks but metapopulations closely related or a single population. This represents a challenge for the management of the resource given that the incorrect delimitation of a stock can lead to inappropriate assessment and management (Le Corre et al. 2018 2020).

Information for the assessment of norther shrimp in Newfoundland and Labrador, comes from the fall multi-species bottom trawl survey conducted by Fisheries and Oceans Canada. A non-parametric method is used to get a probability of distribution of stock size from the survey data (Evans et al. 2000), which is used to estimate indices of total abundance, spawning stock biomass (SSB), fishable biomass, and total biomass. There is currently no accepted population dynamics model to assess this fishery, so a survey index-based precautionary approach has been applied since 2009. This approach categorizes the status of the stock in three zones: critical, cautious, and healthy (Fig. 1.2). These zones are delimited by a limit reference point and an upper stock reference point based on an SSB index. When the SSB index is in the cautious or healthy zone, management actions will depend on the SSB value, on the trajectory of the index, and the socioeconomic aspects of the fishery. Once a stock is in the critical zone, measures are more restrictive, and conservation considerations should prevail (DFO 2009). The precautionary approach and the reference points were revised in 2017 and the conclusion was that shrimp productivity might have changed over time, but there was not enough evidence yet to support any change in the current management approach.

In the 1990’s and early 2000’s, the biomass of northern shrimp in SFA 6 steadily increased until it reached a maximum in 2006. The stock biomass has drastically declined since 2006 (Fig 1.3) and it has been in the critical zone for the last two years. This is particularly concerning because northern shrimp has been one of the most economically valuable fisheries in Newfoundland and Labrador, and the income from shrimp fisheries has been driving the economy of coastal communities and municipalities in Newfoundland (Carruthers et al 2019).

There is no certain explanation of why shrimp biomass has been decreasing; however, there are several hypotheses. One possibility is that there has been too much fishing pressure applied to the stocks. The second is that the modest recovery of the groundfish populations as predators has increased the natural mortality of shrimp, especially given the lack of alternative prey such as Capelin (Sherwood et al. 2007). Finally, a relation between the stock productivity and the environment has been suspected but the mechanisms driving this relation remain unclear (DFO 2017).

Beside the use of a total allowable catch, other regulations have been implemented to achieve sustainability in the fishery. These regulations address gear design, such as the use of a 40 mm mesh size, footgear with bobbins or rubber discs with vertical chains to reduce the impact on the sea bottom, and fish exclusion devises like the Nordmore grate to reduce bycatch. As a result, the fishery has on average less than 3% of bycatch by weight. Furthermore, there are several areas closed to fishing to protect sensible habitats and to maintain the shrimp population (Powles 2016). Because of all these measures and despite the current decline in biomass, the northern shrimp fishery in Newfoundland and Labrador currently holds a certification of sustainability given by the Marine Stewardship Council (MSC) valid until 2021 (Powles 2016).

1.3. Life history variability

The series of events in the lifecycle of the organisms are called life history. We can easily identify contrasting life histories, for example, between a whale and a sardine, the first one has a long lifespan and very low fecundity, while the later have a short lifespan and high fecundity. They are usually defined by life-history traits, which are phenotypic characters that affect the fitness of a species or individual (Stearns 1992), for example, size at birth, age at maturity, or maximum size. Like most other phenotypic traits, life history traits are determined by genetics, environment, and genetic-environment interactions. Life-history traits are known to show a high degree of variation and phenotypic plasticity (Stearns 1992). For example, the porcellanid crab *Petrolisthes armatus* occurs on the pacific and Atlantic sides of South and Central America, but individuals on the Atlantic side reach larger sizes and produce 3 times less eggs than their pacific equivalent because of the conditions in each environment (Wehrtmann et al. 2012).

Life history theory predicts that the evolution of the traits is an optimization problem; each individual should find the balance of energy to allocate between reproduction, growth and survival to maximize its reproductive success (Stearns 1992). According to classical life history theory, this is a complex optimization problem not just because of the trade-offs among contradicting life history traits but also because there is also the effect of extrinsic factors that can affect the fitness (Chen et al. 2020). So, there is not a single ideal set of traits, as this ideal changes constantly as the environment or the population change.

Life history traits are related to population dynamics; hence they are often used to make generalizations about the relation between one set of traits and the extinction risk of the species. For example, traditional conservation biology suggests that slow growing, late maturing individuals are more vulnerable; however, evidence suggest that in the ocean that is not always the case (Pinsky and Byler 2015). Fast growing organisms have more population oscillations, so they are more likely to suffer from a depensation product of stochastic environmental processes (Pinsky and Byler 2015).

Fishing can be considered an extrinsic factor that affects life-history traits. Fishing is size selective and tends to remove the bigger individuals, truncating the size and age distributions of a population. Because larger females are generally more fecund, fishing tends to reduce the population reproductive potential and can also generate a selective pressure towards fast growing and early maturing organisms (Hsieh et al. 2006). Fishing also reduces abundance, and hence competition. Further, fishing can select for fast-growing individuals and, as mentioned before, this puts the population in more risk of collapse in a catastrophic event (Pinsky and Byler 2015). For these reasons, overfishing is often associated with changes in life history traits (Engelhard & Heino 2004).

In the case of northern shrimp, there are some reports of environmental effects on life history traits. Over time, shrimp from all over the North Atlantic have changed the length and date of their hatching period to synchronize with the phytoplankton bloom of the region (Koeller et al 2009), and there are reports of decreases in size at sex transition in warmer waters (Koeller et al. 2007). So, given that 1) shrimp stocks in Atlantic Canada have been exposed to periods with variable environment and fishing pressure, 2) biomass has drastically increased and then decreased over the last 30 years and 3) there is evidence that the life-history traits are varying, and that it could be related to the declining stock.

1.4. Objective

The general objective of this study was to describe the spatiotemporal patterns of life-history traits of northern shrimp in Newfoundland and Labrador and evaluate how they can affect the estimation of reproductive potential. In chapter two, I specifically looked at the spatiotemporal patterns in size at sex transition in northern shrimp in Newfoundland and Labrador and assessed the factors driving those patterns. In chapter three, I updated the prior estimates of the fecundity at size for northern shrimp to evaluate how shrimp fecundity has changed over the las 40 years. Using the updated estimates, I evaluated if changes in life-history (fecundity and size at sex transition) have affected the estimation of the indices of stock reproductive potential and, therefore, the perception of the status of the stock.

1.5. Co-authorship statement

I designed the project, did all analyses and the writing of the thesis. I received shrimp samples for fecundity analysis through Catherine Skanes from Fisheries and Oceans Canada. I processed the samples with the help of the summer interns Taylor Hughes, Elanor Dillabough and Mechaella McDonald. Frederic Cyr form Fisheries and Oceans Canada provided temperature data for the study area. Eric Pedersen from Fisheries and Oceans Canada provided the spatial polygons and the data of predictive variables (eg. Predator biomass, fishing pressure, etc.). Arnault LeBris helped me in the conceptualization of the project and critically reviewed the analyses and manuscript.

The results of this document were presented at different meetings and conferences as the following oral presentations:

Beita-Jiménez, A. Shrimp size at sexual transition based on two data sources and estimates of fecundity at size. *Northern Shrimp Assessment 2019.* St. John`s, Newfoundland, Canada. February 2019.

Beita-Jiménez, A., A. LeBris & E. Pedersen. Spatiotemporal patterns of northern shrimp (*Pandalus borealis*) life-history traits and its relation to density and environmental variability. *Benthic Ecology Meeting.* St. John`s, Newfoundland, Canada. April 2019.

Beita-Jiménez, A., A. LeBris & E. Pedersen. Spatiotemporal patterns of northern shrimp life-history traits and its relation to fishing and environmental variability. *IMBeR Open Science Conference*, Brest, France, June 2019.

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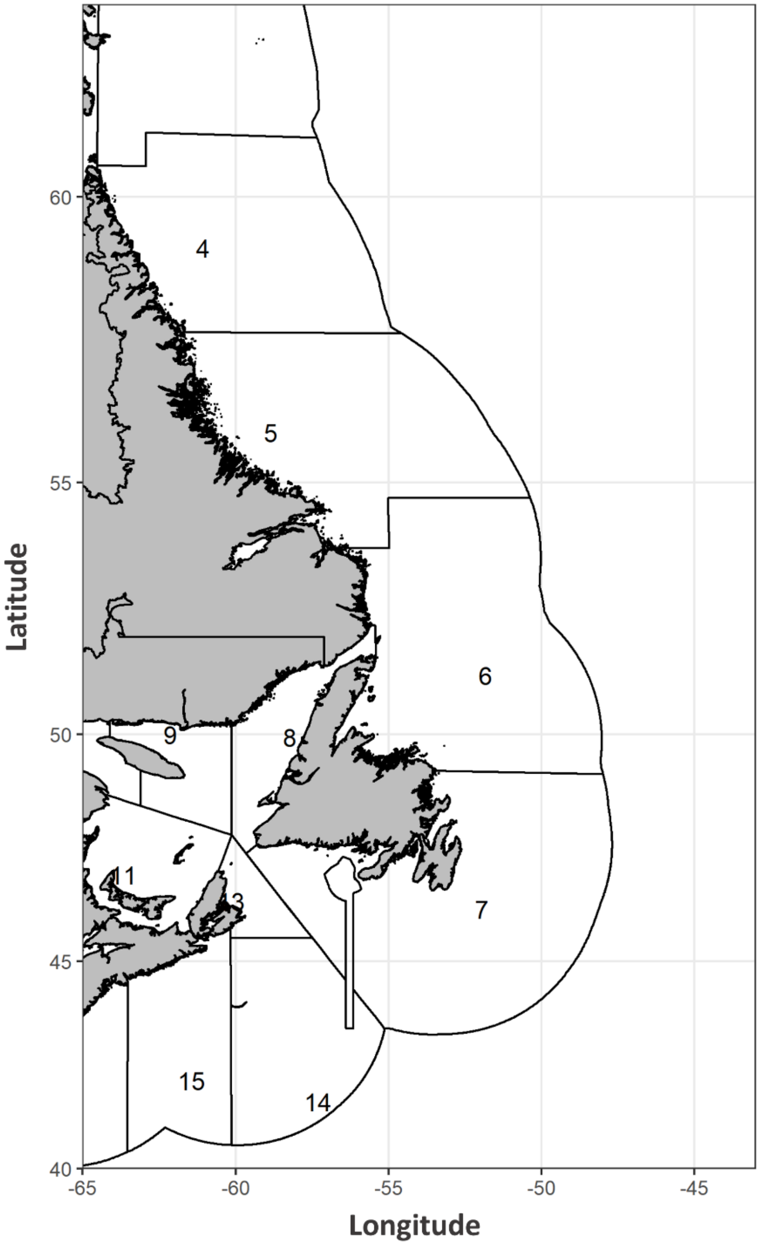

Figure 1.1. Shrimp Fishing Areas (SFA) around Newfoundland and Labrador.

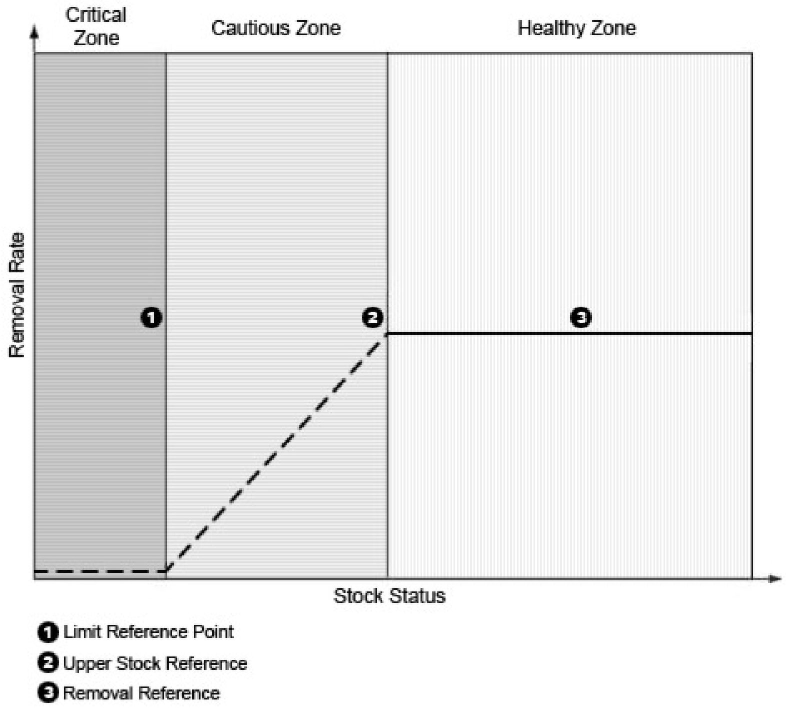

Figure 1.2. Three-zoned diagram defined by the precautionary approach. Reproduced from DFO 2009.

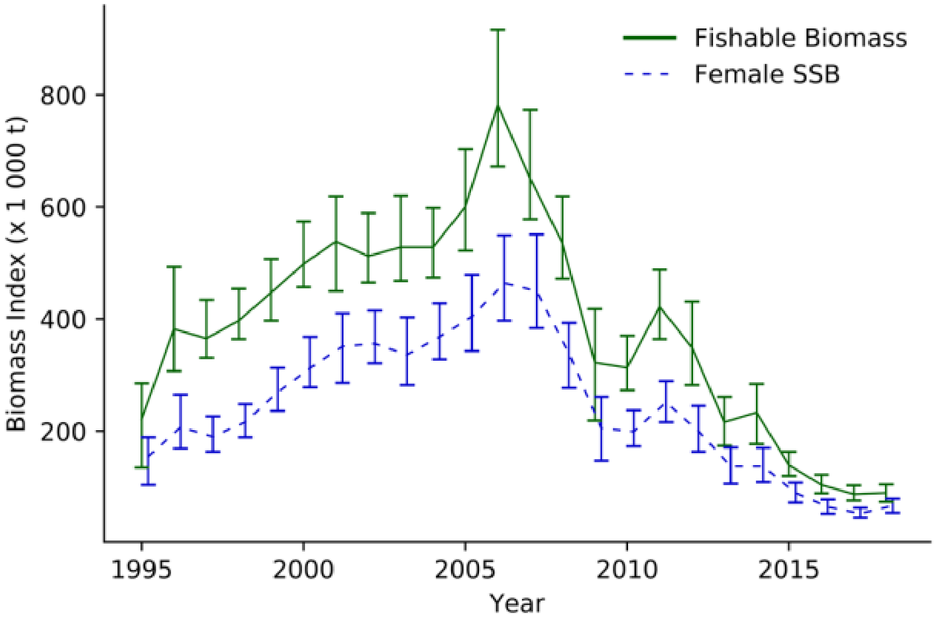

Figure 1.3. Fishable biomass (green solid line) and female SSB (blue dashed line) indices in SFA 6. Error bars indicate 95% confidence intervals. Reproduced from DFO 2019.

Chapter 2. Spatiotemporal patterns of size at sex transition in the northern shrimp and its relation to fishing and environmental variability

2.1. Abstract

Northern shrimp (*Pandalus borealis*) has been one of the most economically valuable fisheries in Newfoundland and Labrador since the collapse of the northern cod; however, it is now experiencing a sharp decrease in productivity. Numerous stock collapses worldwide have revealed that declines in stock productivity are often preceded or accompanied by significant changes in species life-history traits such as size or age at maturity. In this chapter, I described the spatiotemporal patterns in size at sex transition in northern shrimp in Newfoundland and Labrador from 1996 to 2016 and assessed the factors driving those patterns. I used data from onboard observers and scientific surveys to estimate two time series of size at sex transition. Then I tested several environmental and fishing related variables in a generalized additive mixed effect model to identify the drivers of change. Results revealed that the areas with more intense fishing effort showed a declining trend in size at sex transition. In contrast, areas with less fishing effort showed variation with no trend or even a modest increase. The sex transition happened at a smaller size in warmer waters and with the increase of fishing effort. I suggest that the decrease in size at sex transition in intensively fished areas is a compensatory response to reduced local abundance caused by fishing and that trends in sex transition could be reversible with reduced fishing effort.

2.2. Introduction

Northern shrimp (*Pandalus borealis*) has been one of the most economically valuable fisheries in the province of Newfoundland and Labrador since the collapse of the groundfish stocks in the early 90’s (DFO 2017). However, shrimp stocks are now experiencing a sharp decrease in productivity with substantial socio-economic consequences for the coastal communities in the region (Carruthers et al. 2019). The causes for that decrease in stock productivity remain unclear but several hypotheses have been advanced including temperature variability in the North Atlantic, high fishing pressure, and the recovery of groundfish populations such as cod and redfish that are important predators (DFO 2017). The variation in life-history traits can have significant demographic effects, despite that, the relationship between such variation and the stocks productivity has not been explored in this fishery.

Numerous stock collapses worldwide have revealed that declines in stock productivity are often preceded or accompanied by significant changes in species life-history traits such as length, or age at maturity (Trippel 1995, Bromley 2000, Engelhard & Heino 2004). Fishing can truncate size and age distributions of a population because, fishing tends to preferentially remove larger more fecund females, which can result in higher variability in recruitment, biomass, or abundance (Hsieh et al. 2006). This can destabilize populations by increasing the risk of collapse from stochastic environmental events and reducing the chance of recovery. This phenomenon has been one of the hypotheses advanced to explain the collapse and slow recovery of northern cod stocks in

Newfoundland and Labrador and in pink salmon in in western North America (Hutchings and Reynolds 2004).

The northern shrimp (*Pandalus borealis*) is a sequential hermaphrodite; all the shrimps are born males and later transition to females. The medium size at the sex transition (L50) is the size at which 50% of the individuals have transitioned to females. This is easily quantified but it is highly variable in response to environmental variations or population dynamics (Wieland 2004, Jónsdóttir et al. 2018). The consequences of changes in size at sex transition on the reproductive potential of a species and whether these changes are reversible remain unclear. Charnov & Anderson (1989) suggested that L50 tends to decrease during periods of low female abundance to compensate for decreased reproductive capacity; however, Charnov and Skúladóttir (2000) found that there is an invariant ratio between L50 and maximum length. They suggested that this is an indicator of slow growth or a terminal molt after the sex change. In that case, a reduction in L50 could induce faster growth rates in females but reducing smaller maximum lengths, which would result in lower lifetime egg production. This lack of clear understanding of the mechanisms governing changes in L50 prevents us from adopting appropriate measures to manage the effects of the changing life-history on population productivity.

Variables such as fishing pressure and changing environment can affect a species' life-history, and potentially its productivity. In the case of size at sex transition, the relation with fishing mortality can be explained by the hypothesis of a compensatory response (Engelhard & Heino 2004). A population that is being exposed to intense fishing can experience a reduction in density and intraspecific competition and an increase in growth rates, which may cause them to reach maturation or size at sex transition at smaller sizes. (Koeller et al. 2007). A similar mechanism happens with environmental changes like warming waters; increasing water temperatures favor earlier maturation or sex transitions (Koeller et al. 2007, Forster et al. 2012). Decrease in size at maturity has been observed in several crustacean fisheries in the Northwest Atlantic, such as snow crab (Mullowney et al. 2014), American lobster (Le Bris et al. 2017), and potentially northern shrimp (DFO 2017).

The relation between temperature, fishing pressure, and the size at sex transition has been studied in several populations of northern shrimp. Some studies have found that higher temperature increases metabolic requirements in shrimps, affecting growth rates and reducing the size at sex transition (Wieland 2004, Koeller et al. 2007, Jónsdóttir et al. 2018). There is a consensus that warming waters have a negative relation to L50 in *Pandalus borealis*, but the effects of fishing are not so clear. For instance, no effect of density was observed in West Greenland stocks (Wieland 2004), but a positive relationship between L50 and density has been described for the stocks in Iceland (Jónsdóttir et al., 2018), whereas in Newfoundland and Labrador, a negative relationship was found (Koeller et al. 2007).

Environmental conditions, fishing pressure, and their interactions are not homogeneously distributed in time and space. As a result, identifying the factors driving change in life-history traits can be difficult. Furthermore, environmental and life history correlations in fish species are often weak and do not hold up upon reexamination (Myers 1998). Previous studies on northern shrimp sex transition in Newfoundland and Labrador were done in a period of increasing biomass (1990-2002) using the fishing area as the spatial scale (Koeller et al. 2007). Stock biomass in the southern fishing areas have declined, and there is evidence suggesting that the fishing areas are strongly connected and might not correctly represent the underlying biological patterns (Le Corre et al. 2018). These different conditions represent an opportunity to reassess the variation in the life history of northern shrimp in Newfoundland and Labrador, with more data at a finer spatial scale.

The objective of this study is to describe the spatiotemporal patterns in L50 in northern shrimp in Newfoundland and Labrador. First, I wanted to update estimations of temporal trends in L50 at the scale of the management unit and to compare with previous studies (Koeller et al. 2007) but with more recent data now covering periods of increase and decrease in stock abundance. Then, I estimated L50 trends at finer scale using information from onboard observers as well as scientific surveys to characterize the spatial variability in the trend in L50 of northern shrimp from 1996 to 2016, and I evaluated the relationship of L50 with environmental, ecosystem, and population dynamics factors.

2.3. Materials and methods

2.3.1. Data collection: Size and sex data were collected from two sources; the fall multispecies survey (Chadwick et al. 2007) and onboard observers deployed during commercial fishing trips, both conducted by Fisheries and Oceans Canada (DFO). I analyzed the data from 1996 to 2016 in the shrimp fishing areas (SFA) 5 and 6, because that is the period covered by both data sources. The bottom trawl net used in the multispecies survey changed in 1995, and the net used until 1995 did not catch shrimp, hence I used the survey data starting in 1996. For each fishing set, a maximum of 300 shrimps were measured to the nearest millimeter. Each individual was categorized as male, transitional female, or female based on morphologic characteristics. For the survey data, the ratio between the weight of the sample and the total catch was also taken.

To assess variation in L50 at a finer spatial scale than the level of SFAs, I used a set of polygons previously used by Fisheries and Oceans for modelling Northern Shrimp population dynamics (Pedersen et al. 2020). These polygons were developed using a Voronoi tessellation scheme based on a fixed number of survey trawls, so that points in each polygon were similar in depth. Fisheries and Oceans divided the shrimp fishing areas in polygons to have a more detailed spatial structure for future assessments. Fisheries and Oceans Canada provided a shapefile with the polygons and a time series of several variables (see Table 2.1) that had been averaged across all trawls measured within each polygon in each year. I examined the relationship between these variables and the observed trends in the size of sex transition.

2.3.2. Data analysis: The size at sex transition was modeled separately for survey and observer data using generalized linear models with a logit link functions and binomial errors as follows:

$$log\left(\frac{p}{1-p}\right) = \alpha + \beta L + \gamma_i \qquad (2.2.1)$$

Where p is the probability of being female, α is the intercept, β is the coefficient for the length effect, and γ_i is the coefficients for the year effects, where *i* is the year. Sex was included in the model as a binomial response, 0 for males and 1 for transitional individuals and females. The size at which 50% of the shrimp are females (L50) was estimated using the following equation:

$$L50_i = -\frac{\alpha + \gamma_i}{\beta} \tag{2.2.2}$$

I estimated L50 per year i for each shrimp fishing area (SFA5 and SFA6) using first observer data and second survey data. To allow L50 to have some spatial variation, I also estimated it for each year in each polygon using only the survey data. This is because the survey data covers a wider spatial range than the observer data.

Given that the estimation of L50 and its trend over time varies depending on the use of observer data or survey data, I tested if the differences in spatial coverage of both sets of data can explain these differences. To do so, I estimated the relative effort in each polygon, dividing the number of tows by the maximum number of tows observed in any polygon. I did this estimation for both sources of data, separately. I then estimated the relative difference subtracting the relative effort of the scientific survey to the relative effort of the observer data, obtaining an index from -1 to 1 where negative numbers indicate a higher relative number of survey tows than observer tows in a polygon, and positive numbers mean a higher relative number of observer tows than survey tows in a polygon. I also estimated a Pearson`s correlation coefficient between the year and the estimation of L50 to have a quantitative index to describe the trend, so positive correlations indicated increasing L50 and negative numbers indicated a declining trend in L50. Finally, I regressed trends in L50 and the relative difference in data coverage.

To quantify the factors affecting the size at sex transition, I used a Generalized Additive Mixed Model (GAMM) using the function *gam* from the package *mgcv* (Wood 2011) in R software (R Core Team 2020). This analysis was done only with the survey dataset because it has a wider spatial coverage. An initial full model included all the variables in Table 2.1 as predictors, according to the following equation:

$$\begin{aligned} L50_{i,j} = \; & \beta_0 + \mathrm{s}\big(\mathrm{D}_{i,j-l}, k = 10\big) + \mathrm{s}\big(\mathrm{T}_{i,j-l}, k = 15\big) \\ & + \mathrm{s}\big(\ln\big(\mathrm{C}_{i,j-l} + 1\big), k = 15\big) + \mathrm{s}\big(\ln\big(\mathrm{P}_{i,j-l} + 1\big), k = 15\big) \\ & + \mathrm{s}\big(\ln\big(\mathrm{E}_{i,j-l} + 1\big), k = 15\big) + \mathrm{s}(\mathrm{j}, bs = "re") \end{aligned} \tag{2.3}$$

Where s are the smooth functions, i are the polygons, j are the years, l is the lag, k is the number of basis functions, D is the depth in meters, T is the bottom temperature in ºC, C is the catch kg/km^2, P is the sum of the weights of the four key predators in kg and E is the fishing effort in hours/km^2. To avoid estimation errors due to the difference in the covariate units, depth and temperature were standardized, while catch, predators, and effort were log-transformed. Year was also included as a random effect (bs=”re”). The value of k for each smooth function was set trying different ascending values and checking the model until effective degrees of freedom (edf) was significatively lower than the selected value of k, as suggested by Wood (2017). GAMM was preferred because it allows for non-linear responses which is more realistic. I tested lags of 0 to 4 years between the year of the estimation of L50 and the year of the explanatory variables. For each lag, I fitted the model with all the variables and used an automatic selection routine to determine the variables to include in the model. The automatic selection routine was done using the function *dredge*, available in the package *MuMIn* in R (Barton 2019), that selects based on the AIC. Once I selected a set of variables for each lag, I chose the model with the best fitting lag based on the AIC and BIC. I estimated the variance inflation factor (VIF) and tolerance and I did not detect evidence of multicollinearity (Miles 2014).

2.4. Results

Size at sex transition differed between shrimp fishing areas (SFA) 5 and 6, and estimations varied between data from onboard observers or scientific surveys (Fig. 2.1). Estimations of L50 based observer data showed clear declining trends with individuals transitioning at smaller sizes in more recent years in both SFA 5 and 6. In contrast, estimations using scientific survey data showed L50 varying without trends for both SFA 5 and 6 (Fig. 2.1). From 1990 to 2009, there was a reduction of about 0.1 mm per year in fishing area five and 0.05 mm per year in SFA 6. Onboard observers and scientific surveys data revealed similar trends in L50 at the beginning of the time series; however, after 2009, the trends diverged with observer data showing a continued negative trend in L50 while survey data showed a positive trend.

Temporal trends in size at sex transition showed substantial spatial variation with negative trends in some areas and no trend or slightly positive trends in other areas. In general, coastal and southern areas showed no changes or increasing L50, while northern and deeper areas showed a decline in L50 (Fig. 2.2a). The survey data had a wider spatial distribution, while the observer data covered mostly the fishing areas (Fig. 2.2b). This difference in coverage could explain the differences in L50 trends observed in fig 2.1. Areas with a positive difference in relative sampling effort between observer and survey data, meaning that there was a higher survey coverage than observer coverage, corresponded to areas with no or positive trends in L50. However, areas with a negative difference in relative sampling effort, meaning that there was a higher observer coverage than survey coverage, and thus correspond to fishing areas, had declining trends in L50 (Fig. 2.2c).

To identity which variables were driving the size at sex transition, a GAMM with a lag of 4 years was selected as the best model. Fishing effort and bottom temperature were the predictors chosen for the model (Table 2.2), however, even in the best model, the variance explained was low (33%) but looking at the residuals it seems like the model makes a good fit to the data (Fig. 2.3). Sex transition occurred at a smaller size in warmer waters and in areas with higher fishing effort (Fig. 2.4). The inclusion of depth, predator biomass or catch, did not improve the model fit.

2.5. Discussion

Here I present an analysis of the temporal and spatial patterns of size at sex transition in northern shrimp in Newfoundland and Labrador. Similar to previous work on northern shrimp size at sex transition (Koeller et al. 2007), I found that L50 decreased from 1996 to 2002. However, the incorporation of more recent data from 2003 to 2016 revealed contrasting trends. L50 showed variability with no trend when it was estimated using data from scientific surveys. L50 had a clear decreasing trend to reach the smallest size in recent years when estimated with observer data. Koeller et al. (2007) had already noted some effect of the data source on the size structure; however, those differences were on the scale, not on the trend. The analysis of the spatial trends in L50 conducted in this study indicated that these contrasting trends are caused by the differences in spatial sampling effort between surveys and observer data. Indeed, the survey coverage is more widely distributed, while observer coverage is more localized in fishing areas. This suggests that trends in L50 varied across the spatial domain and that L50 has been decreasing in areas with intense fishing pressure.

The potential impact of fishing on size at sex transition was demonstrated by the spatial generalized additive mixed model. The model revealed that the two variables that best correlated with the spatiotemporal variation in shrimp L50 were bottom temperature and fishing effort. Shrimp transitioned at a smaller size in warmer waters and in areas with high fishing pressure. There are two non-exclusive hypotheses to explain why fishing produces earlier sex transition. The compensatory response hypothesis suggests that, as fishing reduces population density and subsequently competition, it leads a phenotypical plastic response (Engelhard & Heino 2004) characterized by an increased growth rate and earlier maturation or sex transition. The other hypothesis is the evolutionary response, which predicts that earlier maturation or sex transition is the result of a genetic change in the population induced by fishing. High mortality rates prevent individuals maturing later and at a larger size to reproduce before they are caught in the fishery, so they do not transmit their genes. In contrast, individuals maturing at a smaller size can reproduce before being targeted by the fishery and thus the frequency of genes favoring smaller sizes increases in the population (Engelhard & Heino 2004).

Depending on the relative strengths of these mechanisms on the stock, the consequences for management are different. If the declining L50 is primarily an evolutionary response, then the trend will take longer to reverse. If declining L50 is a compensatory response, then it can be reversed more rapidly by reducing fishing effort. Given the high degree or larvae connectivity in the region (Le Corre et al. 2018) and resulting potential genetic mixing, I suspect that if the change in L50 was evolutionary response, I would have be observed a decline in L50 across a wide spatial scale. However, the decrease in L50 was observed in some areas but not others, which suggests local compensatory responses. Furthermore, the fact that some areas have observed an increase in L50 in recent years suggests that trends in size at sex transition is relatively easily reversible in northern shrimp, which support the phenotypic response hypothesis. To determine with more confidence which of the two hypotheses explain the trends in L50 in a stock, specific studies of the reaction norms of size at sex transition would be necessary (Wheeler et al. 2009).

Earlier sex transition or maturity as a compensatory response has been reported in several stocks including northern shrimp (Koeller, Mohn & Etter 2000), spiny and slipper lobster (DeMartini 2006), black sea bass (Provost, Jensen & Berlinsky 2017) and coral reef fishes (Easter et al. 2020), among others. This plasticity represents a good advantage to the stocks because it reflects the capacity to adapt temporarily to new conditions or intense fishing pressure, but also the reversibility of the compensatory response can allow the stock to revert back in response to management (Easter et al. 2020). Here I showed that fishing could trigger a compensatory response in the northern shrimp. In the last years, the harvest rate of the stock has been increasing, and the biomass has been decreasing (DFO 2018). Extended periods of high fishing pressure can affect the stocks permanently, moving it from a reversible compensatory response to a permanent evolutionary response. This type of change reduces the resilience of the stocks and increases their vulnerability (Enberg, Jørgensen & Mangel 2010, Kuparinen et al. 2016). The variation in size at sex transition is easy to estimate and it responds to changes in fishing pressure, and it has been proposed as a promising index to measure the effects of fishing on the biology of the target species (Lappalainen et al. 2016). It is worth the effort to monitor the L50 annually in order to identify changes and take appropriate measures.

I found a significant negative effect of the bottom temperature on shrimp size at sex transition. Previous studies have also documented a negative relationship between L50 and temperature in northern shrimp stocks in Newfoundland and Labrador (Koeller et al. 2007), in Iceland (Jónsdóttir et al. 2018) and in Greenland (Wieland 2004). This is a widespread pattern in ectotherms and is has been called the temperature-size rule (Forster et al. 2012). Warmer water temperatures limit the oxygen diffusion to the organisms and because it disproportionally affects the larger individuals in a population, it creates a selective pressure that can lead to a reduction in size of maturity or sex transition. This mechanism has been used to explain variation in maturity in numerous species as American lobster (Le Bris et al. 2017), snow crab (Mullowney et al. 2014), salmon (McMillan et al. 2012) or herring (Hunter, Speirs & Heath 2019).

In this study I show that there is a variability of the L50 but the declining trend is observed in areas with high fishing pressure. The local trends in temperature can help to explain why there is not a more generalized decline. The sea surface temperature (SST) in the Newfoundland Shelf and the Labrador Sea have been increasing by 0.13 ºC per decade; however, unlike the SST, the temperature in the water column and in the deeper areas are not evident (Greenan et al 2018). This means that maturing shrimp have not been exposed to a consistent temperature changes that can lead to constant reductions in size at sex transitions. It is possible that in the fishing areas, the variability in temperature on top of the compensatory response to the fishing pressure are forcing more the changes in sex transition. This is important because the trend can be exacerbated with future variations in temperature.

Life-history traits are often related to decline in biomass; therefore, they have been used as indicators for collapsing stocks (Trippel 1995). I identified water temperature and fishing pressure as drivers of change in sex transition, however there is not a general decline in L50 as expected if temperature was the main driver. In contrast, this study reports a reduction in size at sex transition of northern shrimp in the fished areas of Newfoundland and Labrador, where the biomass has been steadily declining in the last decade (DFO 2018). The compensatory response hypothesis suggests that the decline in L50 is more a consequence than the cause of the northern shrimp biomass decline. However, the subsequent impact of the changes in size at sex transition observed in this remains to be studied to better understand the dynamics of this fishing resource.

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Table 2.1. Description of the variables used to predict variation in size of the sex transition in northern shrimp in Newfoundland and Labrador from 1996 to 2016.

Variable	**Description**	**Unit**
Depth	Average depth of the bottom of all the trawl tows that occurred in each polygon	m
Bottom temperature	Average temperature of all trawl tows in each polygon per year	°C
Catch	Total shrimp caught in each polygon per year scaled by the area of the polygon	kg/km^2
Effort	Total fishing effort recorded in each polygon per year scaled by the area of the polygon	Hours/km^2
Predators	Weights of the four key predators observed by the trawl survey in each polygon per year.	Kg

Table 2.2. Models with the lowest AIC from the automatic model selection routine and the null models. Columns indicate the variables included in each model, the degrees of freedom (df), Akaike's information criteria (AIC), and the delta that corresponds to the difference in AIC compared to the best model. The variable year was included in the model as a random effect (re)

Variables included						df	AIC	delta
Depth	**Catch**	**Effort**	**Predators**	**Temperature**	**Year (re)**			
		+		+	+	14	2468.570	0.000
+		+			+	14	2469.602	1.031
				+	+	14	2470.545	1.975
	+	+		+	+	15	2470.683	2.113
		+	+	+	+	17	2471.294	2.724
+				+	+	14	2471.529	2.959
			+	+	+	16	2472.819	4.249
		+	+		+	16	2473.291	4.720
	+	+	+	+	+	18	2473.384	4.813
+					+	13	2473.508	4.938
+		+		+	+	18	2474.692	6.122
	+	+	+		+	17	2475.265	6.695
+		+				4	2476.090	7.519
			+		+	15	2476.135	7.565
					+	12	2491.609	23.039
						2	2498.874	30.303

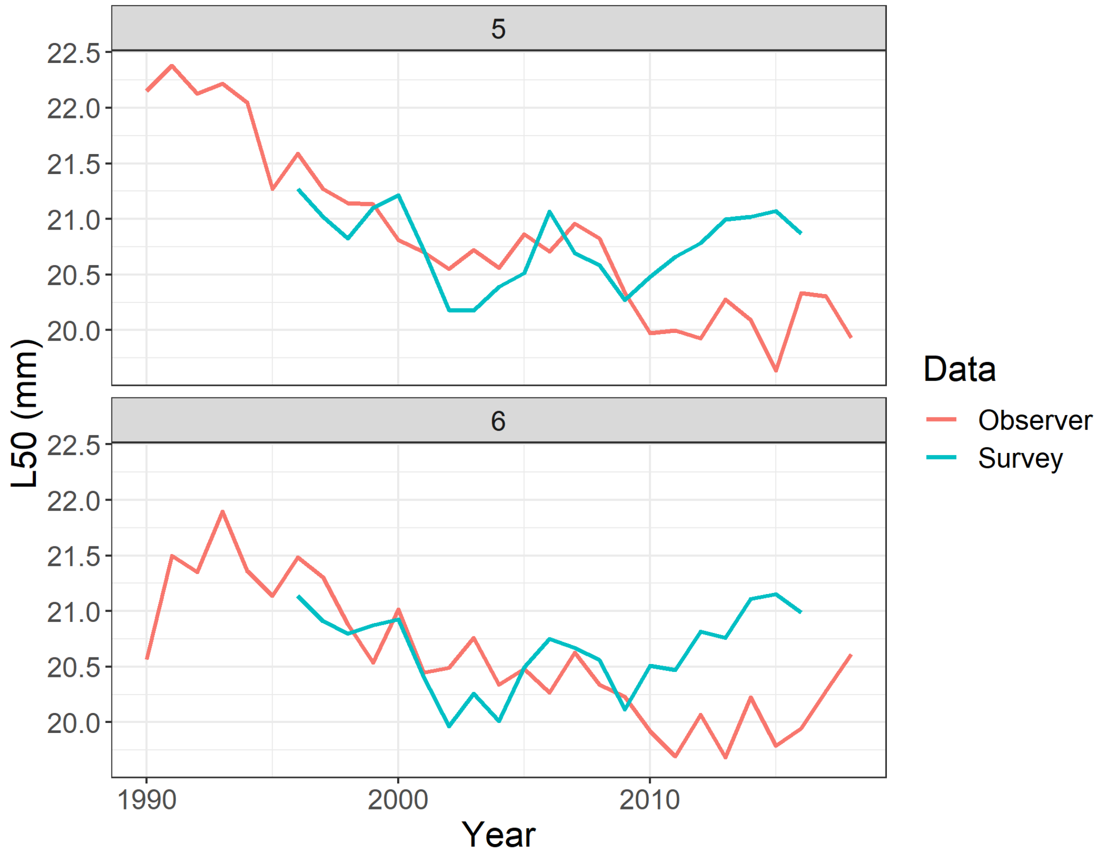

Figure 2.1 Estimation of the size at sex transition (L50) for northern shrimp fishing areas 5 and 6 in Newfoundland and Labrador using two different sources of data from onboard observers or scientific surveys.

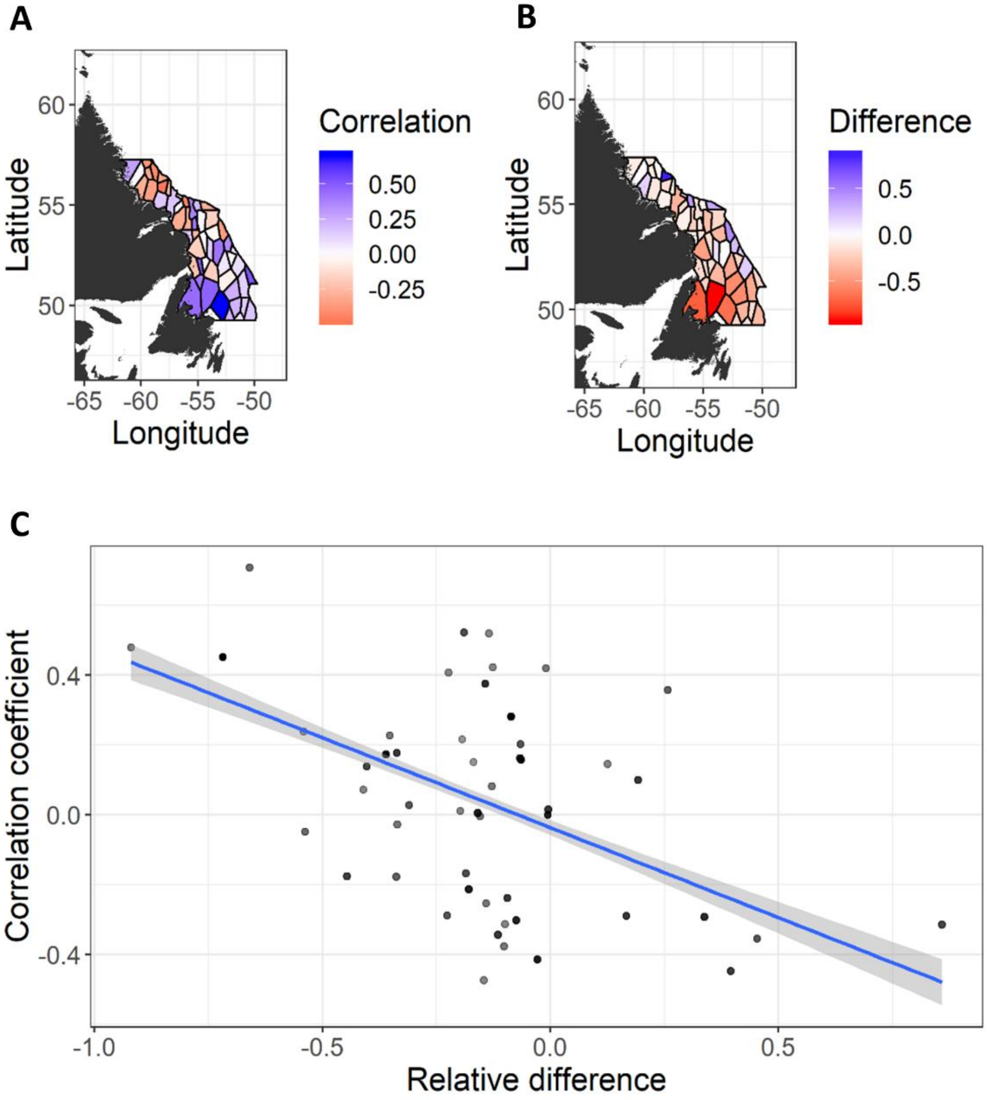

Figure 2.2 (A) Spatial variability in the correlation coefficient between year and size at sex transition of northern shrimp in Newfoundland and Labrador estimated with scientific survey data, where the positive (blue) values represent areas with an increasing trend, and the negative (red) values indicate declining trends. (B) the relative difference in sampling effort of observer data and survey data, where the positive (blue) values represent areas where there is an overrepresentation of observer data relative to the survey, and the negative (red) values indicate areas with an underrepresentation of the survey. (C) relationship between the correlation coefficient and relative difference in effort.

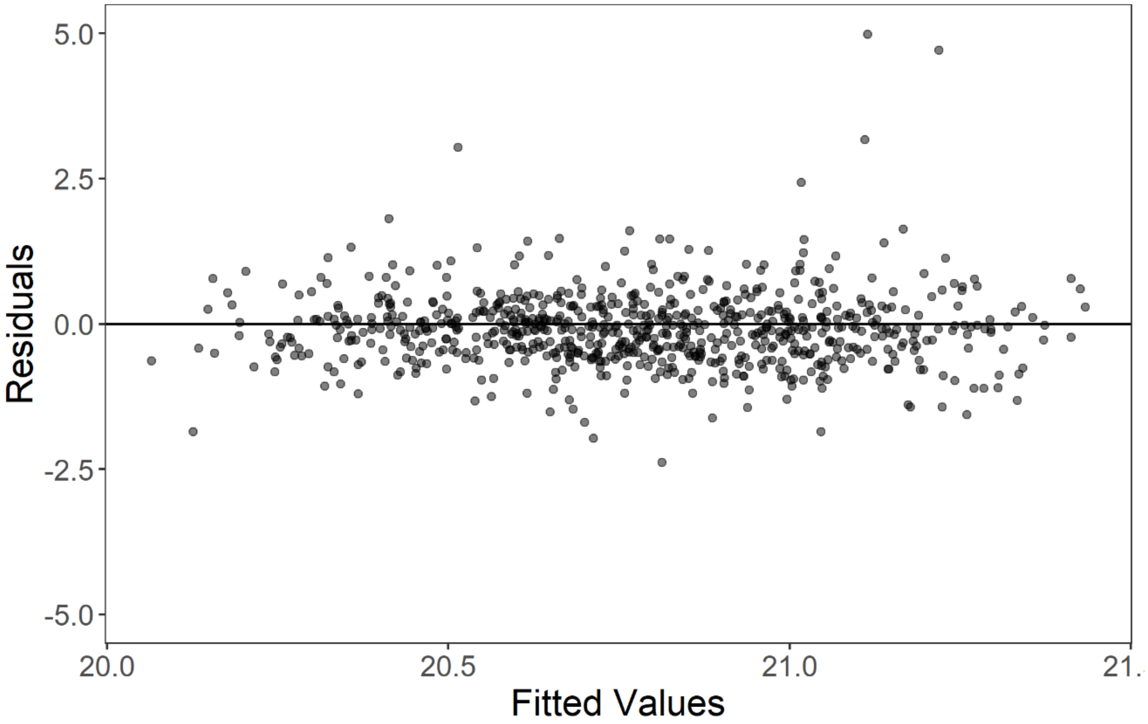

Figure 2.3. Residuals versus fitted values of the generalized additive mixed model.

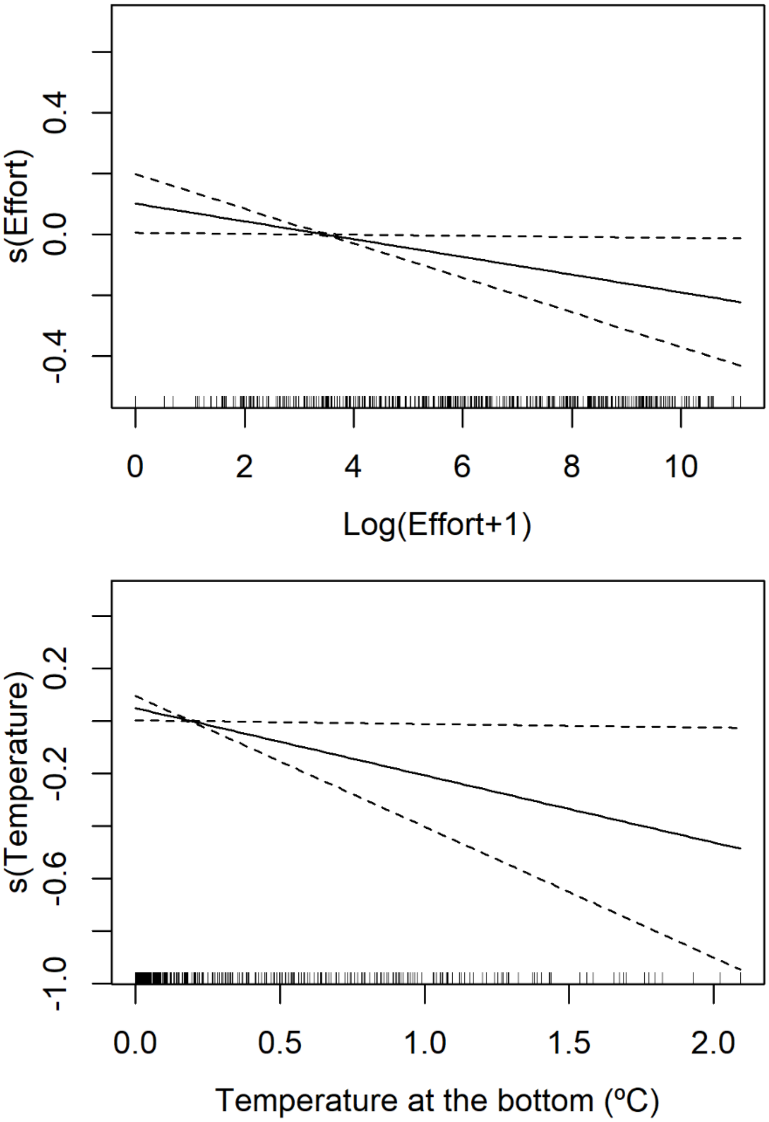

Figure 2.4. Smooth effect of fishing effort and temperature at the bottom on the size at sex transition of shrimp in Newfoundland and Labrador from a generalized additive mixed model.

Chapter 3. The effects of life-history variability on the reproductive potential of northern shrimp (*Pandalus borealis*) in Newfoundland and Labrador

3.1. Abstract

The Spawning Stock Biomass (SBB) has frequently been used as an index of stock reproductive potential when defining biological reference points (BRP). However, using SSB as a measure of reproductive potential depends on several assumptions that when not met, could bias estimates of reference points. Because of the variation in life-history traits, indices such as Total Egg Production (TEP) can better represent the reproductive potential than SSB. In this chapter I estimated individual fecundity at size for northern shrimp in Newfoundland and Labrador, which had not been done for 40 years. Then I evaluated if changes in life-history characteristics such as size structure, size at sex transition and fecundity have affected the estimation of the spawning stock biomass and total egg production of the northern shrimp stocks in shrimp fishing areas 5 and 6. Finally, I evaluated how the perception of stock status changes if TEP is used instead of SSB as the status metric. I found that the number of eggs at size decreased by the 30% since the last estimate. However, the variability in size at sex transition and fecundity did not affect the estimation of reproductive potential enough to cause a major change in the categorization of the status of the stock in the current precautionary approach. For this stock, the SSB and TEP showed very similar trends, hence SSB can be considered as a suitable index to represent the reproductive potential of this stock.

3.2. Introduction

Biological reference points (BRP) are benchmarks that scientists use to classify the status of fish stocks (Collie & Gislason 2001). Some reference points are based on the idea that a relationship exists between the parental stock size and the number of recruits entering the fishery in the future, so one can define limits to the mature biomass that should be left in the population to sustain its productivity. The original formulations for stock-recruitment based BRPs used the annual total egg production (TEP) as a measure of the reproductive potential (Ricker 1954, Beverton & Holt. 1957). Nowadays, most stock assessment and management plans use spawning stock biomass (SSB), relying on the simplifying assumption SSB is proportional to TEP (Marshall et al. 2006, Marshall 2016). For this proportionality to be true, the sex ratio and size at maturity of the population must be constant over time. Furthermore, individual fecundity must increase linearly with body size, with a time-invariant body size-fecundity relationship (Barneche et al. 2018, Marshall 2016). When these assumptions are not met, the use of SSB could lead fisheries managers to set wrong reference points or to make decisions on biased productivity estimates (Barneche et al. 2018, Marshall et al. 2006, Marshall 2016).

Assumptions of constant or allometric life-history traits are often violated because these characteristics vary in a population over time due to phenotypic plasticity or genetic changes, driven by factors such as fishing and natural mortality, size selectivity, food availability, or environmental variability (Stearns 1992). The northern shrimp (*Pandalus borealis*) is an example of a species with variable life-history traits (Haynes & Wigley 1969, Parsons & Tucker 1986, Charnov & Skúladóttir 2000). For example, an annual variation in fecundity at a size of 30% has been observed in the Gulf of Maine (Haynes & Wigley 1969), and seasonal, annual, and spatial variation were reported in Newfoundland shrimp (Parsons & Tucker 1986). Despite this potential for variation, the fecundity of northern shrimp in Newfoundland and Labrador has not been evaluated since 1982 (Parsons & Tucker 1986). If the variability in fecundity over time or space is significant, this should be considered in the calculation of the reproductive potential to have a better understanding of the stock productivity (Mehault et al. 2010).

Northern shrimp is a species with sequential hermaphroditism. Shrimp are born as males, grow and later transition to females. The size at which the sex transition occurs varies over time (previous chapter of this thesis), which can affect the reproductive potential of the stock and is therefore relevant to stock status assessment and management (Mehault et al. 2010). If the size at sex transition is constant over time, but the fishing pressure or selectivity reduce the number of big individuals, the population will increase the male-female (M: F) ratio potentially leading to a loss of reproductive potential. In contrast, if the size structure is constant but the size of sex transition decreases, then the M:F ratio would decrease (Haynes & Wigley 1969), which would increase the reproductive biomass of the population. Previous work in this thesis revealed that northern shrimp of Newfoundland transitioned from males to females at a smaller size in warmer waters and under high fishing pressure (Chapter 2), and we can expect that this variation in size at sex transition may affect stock productivity.

The precautionary approach used to assess and manage the northern shrimp stock in Newfoundland and Labrador since 2009 is based on SSB. It defines a lower reference point

(LRP) and upper stock reference (USR) at 30% and 80% of the geometric mean of the SSB of the period when the stock was considered productive (DFO 2009). The precautionary approach was revised in 2017, and it was concluded that shrimp productivity has changed over time, but that there was not enough evidence to support changing the reference points at the time.

The objective of this study is to evaluate if changes in life-history traits have affected the stock reproductive potential and; therefore, the accuracy of current reference points and the understanding of the status of the stock. I estimated different indices of reproductive potential of the northern shrimp in Newfoundland and Labrador: i) SSB that considers the temporal variability in size structure, ii) sex ratio, iii) size at sex transition, and iv) TEP. I hypothesized that given the variability in life-history traits in the northern shrimp stocks, the assumptions for the use of SSB might not being met, and that total egg production is a more comprehensive index. To test this hypothesis, I compared the stock status derived of the application of the precautionary approach using SSB or TEP. The main objective was to identify the index that better reflects the productivity of the stock.

3.3. Materials and methods

3.3.1. Data collection: Size, sex, and fecundity data were collected from two sources, during the fall multispecies survey (Chadwick et al. 2007) conducted by Fisheries and Oceans Canada (DFO) and with onboard observers. Both databases covered the period from 1996 to 2016 in the shrimp fishing area (SFA) 6. For each fishing set, a maximum of 300 shrimps were measured to the nearest millimeter. Individual were categorized as males, transitional females, or females based on morphologic characteristics.

During DFO's fall multispecies survey in 2018, 25 ovigerous females for each trawl tow where northern shrimp was present were collected from the subsample taken for carapace length measurements. Only shrimp that were not visibly damaged and that had intact egg clutches were sub-sampled. For each subsample, shrimps were collected trying to include a wide range of size classes, including any extremely large or small ovigerous shrimp. The samples were tagged, deposited in bags, then frozen to posterior transport to the laboratory of the Fisheries and Marine Institute for fecundity analysis.

3.3.2. Size structure: I used the size data to estimate the proportion of individuals of each size bin per year. I extracted the total abundance from the DFO's 2018 stock assessment report (DFO 2019). Multiplying the proportion of individuals per size bin by the total abundance, I estimated the total number of shrimps per size bin in a given year N.

3.3.3. Transition size: The size at sex transition was modeled separately for survey and observer data using generalized linear models with a logit link functions and binomial errors as follows:

$$log\left(\frac{p}{1-p}\right) = \alpha + \beta L + \gamma_i \tag{3.1}$$

Where p is the probability of being female, α is the intercept, β is the coefficient for the length effect, and γ_i is the coefficients for the year effects, where i is the year. Sex was included in the model as a binomial response, 0 for males and 1 for transitional individuals and females. The size at which 50% of the shrimp are females (L50) was estimated using the following equation:

$$L50_i = -\frac{\alpha + \gamma_i}{\beta} \tag{3.2}$$

The resulting model was used to estimate the proportion of females at length.

3.3.4. Fecundity: I measured carapace length (CL) to the nearest 0.1 mm with a caliper as the distance between the posterior margin of the orbit of the eye and the posterodorsal margin of the carapace. I weighted shrimp using a digital scale with a precision of 0.01 g. Then I removed the entire egg mass and deposited it in an aluminum recipient labeled and weighed with an analytical balance (with an uncertainty of 0.0001 g). I counted the eggs for each using a stereoscopic microscope and a click counter. These samples were dried in an oven at 60 ºC for 24 hours and subsequently weighted using a digital scale with an uncertainty of 0.01 g. I quantified the number of eggs was counted for 91 individuals, selected randomly, which were used to calibrate equation 3.3 as follows:

$$E = a + bDW + \varepsilon, \tag{3.3}$$

where E is the number of eggs, DW is the dry weight, *a* and *b* are the intercept and slope respectively, and ε is a normal error. Then, equation 3.3 was used to estimate the total number of eggs produced by each individual based only on the dry weight of the egg mass. This allowed us to speed up individual fecundity estimations. Finally, the estimated total number of eggs (E) was related to carapace length as follows:

$$\log_{10}(E) = a + b \cdot \log_{10}(CL) + \varepsilon, \tag{3.4}$$

where a and b are the intercept and slope. We also used the data to estimate a length-weight relationship using linear regression for later analysis.

3.3.5. Reproductive potential: Two indices of reproductive potential (RP) were calculated to examine the possible impact of changes in size structure, size transition, and fecundity (through changes in length), spawning stock biomass (SSB) and total egg production (TEP). SSB was calculated as follows:

$$SSB_Y = \sum_{L=i}^{j} N_{L,Y} W_L P_{L,Y}, \tag{3.5}$$

where $N_{L,Y}$ is the number of shrimp per size bin in a given year, W_L is the weight of an individual shrimp per size and $P_{L,Y}$ is the proportion of females per size bin (0.1mm) in a given year. i and j are the minimum and maximum size (mm) found in each year.

$$TEP_Y = \sum_{L=i}^{j} N_{L,Y} P_{L,Y} F_L, \tag{3.6}$$

where F_L is the number of eggs at a given size bin.

3.3.6. Comparison of indices of stock reproductive potential: The two BRPs used for northern shrimp are the lower reference point (LRP) and the upper stock reference (USR). They are defined as the 30% and 80% of the geometric mean stock biomass from 1996 to 2006, the period when the stock was considered productive (DFO 2009, DFO 2013). Using the same definition, I calculated LRPs and USRs based on previously estimated SSB and TEP. Using these reference points, I classified the stock each year in the healthy, cautious, or critical zone and assessed if the stock status differed between SSB based BRPs and TEP based BRPs. I used fecundity estimations from 2018 (this study) and from 1978 (Parsons

1985) in the TEP calculations to examine the impact of changes in fecundity. For each index, I used survey and observer data to see if the data source influenced estimations.

3.4. Results

L50 estimated using observer data showed a decreasing trend during the 1996-2016 period, while L50 from survey data varied without a trend (Fig. 3.1) during the same period. L50 estimates between the two data sources differed markedly from 2009 to 2016, with higher L50 values from survey data. there is a considerable variation in proportion of females at size (Fig. 3.2)

The number of eggs increased linearly with the dry weight of the egg mass (Fig 3.3). The linear relationship explained 89% of the variance in the data (Table 3.1), confirming that this relationship can be used to predict the number of eggs based only on the dry weight of the egg mass. Individual fecundity was significantly related to carapace length, but the model explained only 30% of the variability of the data (Table 3.1, Fig. 3.4). This model estimated lower fecundity at all sizes (Fig. 3.5) compared to 1978 (Parsons 1985). At an individual level, this corresponded to a loss of around 30% of egg production. There was a significant positive relationship between carapace length and weight with an r^2 of 0.58 (Table 3.1., Fig. 3.6).

All reproductive potential indices showed increasing productivity from 1996 to 2008, followed by a period of decline (Fig. 3.7). The SSB and TEP shows similar trends when size at sex transition was estimated with the same data source (i.e., observer or survey). The largest difference was observed when comparing indices estimated with survey data to indices from observer data (Fig. 3.7). Surprisingly, the lower fecundity at size observed in 2018 in comparison to 1978 did not lead to lower stock productivity indices.

The similar variation over time of SSB and TEP resulted in a similar categorization of the stock status in the precautionary approach (Fig. 3.8.A). For all but two years (e.g. 2010 and 2016), there was a match in the status of the stock when used in the precautionary approach (Fig. 3.8.B), despite that SSB estimated using survey data and SSB estimated using observer data produced slightly different results (Fig. 3.8.B). For the years 2010 and 2016, the SSB estimates using observer data produced a more optimist perception.

3.5. Discussion

Variation in life-history traits affects population dynamics and can bias the perception of stock status when this variation is not adequately accounted for. It has often been suggested that spawning stock biomass does not appropriately reflect the productivity of a stock because it does not consider size specific variation in fecundity or maturity (Barneche et al. 2018, Marshall et al. 2006, Marshall 2016). In this chapter, I assessed how changes in size at first sex transition and fecundity affected the reproductive potential estimates of northern shrimp in Newfoundland and Labrador. Overall, I found that despite important temporal variations in fecundity and size at maturity, SSB and TEP showed very similar trends indicating that SSB is a suitable index of northern shrimp stocks productivity.

This study revealed that fecundity at size of northern shrimp in Newfoundland has decreased by 30% since the last estimation in 1978 (Parsons & Tucker 1986). This variation in fecundity over time was not unexpected. Several studies have shown that fecundity varies around 30% to 40% in shrimp (Haynes & Wigley 1969, Jónsdóttir 2018, Parsons & Tucker 1986) and fish throughout the region (Kjesbu et al. 1998). One possible contributing factor is that there have been reports of parasites in the egg masses of northern shrimp in Newfoundland and Maine that can cause a reduction in fecundity (Haynes & Wigley 1969, Parsons & Tucker 1986). In the fecundity estimation process for this study, the majority of the egg masses had from a couple to tens of white, inviable eggs that matched the description of parasitized eggs (Parsons & Tucker 1986). Chang et al. (2020) recently reported that higher bottom temperatures are related to the increase of parasitized eggs, suggesting that this can produce egg mortality and could eventually affect recruitment. Because of the high prevalence of parasitized eggs observed here and in other populations of the same species (Chang et al. 2020), the causes and consequences of this issue are worthy of further study.

Egg production is an intrinsically variable trait. It depends on environmental conditions, competition, food availability, etc. Haynes and Wigley (1969) observed a temporal and spatial variation in fecundity of northern shrimp from Maine of about 30%, similar to the change documented here. This type of variation has been also reported in lobsters, where the reduction in fecundity is driven by increases in water temperatures (Koopman et al. 2014). Temperature can increase the growth rates which leads to smaller sizes at sex transition (Forster, Hirst & Atkinson 2012). When there is an increase in growth caused by an extrinsic factor, the organism allocates more energy to the growth process, reducing the energy invested in reproduction, which can lead to a decrease in fecundity.

This mechanism has been observed in fish stocks (O'Brien 1999) and can also apply to situations where fishing is decreasing population density, accelerating growth, reducing size at sex transition and eventually affecting egg production (Charnov & Anderson 1989, Koeller, Fuentes-Yaco & Platt 2007). The reduced L50 presented in some areas can be an indicator of a change towards faster growth and earlier reproduction in the stock, and this could be one reason for the reduced fecundity.

I cannot rule out the effect of the differences in the methodology used in this study and the study from Parson and Tucker (1986). Parson and Tucker (1986) directly counted the dried eggs for each individual while I used an indirect estimation, using a previously calibrated equation to predict the number of eggs based on the dry weight of a subsample of the egg mass. Also, their sampling was focused on the deep channels while sampling was spread throughout the fishing area 6 in this study. Spatial differences in fecundity have been found in northern shrimp stocks in Maine (Haynes & Wigley 1969) and Iceland (Jónsdóttir 2018). One possible hypothesis to explain the spatial difference in fecundity is temperature effects. Perhaps shrimp in deeper waters have higher fecundity at size so that the difference in spatial sampling effort may explain the difference fecundity between the two studies. Chang and Chen (2020) recommend the use of size-based stratified random sampling to select the shrimps for the egg counts, arguing that the sampling method can introduce biases in the fecundity estimation. Neither Parson and Tucker (1986) nor I used size-based stratified random sampling and there can be subtle differences in sampling that could contribute to the observed differences in fecundity.

Despite the importance of fecundity for the estimation of reproductive potential, most of the stocks in the North Atlantic have few and outdated data on egg production (Parsons & Tucker 1986, Tomkiewicz et al. 2003). Here I mentioned several factors that can possibly affect the fecundity, but because of the lack of a time series, I cannot conclude if this is a consistent reduction in fecundity or if the reduction observed here is part of a normal variability of the trait. It is important to monitor egg production more often so we can better detect changes, and to improve the understanding of the effect of this variability on the overall reproductive potential of the stock. In this study I used equation 3.3 to estimate the number of eggs based on the dry weight of the egg mass, which makes the estimation less time consuming than traditional methods. Hence, it can be used to facilitate the process and make future monitoring of shrimp fecundity easier.

Finding the appropriate index to represent the reproductive potential of stocks has been a long debate in fisheries sciences. The use of SSB is more common but it has some underlying assumptions, mainly that fecundity increases linearly with mass. The TEP is an alternative method that explicitly considers size-based fecundity and does not assume a linear fecundity and constant maturity (Marshall et al. 2006, Marshall 2016). The use of an inappropriate index can affect the understanding or estimation of stock-recruitment relationships or biological reference points (Marshall 2016). Given that both the size at sex transition and fecundity are essential information that can affect the estimation of reproductive potential, it is often recommended that SSB should be used with caution, or that the use of other indices, such as TEP, should be considered to better represent the reproductive capacity of the stock (Barneche et al. 2018, Jónsdóttir 2018, Marshall 2016).

In this study, I found that, despite the variability in size at sex transition and fecundity, the SSB and TEP produced very similar results and that changing the fecundity estimation did not have much effect either.

The fecundity variation observed in this study is not large enough to cause differences among the indices of reproductive potential I studied. One possible reason is that the shrimp have low fecundity compared to the species usually studied in the literature (e.g. Barneche et al. 2018). For example, I found that the variation in size at sex transition is small, only a few millimeters, and a shrimp of 21mm will have only around 100 more eggs than an individual 1 mm smaller, while in very fecund fishes like cod a small difference can represent a substantial change in the number of eggs. Also, although the relationship in Figure 3.3 is potential, perhaps it does not depart much from a linear relationship, so its effects are not as impactful. However, it is important to keep in mind that in this study, I did not have the data to allow the fecundity to vary over time. Instead, I used scenarios where the fecundity is constant over time but using estimations from two different periods. The ideal is to use methods that include the interannual variability of egg production to have a good understanding of the effect of fecundity on the estimation of reproductive potential (Marshall et al. 1998, Morgan & Brattey 2005)

The data source for the estimation of the proportion of females also has a bigger effect on the indices of reproductive potential than fecundity. The size at maturity or sex transition is a key element to define the spawning biomass. The use of outdated or biased sex transition ogives produce unreliable spawning stock biomass estimates that can lead managers to make wrong decisions (Enberg, Jørgensen & Mangel 2010). For example, ignoring a declining trend in L50 can lead to an under or overestimation of the spawning stock biomass if the size structure is constant or has been truncated, respectively. When the bias is consistent and predictable, managers can directly consider this bias into management advice; however, for northern shrimp, estimation of L50 from then two different data sources produces an inconsistent bias that is not easy to account for. The data obtained from scientific surveys are more comprehensive and probably represents the entire stock better, however the declining size at sex transition observed in fished areas should be studied further to determine whether this has a significant effect on the reproductive potential of the stock. It is important to consider that SSB in the stock studied here is estimated by summing the total biomass of transitional individuals and females without involving any model; however, in order to advance towards the development of an age or length-based population dynamic model, it is important to continue modeling the sex transition ogive and using this to estimate SSB (Cao et al. 2017).

The variations in reproductive potential caused by changes in life history traits do not seem to cause a major change in the categorization of the status of the stock with current precautionary approach. Several studies have argued that SSB is not a good proxy for the productivity of a stock and recommend the explicit accounting of egg production; however, perhaps the relatively low fecundity of the shrimp compared with some fish species (Barneche et al. 2018) makes SSB a suitable proxy for shrimp in Newfoundland and Labrador. However, because of spatial and temporal variability in fecundity, this may not be the case for stocks in other areas or the same area in the future. Due to the importance of the shrimp fishery and as the science around northern shrimp progress, management will probably be based on a more quantitative approach to assess the stock. The variability on life-history trait discussed here would need to be carefully considered in such approach.

3.6. References

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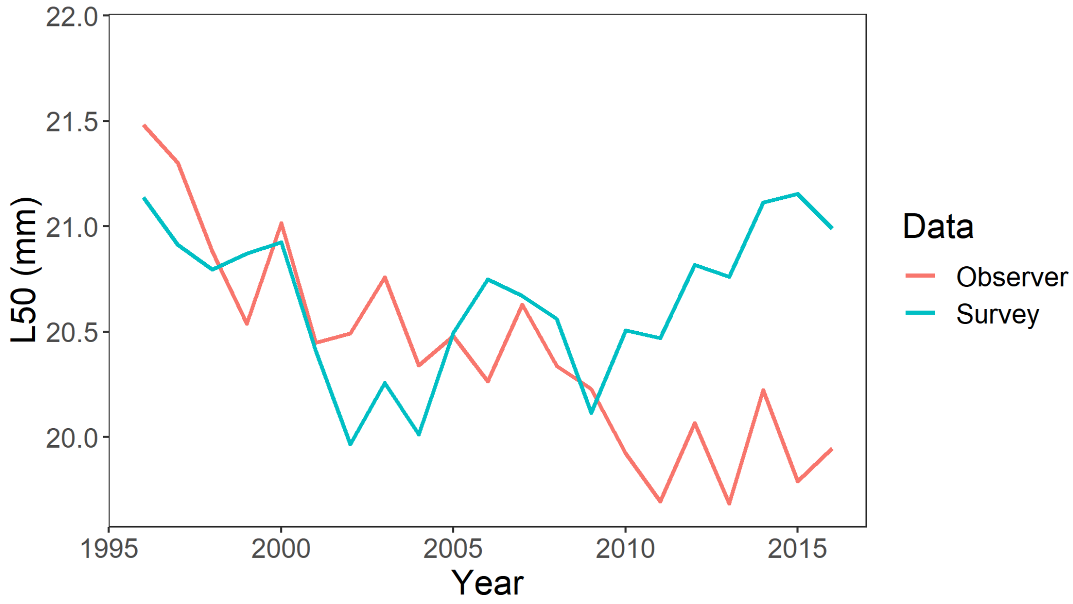

Figure 3.1. Time-series of estimated length at first sex transition (L50) of northern shrimp in Newfoundland and Labrador for the period of 1996 to 2016 estimated using survey and observer data.

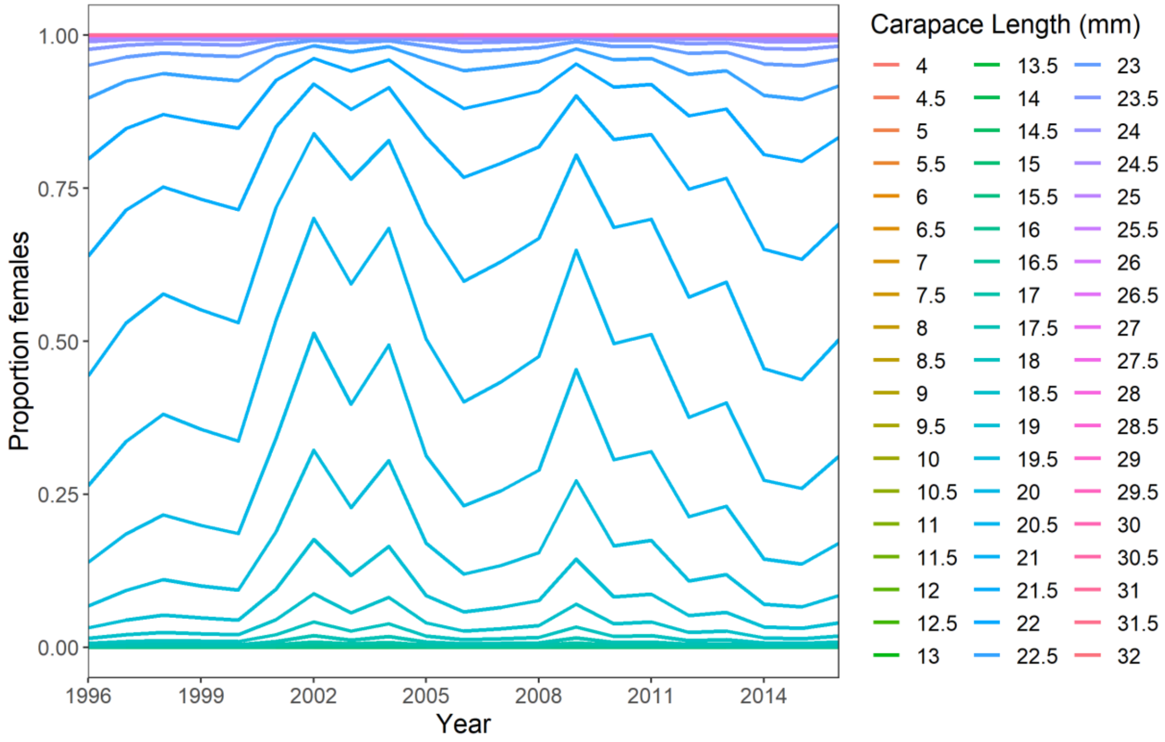

Figure 3.2. Temporal changes in proportion of females of northern shrimp per size in Newfoundland and Labrador using estimations from survey data

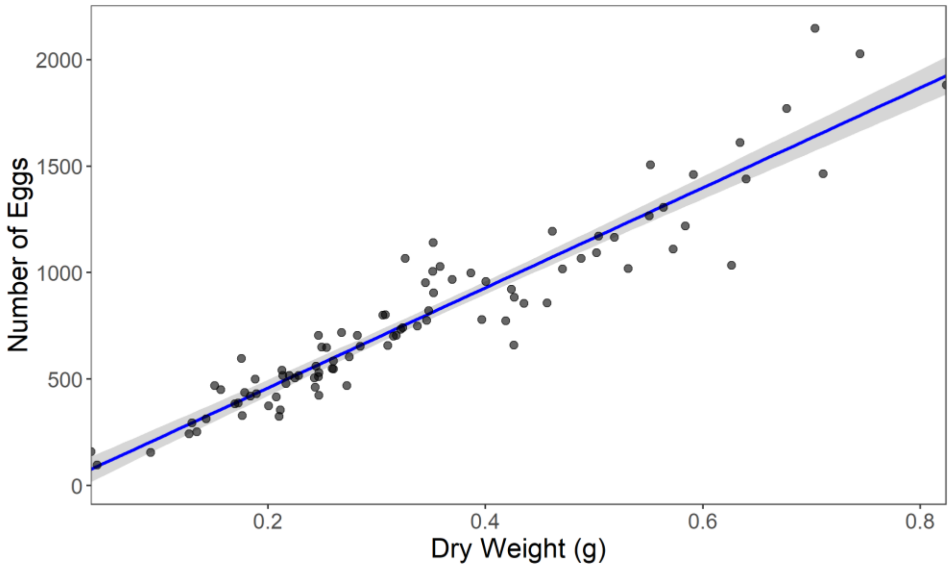

Figure 3.3. Linear relationship between dry weight (DW) and the number of eggs of northern shrimp in Newfoundland and Labrador.

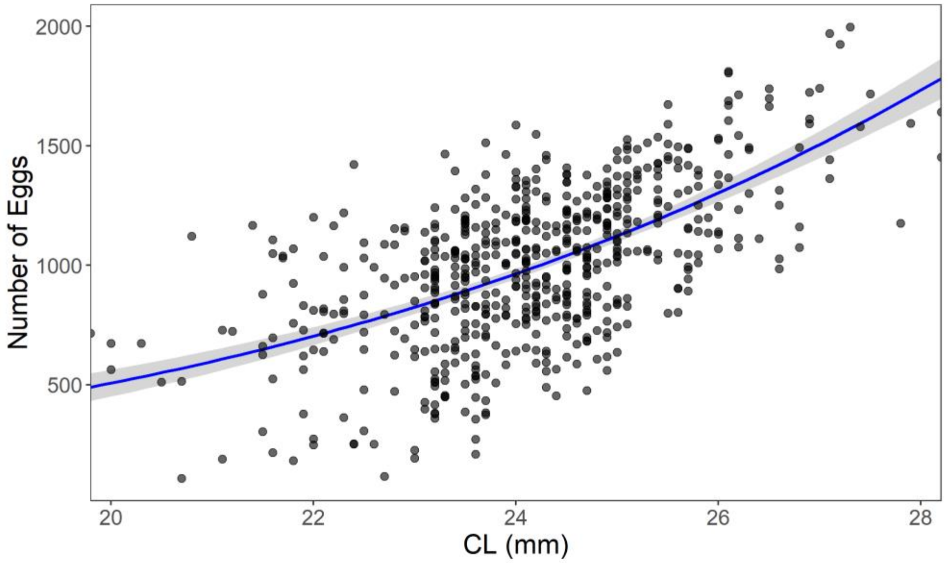

Figure 3.4. Relationship between carapace length (CL) and number of eggs of northern shrimp in Newfoundland and Labrador.

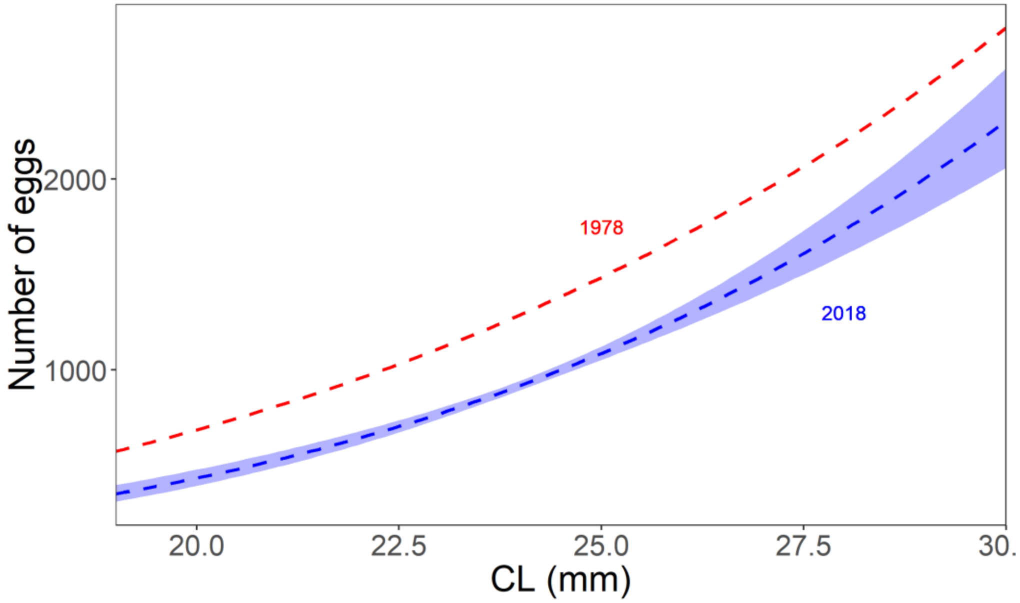

Figure 3.5. Comparison of fecundity at size if northern shrimp in Newfoundland and Labrador in 1978 and 2018.

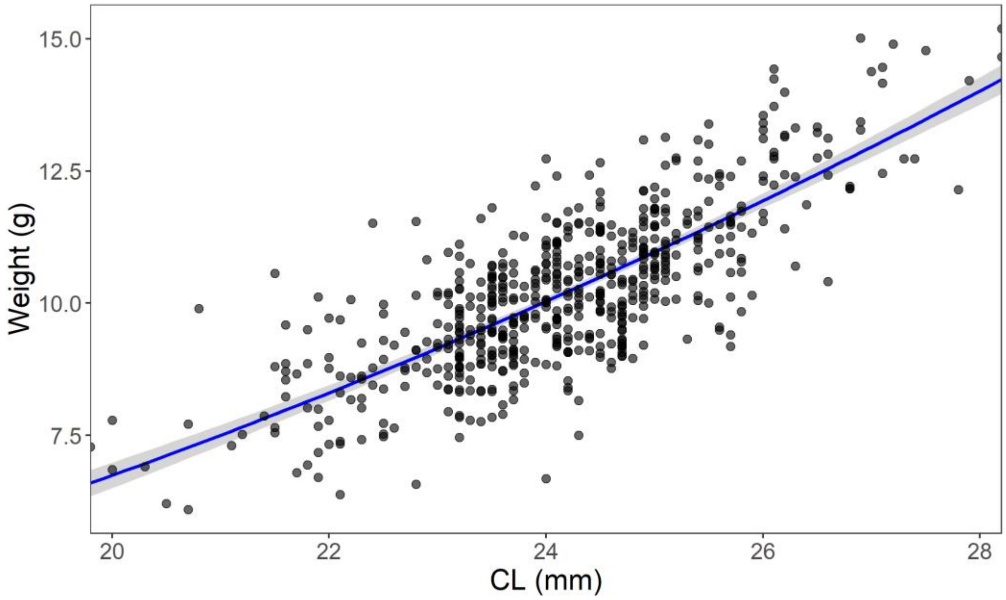

Figure 3.6. Relationship between carapace length (CL) and weight (W) of northern shrimp in Newfoundland and Labrador.

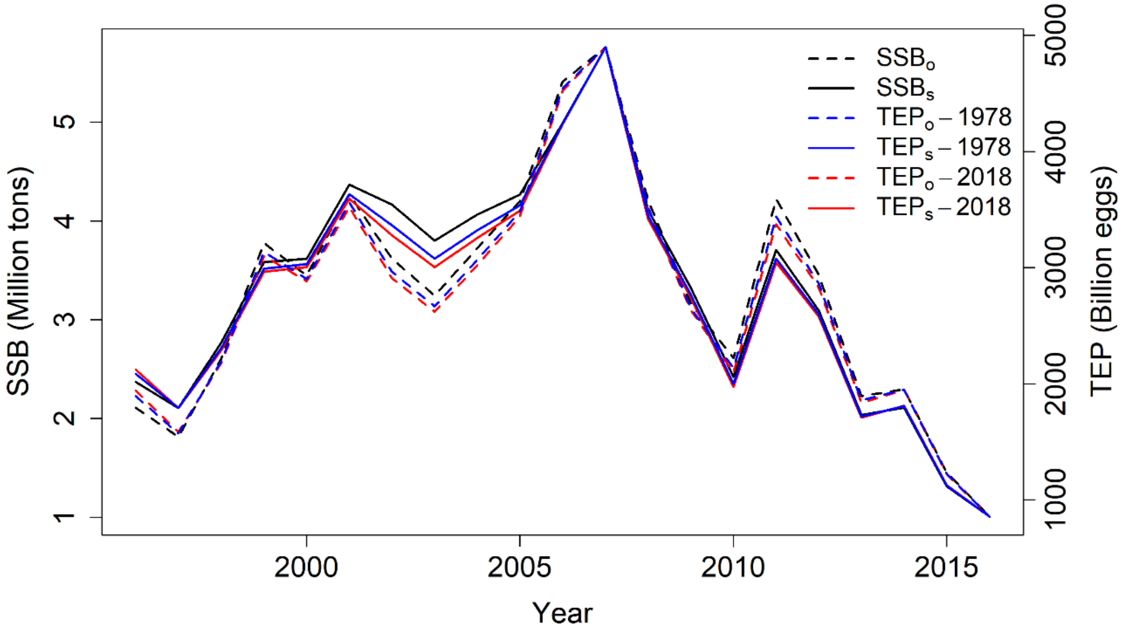

Figure 3.7. Comparison of the estimated spawning stock biomass (SSB) and total egg production (TEP) of northern shrimp in Newfoundland and Labrador based on observer (o) or survey (s) data and using fecundity estimations for years 1978 and 2018.

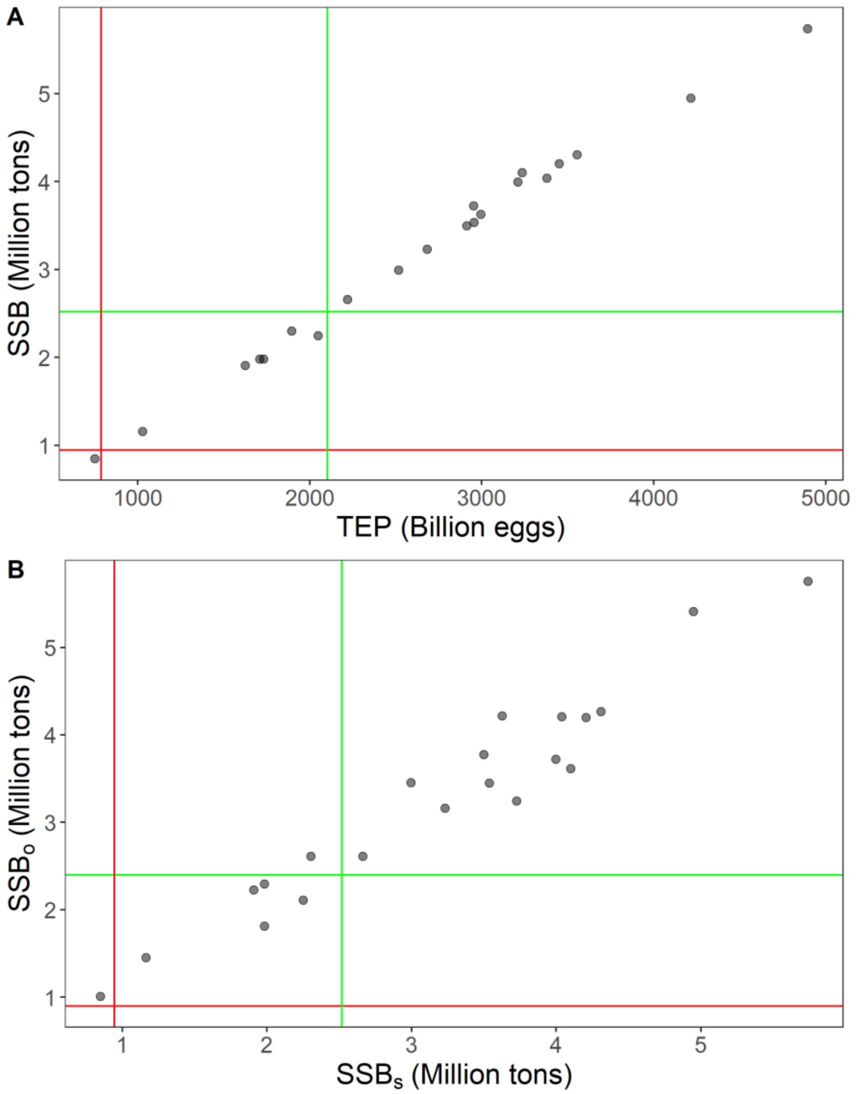

Figure 3.8. Comparison of A) spawning stock biomass (SSB) estimated using survey data and total egg production (TEP) estimated using fecundity of 2018, and B) spawning stock biomass estimated using observer or survey data (o and s subscripts respectively). Red lines are the lower reference point (LRP), and green lines are the upper stock reference (USR).

Table 3.1. Results of the models

Relationship	Equation	a (min, max)	b (min, max)	R^2	N
Dry Weight (DW) – Number of Eggs (E)	$E = a + bDW$	-9.53 (-74.15, 55.10)	2347.45 (2176.67, 2518.23)	0.89	91
Carapace Length (LC) – Number of Eggs (E)	$\log_{10} E = a + b \cdot \log_{10} CL$	-2.73 (-3.42, 2.03)	4.12 (3.62, 4.63)	0.30	604
Carapace Length (LC) – Weight (W)	$\log_{10} W = a + b \cdot \log_{10} CL$	-1.95 (-2.15, -1.746)	2.13 (1.99, 2.23)	0.58	601

Chapter 4. Conclusions

In this thesis I investigated how variations in northern shrimp life-history traits were related to variations in stock biomass and if these life-history traits can be used as indicators for collapsing stocks. I found that size at sex transition declined a few millimeters in areas with high fishing activities while the same trait varied without trend in areas with less fishing pressure. Fishing effort and temperature are the factors negatively affecting the size at sex transition. I suggest that the observed trends are mainly explained by the compensatory response hypothesis.

I estimated the fecundity at size of the northern shrimp in Newfoundland and Labrador. It had been 40 years since the last estimation. I found that the number of eggs per size has decreased by about 30%. This information is starting to fill a gap and helps to understand the reproductive potential of the stock. Importantly, the method used in this chapter, including Equation 3.3, is a good approach to help facilitate future estimation of fecundity because it simplifies the process, reduces laboratory time, and gives reasonable results.

I combined the information on L50 and on fecundity with the size structure and estimated the spawning stock biomass and the total egg productions. Although several studies have argued that SSB is not a good proxy for the reproductive potential (Barneche et al. 2018, Marshall et al. 2006, Marshall 2016), I tested its reliability compared with the TEP. Both indices produced very similar results and did not significantly affect the categorization of the stock under the precautionary approach. Perhaps the relatively low fecundity of shrimp compared with some other fish species makes the SSB a good and parsimonious index to represent the reproductive potential of this stock. However, because of spatial and temporal variability in fecundity this may not be the case for stocks in other areas or in the same area in the future. In general, the variability of life history traits for northern shrimp in Newfoundland and Labrador is related to the decline, but it seems to be more a consequence than the cause of recent biomass decline.

My results show that the life history traits of northern shrimp are variable and can be affected by fishing pressure. The decline in size at sexual transition in some areas and the reduction in fecundity at size are worrisome indicators, because they can affect the productivity of the population in the future and its capacity to recover from the low biomass period that it is experiencing. I suggested that some of these changes are the result of a compensatory response to fishing, although more research into that hypothesis is needed. Nonetheless, this suggests that the harvest rate should be reduced not only to recover the biomass but also to avoid more permanent changes in the life history.

Currently, there is not an accepted population dynamics assessment model for northern shrimp in Newfoundland and Labrador. Future attempts to assess this fishery should consider that aggregated biomass dynamics models or stage based models could be missing important information like the changes in size at sexual transition and fecundity, that affect the population but are not considered explicitly in those kinds of models. A size-based assessment approach should be considered for this fishery, although there are many challenges in doing this because of the lack of information and complexity of the species biology and available data.

Based on the results of my work, I can recommend some future research. First, the changes in the size at sexual transition should continue to be monitored to detect further declines. I suggest the compensatory response as an explanation of the fishing effects on the sex transition, but to prove or discard this, a more specific study of the reaction norms is required. It is also important to continue the monitoring of the fecundity at size to determine whether the decrease I found is real or if it is normal variation. I tested the effect of the size at sexual transition and fecundity on the estimation of indices of reproductive potential, but it would be important to re-evaluate my results using time varying fecundity, once more data are available. Also, it would be very informative to test the effects of variation in life history traits on more complex processes of the population dynamics in order to better understand the mechanisms and to help with the development of a new assessment model that include all these sources of variability.

4.1. References

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