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SPAM (Sex-structured Pandalus Assessment Model): a stock assessment model for *Pandalus* stocks

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Abstract

Despite the economic importance of *Pandalus* shrimp fisheries, few analytical tools have been developed to assess their stocks and traditional stock assessment models are not appropriate because of biological specificities of *Pandalus* species. In this context, we propose SPAM, a model dedicated to protandric hermaphrodite Pandalids stock assessment. Pandalids are difficult to assess because the cues affecting sex-change, size at recruitment and mortality variability are not well understood or characterized. The novel structure of the model makes it possible to adequately describe variability in natural mortality by stage and in time, as well as variability in size at sex-change and recruitment. The model provides traditional stock assessment outputs such as fishing mortality estimates, numbers of individuals, and provides in addition yearly natural mortality estimates. The model is applied to the exploited shrimp stock of *Pandalus borealis* in Sept-Îles as an illustrative example of the utility of the approach.

Introduction

Shrimp fisheries are becoming more and more important throughout the world. According to FAO, 3,120,566 t of shrimp were caught in marine waters in 2008, representing about 60% of the total crustacean production and 3.9% of the world capture fisheries production (FAO 2009). A Pandalidae, *Pandalus borealis*, is the second most important exploited shrimp species globally, counting for 12.3% of the global shrimp catches (FAO 2010).

Shrimp of the genus *Pandalus* are exploited in the North Atlantic and the North Pacific oceans mainly by trawl fisheries on large individuals given that shrimp price is often directly linked to its size. This characteristic of the fisheries becomes important because most species of the genus *Pandalus* (including *P. borealis*) are protandric hermaphrodites, i.e. they reproduce first as males and then change sex and become females (Bergström 2000; Berkely 1930) (Fig. 1). Sex-change is thus critical for fishery management (Fu et al. 2001) since females are primarily targeted by the fishery because of their size. Despite a large literature investigating the factors which potentially influence the activation of the sex-change process, there is currently no clear consensus. Density-dependence effects (Koeller et al. 2000a), size or age (Koeller et al. 2003; Wieland 2004), environmental factors (Wieland 2004) and evolutionary processes (Charnov and Skuladottir 2000) have been studied but none of them alone is a powerful predictor of the yearly variability observed in sex-change. However, sex-change always occurs within a certain length interval, albeit a relatively large one, and consequently, length appears to be a required basis when modelling sex-change.

Individuals of *P. borealis* remain as males for some years. Sex-change occurs in winter and newly transformed females can be identified as primiparous females in the following spring and summer. Primiparous females spawn the following fall. Larvae hatch in spring and reproductive females that survive breeding are then identified as multiparous females. Multiparous and primiparous females can be distinguished by the presence of sternal spines that start disappearing during summer and are definitively lost little time before their first mating (mating occurs few hours/days before spawning - McCrary 1971).

Direct determination of age is not possible for *P. borealis* and age can be approximated by the identification of the first modes in length frequency distributions and by the examination of sex related characteristics (Bergström 2000). Growth of males can be adequately modelled with a von Bertalanffy curve (Bergström 2000); however size at recruitment is variable through time (Hvingel and Savard 1997) probably as a consequence of varying environmental conditions during the larval and juvenile phases (Daoud et al. 2010). Male growth rate decreases for oldest males and consequently the largest male length modes can contain individuals of different ages. Absence of direct hard pieces such as otolith combined with the difficulty to distinguish cohorts for largest males hinders the development of reliable aging techniques. Tagging techniques is often used but this technique is more difficult to apply to shrimps because of frequent moulting, small size of the individuals, and is generally expensive. Primiparous females are considerably larger than males of the same age because moult frequency increases during the sex change period. Growth of females is then slow and modes of primiparous and multiparous in length-frequency samples are often difficult to distinguish.

Despite the economic importance of crustacean fisheries, few analytical methods have been developed for crustacean stock assessments (Smith and Addison 2003) and more specifically for shrimp stocks. Age structured models have been applied for some crustacean stocks (ICES 2003), including shrimp (ICES 2001), but in most cases they were found inappropriate because of the uncertainties in aging techniques and the difficulties to track the cohorts after sex-change.

Catch-Survey-Analysis (Cadrin 2000; Cadrin et al. 1999) and surplus production models have also been applied (Cadrin et al. 2004; NAFO/ICES 2008) to carry out shrimp assessments. They have the advantage of being simple and rather robust, requiring few data. However, a major limitation is that they do not provide any information on the demographical, and especially sex stock structure which can be considerably altered by commercial harvesting and is essential for fishery management. Consequently, shrimp stock assessments often consist of a descriptive analysis of various indicators and trends (for example commercial catch rates and/or survey abundance indices) through time, sometimes formalized in a traffic light approach (Koeller et al. 2000b).

Length (Drouineau et al. 2008; Drouineau et al. 2010) and age-length structured (Fournier et al. 1998; Quinn et al. 1998; Froysa et al. 2002) models have recently raised more and more interest, especially for species such as shrimp, for which growth is poorly known and aging is difficult. Such models would have several advantages for *Pandalus* stocks. Indeed, this kind of models can be fitted directly to length-structured data, obviating the need of an uncertain and often expensive length to age data conversion. Moreover, a sex and age-length structured model would enable one to model sex-change in a length interval and to provide valuable information on the demographic structure of the stock. A simulation length-based model with explicit sex-change was first proposed by Fu et al. (2001) to quantify the importance of some biological processes, especially growth, sex-change and natural mortality, but the model was dedicated to understanding the sex-change process rather than as an assessment method.

This paper presents SPAM, a model dedicated to protandric hermaphrodite Pandalids stock assessment, that incorporates (i) a length based submodel for male, (ii) a constant growth model but time varying size at recruitment, (iii) a time varying length at sex-change relationship function and (iv) a stage structure (primiparous/multiparous) submodel for females. Contrary to Fu et al. (2001), a simple two stage structure is used for females whereas the male component relies on a length and age structure. The model is then applied to the exploited *Pandalus borealis* stock of the Gulf of Saint-Lawrence as an illustration showing the relevance of SPAM to assess a commercially harvested shrimp population.

Material and methods

Population model

The model has a seasonal time step (Fig. 1) which is required to properly describe male growth, seasonal biological processes (sex-change, reproduction) and fishing patterns (variability in catchability linked to seasonal migrations). The first season, namely spring, extends from April to May (hatching season). Summer extends from June to August. Fall starts in September and ends in November (spawning). Finally, winter extends from December to April (sex-change and egg incubation period).

The population is primarily divided into male and female components. Male component is age (from age 1 to age A) and length (from length class 1 to L) structured. We assume that males are recruited to the population at age 1 at the beginning of spring; they progress from age a to age a+1 also at the beginning of spring (Fig. 1). Quantities related to the male component are subscripted with a *m*, quantities related to the primiparous component are subscripted with *primi*, quantities related to the multiparous component are subscripted with a *multi* and quantities related to the female component (both primiparous and multiparous females) are subscripted with a *fe*.

The number of males for a given time step *t*, a given age *a* and a given length class *l* is $N_m(t,a,l)$. The total number of males per time step and length class is denoted by $N_m(t,\cdot,l)=\sum_a N_m(t,a,l)$, while the total number of males per time step and age is $N_m(t,a,\cdot)=\sum_l N_m(t,a,l)$. Male can change sex at different length and age following a sex-change at length transition ogive.

Females are subdivided into primiparous and multiparous maturity stages (Fig. 1). Although length-frequency data are also available for females, we consider a two stage structure instead of an age structure because female growth is slow and modes are often confounded. All females go through the primiparous stage before reaching the multiparous stage.

$N_{primi}(t)$ and $N_{multi}(t)$ stands respectively for the number of primiparous and multiparous females at time step *t*.

Assumptions regarding length-at-age

Male growth is assumed to follow a von-Bertalanffy growth curve. Consequently, the mean size of the year class *y* at time step *t* is:

(1) $\mu_y(t+1)=\mu_y(t)+\left(L_\infty-\mu_{y,r}\right)\cdot\left(1-\exp^{-K\cdot(\Delta t)}\right)$

with $\mu_{y,r}$ the size at recruitment (size at age 1 at the beginning of spring) of the year class and Δt the duration of time step *t*.

L_∞ is assumed to be known and constant and could be approximated by the maximum length observed for males since growth at age 3 is slow and nearly null at age 4. Following Fournier et al. (1998) and Maunder and Watters (2003), length distribution of an age group at time step *t*, is assumed to follow a normal distribution with a mean $\mu_y(t)$ and a constant coefficient of variation *cv*.

Assumptions regarding sex-change

Quantities related to the sex-change are subscripted with *sex*. Sex-change is assumed to be length dependent. We assume that the sex-change process is completed at the end of winter before the beginning of the new biological year. The proportion of males that change sex in a given year y is modelled by a sigmoid function of length, characterised by two parameters $L_{50sex}(y)$ and R_{sex} (interquartile range). $L_{50sex}(y)$ is assumed to follow a lognormal random walk to account for inter-annual variability in sex-change:

$$(2)\quad L_{50sex}(y) = L_{50sex}(y-1)\cdot e^{\varepsilon_{sex}(y)} \qquad \text{with } \varepsilon_{sex}(y) \sim N\left(0, \sigma^2_{sex}\right)$$

The proportion $p(y,l)$ of males of size l that change sex is given by:

$$(3)\quad p(y,l) = \frac{1}{1+\exp\left(-2\dfrac{\log(3)}{R_{sex}}\cdot\left(l - L_{50sex}(y)\right)\right)}$$

However, all males of last age A are forced to change sex.

It is necessary to make an assumption about sex-change during final year Y to provide abundance estimates in year Y+1. Since sex-change is assumed to follow a random walk, it is logical to assume that the sex-change ogive in year Y is similar to year Y-1.

Survival equations

Survival *Sr* is the result of the natural and fishing mortality. Mean natural mortality *M* is assumed to be constant over age groups and stages, and is equal at 0.5 year^{-1}. Yearly deviations are allowed to account for inter-annual variability:

$$(4)\ M(y) = M \cdot e^{\varepsilon_M(y)} \quad \text{with } \varepsilon_M(y) \sim N\left(0, {\sigma_M}^2\right)$$

M(y) denoting the natural mortality in year *y*.

$F_m(t,l)$, $F_{primi}(t)$ and $F_{multi}(t)$ stand for fishing mortality applied respectively on males of length *l*, primiparous and multiparous females at time *t*. Their calculation is explained in the next section. Survival is computed with the following equations:

$$(5)\ \begin{cases} Sr_m(t,l) = e^{-\left(M(y)+F_m(t,l)\right)\Delta t} \\ Sr_{primi}(t) = e^{-\left(M(y)+F_{primi}(t)\right)\Delta t} \qquad t \in y \\ Sr_{multi}(t) = e^{-\left(M(y)+F_{multi}(t)\right)\Delta t} \end{cases}$$

Fishing activity and survey models

Fishing mortality and catches

Quantities related to the commercial fishery are subscripted with a *f*. Male fishing mortality is assumed to be the product of a selectivity $s_f(l)$, a fishing effort *E(t)* and a year effect *q(y)* which corresponds to a catchability. Selectivity $s_f(l)$ is modelled as a traditional sigmoid function, characterised by two parameters $L_{50\,f}$ and R_f (interquartile range):

$$(6)\ s_f(l) = \frac{1}{1+\exp\left(-2\dfrac{\log(3)}{R_f}\cdot\left(l - L_{50\,f}\right)\right)}$$

Male fishing mortality is equal to:

$$(7)\ F_m(t,a,l) = q(y)\cdot s_f(l)\cdot E(t)$$

Concerning females, it is assumed that selectivity is equal to 1 given that the newly transformed females reach the sizes that are usually fully recruited to the fishing gear (Shumway et al. 1985). Therefore, primiparous females fishing mortality is equal to:

$$(8)\ F_{primi}(t)=q(y)\cdot E(t)$$

Females that bear eggs might have, in certain areas, a more specific behaviour than males or primiparous females. In winter and spring, egg bearing females (named multiparous in the model) aggregate inshore, and consequently have a higher catchability (Shumway et al. 1985). A targeting factor $T_{spring,multi}$ is thus introduced into the calculation of multiparous females fishing mortality in spring to describe this interaction:

$$(9)\ F_{multi}(t)=\left\{\begin{array}{ll} q(y)\cdot T_{spring,multi}\cdot E(t) & \text{in spring} \\ q(y)\cdot E(t) & \text{the rest of the year} \end{array}\right\}$$

Year effect is assumed to follow a random walk to avoid unrealistic inter-annual variations:

$$(10)\ q_f(y)=q_f(y-1)\cdot e^{\varepsilon_f(y)} \qquad \text{with } \varepsilon_f(y)\sim N\left(0,\sigma_f^2\right)$$

Given the population numbers and the fishing mortality, expected catches are calculated using traditional Baranov equations:

$$(11)\left\{\begin{array}{c} C_m(t,l)=N_m(t,,l)\cdot\dfrac{F_m(t,l)}{M+F_m(t,l)}\cdot\left(1-\exp\left(-\left(M+F_m(t,l)\right)\cdot\Delta t\right)\right) \\ C_m(t)=\sum_l C_m(t,l) \\ C_{primi}(t)=N_{primi}(t)\cdot\dfrac{F_{primi}(t)}{M+F_{primi}(t)}\cdot\left(1-\exp\left(-\left(M+F_{primi}(t)\right)\cdot\Delta t\right)\right) \\ C_{multi}(t)=N_{multi}(t)\cdot\dfrac{F_{multi}(t)}{M+F_{multi}(t)}\cdot\left(1-\exp\left(-\left(M+F_{multi}(t)\right)\cdot\Delta t\right)\right) \end{array}\right.$$

Harvest rates H are computed as a ratio of catches in year y over the abundance of the stock at the beginning of that year, i.e. at the beginning of spring, the first seasonal step of a year:

$$(12)\quad \begin{cases} H_m(y)=\dfrac{\sum\limits_{t\in y}\sum\limits_{a}\sum\limits_{l}C_m(t,a,l)}{\sum\limits_{a}\sum\limits_{l}N_m\left(t_{1,}al,l\right)} \\ H_{primi}(y)=\dfrac{\sum\limits_{t\in y}C_{primi}(t)}{N_{primi}(t_1)} \\ H_{multi}(y)=\dfrac{\sum\limits_{t\in y}C_{multi}(t)}{N_{multi}(t_1)} \end{cases}$$

Assumptions regarding survey abundance indices

Quantities related to the survey are subscripted with an *s*. Survey abundance indices are assumed to be a relative measure of the stock abundance. Abundance indices are the product of a selectivity $s_s(l)$, a catchability q_s and numbers of shrimp. We use a sigmoid function, characterised by two parameters L_{50s} and R_s (interquartile range), to model selectivity for males. Therefore, $s_s(l)$ is given by

$$(13)\quad s_s(l)=\frac{1}{1+\exp\left(-2\dfrac{\log(3)}{R_s}\cdot\left(l-L_{50s}\right)\right)}$$

Selectivity is assumed to be equal to 1 for the females which are large enough to be totally recruited to the survey trawl. Abundance indices of primiparous and multiparous females estimated by the model are summed into a single female abundance index IA_f to be consistent with surveys that are often conducted in fall when the distinction between the two stages of females is difficult or impossible. Given these assumptions, expected abundance indices are given by:

$$(14)\quad \begin{cases} IA_m(t,l)=s_s(l)\cdot q_s\cdot N_m(t,\cdot,l) \\ IA_{fe}=q_s\cdot\left(N_{primi}(t)+N_{multi}(t)\right) \end{cases}$$

Observation model and likelihood function

The model is fitted by maximising a likelihood function which is derived from an observation model that describes the uncertainties around observed data.

Contribution of length-frequency data

Length-frequency samples are available from both commercial and survey catches. A sample consists of the frequencies of males in each length class. Following Fournier et al. (1990, 1998) and Drouineau et al. (2010), a robust likelihood is used to account for the samples. Basically, it is based on the property that a proportion in a sample follows a normal distribution, and the likelihood is modified to limit the influence of high and low frequencies. The length-likelihood of a sample *samp* is:

$$logL\left(samp(t)\,|\,\theta\right)=\sum_{l}-\frac{1}{2}\cdot\log\left(v_{samp}(t,l)\right)+\log\left(e^{-\frac{1}{2}\cdot\frac{\left(f(t,l)-f_{obs}(l)\right)^{2}}{v_{samp}(t,l)}}+10^{-6}\right) \tag{15}$$

$$\text{with } v_{samp}(t,l)=\left(\left(1-f(t,l)\right)\cdot f(t,l)+\frac{0.1}{L+2}\right)\cdot\frac{1}{n_{samp}(t)}$$

where $n_{samp}(t)$ is the number of sampled shrimps and $f(t,l)=C_m(t,l)/\sum_{i=1}^{L}C_m(t,l)$ and $f(t,l)=IA_m(t,l)/\sum_{i=1}^{L}IA_m(t,l)$ are the expected frequency of length class *l* estimated by the model for a sample from the commercial fishery and from the scientific survey respectively, and $f_{obs}(l)$ the observed frequency in the sample.

Contribution of total catches and total abundance indices

Total commercial catches per time step ($C_m(t), C_{primi}(t), C_{multi}(t)$) and total survey abundance indices per time step ($IA_m(t,l), IA_{fe}(t)$) are assumed to follow a gamma distribution. The gamma distribution is a distribution function that is increasingly used in population dynamic models because of its great flexibility (Froysa et al. 2002; Haddon 2001).

The loglikelihood is given by:

(16)

$$LogLC(t\,|\,\theta) = v_{com}\left[\log\left(\frac{C_{m,obs}(t)}{C_m(t)}\right) - \frac{C_{m,obs}(t)}{C_m(t)} + \log\left(\frac{C_{primi,obs}(t)}{C_{primi}(t)}\right) - \frac{C_{primi,obs}(t)}{C_{primi}(t)} + \log\left(\frac{C_{multi,obs}(t)}{C_{multi}(t)}\right) - \frac{C_{multi,obs}(t)}{C_{multi}(t)}\right]$$

and

(17) $$LogLIA(t\,|\,\theta) = v_{surv}\left[\log\left(\frac{IA_{m,obs}(t)}{IA_m(t)}\right) - \frac{IA_{m,obs}(t)}{IA_m(t)} + \log\left(\frac{IA_{fe,obs}(t)}{IA_{fe}(t)}\right) - \frac{IA_{fe,obs}(t)}{IA_{fe}(t)}\right]$$

v_{com} and v_{surv} equal to the inverse of the square root of the coefficient of variation of the distributions (McCullagh and Nelder 1989).

Parameter estimation

A large number of parameters have to be estimated (Tab. 1). The search domain dimensions quickly increase with the number of years and age groups. Therefore, following Punt (2003), estimation of unknown parameters θ is split into two steps, growth parameters $\theta_1 = \{K, cv, \mu_{1,r}, \ldots, \mu_{Y,r}, \mu_2(t_0) \ldots, \mu_A(t_0)\}$ being estimated before the remaining parameters θ_2 (where Y denotes the number of years in the data set, ranging from y_0 to y_{Y-1}).

Estimating growth parameters

The following procedure is used to estimate the loglikelihood $LogL_2(\theta_1)$:

1. given θ_1, mean size at age $\mu_a(t)$ is computed for each age group and each time step (equation 1).
2. given θ_1 and given the assumptions regarding the length distribution of an age group, theoretical frequency per length class and per age group is computed.
3. The loglikelihood of a length-frequency sample from commercial or survey catches is computed by a modal analysis with the mean size and standard deviation of the modes kept fixed:

$$(18)\ logL_2P_{samp}(t\,|\,\theta_1)=\sum_{l=1}^{L}\left[f(t,l)\cdot\log\left[\sum_{a=1}^{A}\lambda_{samp}(t,a)\frac{1}{2\cdot cv\cdot\mu_a(t)}\exp\left(-\frac{1}{2}\left(\frac{length(l)-\mu_a(t)}{cv\cdot\mu_a(t)}\right)^2\right)\right]\right]$$

with $\lambda_{samp}(t,a)$ estimated for each sample by an Expectation Maximisation algorithm.

4. Repeat steps 1-3 to θ_1 that maximises

$$(19)\ logL_2(\theta_1)=\sum_t\left(logL_2P_{samp}(t\,|\,\theta_1)\right)$$

Estimating other parameters

Given θ_1, other parameters are estimated by maximising the loglikelihood which is a function of 5 components: (i) the length composition of commercial and survey catches (equation 15), (ii) the total commercial catches (equation 16), (iii) the total abundance from survey (equation 17), (iv) assumption regarding the random walk of $L50_{sex}$ and (v) assumption regarding the random walk of the year effect q_f:

(20)

$$logL(\theta_2 \mid \theta_1) = \sum_t LogL(samp_{com}(t) \mid \theta) + \sum_t LogL(samp_{surv}(t) \mid \theta) + \sum_t LogLC(t \mid \theta) + \sum_t LogLIA(t \mid \theta) + LogL_{sex}(\theta) + LogL_M(\theta) + LogL_f(\theta)$$

with:

$$(21)\ \ LogL_{sex}(\theta) = -\frac{1}{2 \cdot \sigma_{sex}^2} \sum_y \varepsilon_{sex}^2$$

$$(22)\ \ LogL_M(\theta) = -\frac{1}{2 \cdot \sigma_M^2} \sum_y \varepsilon_M^2$$

and:

$$(23)\ \ LogL_f(\theta) = -\frac{1}{2 \cdot \sigma_f^2} \sum_y \varepsilon_f^2$$

Following Drouineau et al. (2010), the loglikelihood is maximised using an evolutionary algorithm (Schwefel 1995) that provides a starting point to a quasi-Newton algorithm provided in the autodif library (http://www.otter-rsch.com/). The evolutionary algorithm is a stochastic algorithm which is relevant to explore highly dimensional objective functions and which does not require a starting point to be specified unlike traditional quasi-Newton algorithms. The Hessian matrix is estimated by a finite difference approximation and inverted to get the variance covariance and correlation matrices.

Case study: Gulf of St. Lawrence *Pandalus borealis* stock

Description of the fishery

The northern shrimp (*Pandalus borealis*) fishery began in the Gulf of St. Lawrence (Fig. 2) in the 1960s. The exploitation is conducted by trawlers in four shrimp fishing areas (SFA) (DFO 2009). In 2008, the Gulf landings reached about 36,000 tons. The Sept-Îles area (SFA 10) is the most productive of the four stocks representing about 41% of the total Gulf catch. The fishery is managed by TAC and the number of fishing licenses is regulated. Fishing season starts on April 1st and closes when the TAC is reached or on the 31st of December at the latest. There is no fishing in winter mainly because the ice cover prevents access to fishing grounds.

The fishery mainly targets large individuals which are more economically valuable; therefore fishermen allocate a large part of their effort in spring on reproductive females on hatching grounds. On average, females represented 68% of the Sept-Îles fishing area landings between 1990 and 2008.

Fishers are required to fill out a logbook, indicating the number of hours fished and a dockside monitoring program ensures control over landings. Both log-book and dockside programs have provided very reliable estimates of fishing effort and catches since 1990. The commercial catches are sampled regularly during the fishing season and a bottom trawl survey is conducted each year at the end of summer. The catch sampling program has been running since 1982 and the research survey has been conducted since 1990. The total number of shrimp measured each year varies from 8,000 to 18,000 for the commercial sampling as well as for the survey.

Input data

Catch at length is available for males by time step (except in winter) and abundance at length is available for males for the second time step (in summer), both from 1990 to 2008. Cephalothorax lengths are aggregated into 0.5 mm classes (they are measured at the nearest 0.1 mm) and range from 8.0 to 27.0 mm. In the Sept-Îles area, shrimp larvae hatch in early May (Ouellet et al. 2007). In fall the year after, they are 1½ year old and measure between 8.0 and

12.0 mm. They are between 12.0 and 16.0 mm at 2½ y.o., 16.0 and 19.0 mm at 3½ y.o. and 19.0 and 23.0 at 4½ y.o. The maximum size is 28.0 mm but few males are found at sizes larger than 24 mm. Sex-change occurs after mating (which occurs few hours/day before female spawning), in winter, before they reach the age of 5. Controlled growth experiment studies confirmed this growth pattern (Daoud et al. 2010). Indeed, the authors found that, at 5 °C which is about the bottom temperature of the area, 20.0 mm males are 4 years old.

Female catch and abundance data are available from 1990 to 2008. Females are split into two stages (primiparous and multiparous females) for the commercial catch for spring and summer. The separation is not done for the fall season and for the survey. In the Sept-Îles area, spawning occurs in early October. Primiparous females spawn 6 months or so after having changed sex. Egg bearing females migrate and aggregate inshore in winter and spring. This behaviour has an impact on their availability to the fishing fleet. Therefore, a targeting factor was introduced to the model to account for this migratory behaviour.

Specific parameters values

Some specific parameters values were fixed for the Sept-Îles case study according to expert knowledge (Tab. 2). We set $v_{com}=v_{surv}=100$ which corresponds to a CV of 10%. We set $\sigma_f = 0.05$ which corresponds to a random walk of coefficient of variation to 5%, given that fishing activity is well known and that catchability is not expected to have changed a lot over the period. Although there is little information on natural mortality inter-annual variability, we choose to fix $\sigma_M = 0.05$, to have equivalent weights between natural and fishing mortality deviations. In the absence of information over sex-change, we choose to let more flexibility to the sex-change random walk and fix $\sigma_{sex} = 0.10$.

The model includes 4 male age groups and is fitted over a 19 years data series. Consequently 111 parameters should be estimated (24 in phase 1 and 87 in phase 2 - Table 1).

Results

Fitting observed data

The model properly fits length-compositions of the male component with modes that can be easily detected (Fig. 3a, Fig. 3b and Fig. 4), demonstrating the adequacy of the growth model and of the use of a time step.

The seasonal pattern of landings was captured as well in the fitting (Fig. 5). Each year, a peak of catches is observed in spring that corresponds to the fishery targeting multiparous females which are aggregated on the hatching grounds. The model poorly fits summer catches for the last two years, probably because the estimates rely on only a few data points. More generally, the fits are a bit poorer for the summer season than for the two other fishing seasons since the late 1990’s, perhaps indicating a change in fishing behaviour over the period. Globally, catches have increased through time over the period (Fig. 5) as a consequence of an increase in TAC (DFO 2009).

The global trend in total survey abundance indices estimated by the model is consistent with the observations, except for 2003 (Fig. 6). However, a strong year effect in the survey was detected for many species for that year (DFO 2009). Globally, the model tends to smooth the survey signal, which is not surprising given the random walk employed in the model.

Population numbers

Recruitment at age one (Figs. 7 and 8) estimated by the model is variable with two periods of higher recruitments in early 90's and then in early 2000's. Those strong year classes are especially prominent at 15 mm (2 years old) in the length compositions of the 1992, 1999 and 2001 commercial catches (Fig. 3) and at 10 mm (1 year old) in the 1991, 1998 and 2000 survey length compositions (Fig. 4). The abundance of females (primiparous and multiparous) also shows the same trend with however a few years lag (Fig. 9a). The abundance of females has been gradually decreasing for the last four to five years probably due to the decreasing abundance of males estimated from 2003 to 2007. Recruitment seems to be slightly decreasing in latter years, therefore, a decrease in total abundance is expected in the future (the number of males increased in recent year, but it is probably because of a delayed sex-change).

No obvious stock-recruitment relationship is observed (Fig. 8). The strong year classes are not explained by a high abundance of females and are more likely due to favourable environmental conditions improving larval survival (Ouellet et al. 2011).

Theoretically, the model provides absolute population number estimates, however a rather high correlation is observed between catchability (of both survey and commercial fishery) and recruitment in first year estimates. Consequently, the population number estimates (and therefore the harvest rates) are more likely to be relative abundance estimates.

Natural and fishing mortality rates

The model provides natural and fishing mortality estimates for males and females at each time step (Fig. 9b - male and multiparous female fishing mortality rates are not represented, since they are equal to the primiparous mortality rate multiplied by a constant through time). A high level of both natural and fishing mortality rates at the beginning of the 1990s explains the low abundance of multiparous in the same period. A sudden decrease in natural mortality first, followed by a more limited decrease in fishing mortality with the combination of high recruitment resulted in a period of relatively high female abundance between 1996 and 2001. Similarly, the second peak of female abundance in the 2000's happened after a period of high recruitment, lower fishing mortality, and decreasing natural mortality which continued to decrease till 2006. The recent decrease in the abundance of females is probably due to both an increase in the natural mortality rate estimated for the last two years, and a substantial increase in fishing mortality since 2003.

Year effects do not exhibit strong variations through the period; however a model with a constant year effect was rejected by the Akaike Information Criterion (Akaike 1973).

Sex-change

The model relies on a time-varying sex-change–at-length relationship. A time constant function was tested but rejected by the Akaike Information Criterion, demonstrating that inter-annual variability in sex-change is significant.

The two extreme ogives of sex-change-at-length show that in some years, a significant proportion of males may anticipate sex-change and become females before reaching age 4 or even age 3 (Fig. 10). In other years, exclusively males of age 4 change sex. This may explain why the mode corresponding to age 4 is often hardly distinguished from the mode corresponding to age 3 in length-composition samples. It might also explain why the prediction of the abundance of primiparous females from the abundance of males is uncertain though it would be very important for management. Globally, length-at-sex-change has shown great variations in primiparous length (Fig. 10) which have likely induced variations in female length (DFO 2009).

Discussion and perspectives

This study presents a sex, age and length structured model dedicated to shrimp stock assessment. To our knowledge, it is the first assessment model designed specifically for Pandalid shrimps, a species that changes sex and for whom ageing after the sex-change is difficult, if not impossible. Our model is a sex-structured model with a length-based submodel for males and a simple stage-structured submodel for females. To characterise a Pandalid shrimp fishery, modelling the sex-change process from males to females is critical and this length-stage-sex-structured model should thus be considered as at least a way to take this biological process into account. The age-length structure of the male component is required to properly model sex-change given that the size at sex-change varies over time as indicated by the variations in the size of newly transformed females. A more simple stage-structured submodel is used for females because (i) females growth is slow and it is difficult to distinguish modes in length-frequency samples while the presence/absence of sternal spines provide a more reliable discrimination method between primiparous and multiparous females and (ii) females being fully recruited to the fishing gear, their size compositions are not essential for a stock assessment model. The age structure of females can be approximated by the two stages, primiparous (newly transformed females) and multiparous females which can be distinguished by morphological differences.

The model demonstrates a high inter-annual variability in length at sex-change. Consequently, the numbers of newly transformed females are difficult to predict from one year to the next. We totally agree with Fu et al. (2001) when stating that a better understanding of sex-change would be a valuable improvement for *Pandalus* stocks management, especially for stocks where females are such a large component of the commercial catches. Females represent the spawning population and constitute the main target of the commercial fisheries and thus they need to be effectively managed to prevent stock depletion. Moreover, the results of the model on the yearly variations in size at sex-change will probably help to investigate the process and find relevant explanatory covariables. More specifically, density-dependant influence on the variations in size at sex-change may be investigated in the future, since we observed that periods of high or increasing levels in males abundance correspond to periods with low size at sex-change.

Estimating natural mortality yearly deviations was possible because of the absence of fishing in winter due to ice cover. Natural mortality is then not confounded with fishing mortality during this season. The correlation matrix analysis shows that though year to year natural mortality deviations were slightly correlated, they were not correlated to catchability deviations (year effects), confirming that it was possible to at least partially estimate those deviations. The assumption of yearly deviations around a mean seemed sufficient to catch the main trends in the population numbers. However, shrimp natural mortality is known to be correlated to the abundance of important predators such as cod and redfish, which have decreased substantially in many of the Northwest Atlantic shrimp fishing areas. Consequently, it may prove necessary in the future to describe the predation process in the model to clearly distinguish F and M throughout the time series. Moreover, we assumed that M was constant over age and length in the absence of more precise information, more precise mortality-at-length estimates would be a valuable improvement to the model.

The model has been used to assess the Sept-Îles shrimp stock as an illustrative example. The model provides results which are consistent with existing knowledge on the species and the stock (DFO 2009).

Weights on sex-change (equation 2 - σ_{sex}), natural mortality (equation 4 - σ_M) and year effect random walks (equation 10 - σ_f) were fixed rather arbitrarily. However our objective in this paper was to present an illustrative example. In a formal stock assessment context, those weights should be discussed with experts and adapted to each stock, and sensitivity analysis should be carried out. We think that the model is generic enough to be applied to different *Pandalus* stocks, if reliable data from both scientific survey and commercial fishery are available. Moreover, the model needs reliable fishing effort data to estimate the seasonal pattern in fishing activity.

The present model was specifically developed to assess *Pandalus* shrimp stocks. Traditional models such as stage-structured models (CSA), surplus production models or age-structured models proved to be poorly adapted to such species because of the absence of aging techniques and the non integration of the sex-change process. In SPAM, the age, length and sex structure provides relevant solutions to both problems. However, a rather large amount of data is required to fit the model, which can be justified by the economic importance of the fishery.

On the whole, results are consistent with the traditional assessment (DFO 2009) confirming a present high abundance level compared to the early 1990’s. However, short or medium term projections are possible with SPAM, and consequently, managers may detect more quickly variations in abundance and adapt management measure (TAC) accordingly. More specifically, the detailed male length-structured abundance estimates and sex change at length ogive are valuable information to managers to anticipate more precisely the number of females in the years to come, which are especially targeted by the commercial fishery.

Finally, the model may be used as an operating model in a management strategy evaluation (MSE) framework (Butterworth and Punt 1999; Punt and Donovan 2007; Sainsbury et al. 2000). MSE aims at assessing the robustness of management options regarding various sources of uncertainty. It relies on an operating model that is able to simulate realistic population dynamics under various scenarios. The model seems to be able to reproduce Pandalid shrimp stock trends and is flexible enough (especially if one adds time varying natural mortality and size at sex-change) to simulate various plausible scenarios of stock evolution.

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558 **Table 1.** Unknown parameters and their significance (Y stands for the number of years in the

559 dataset).

Type of parameters	Parameters	Number of parameters
Growth	K	1
	cv	1
	Mean size at recruitment $\mu_{y,r}$	Y
	Mean size of male age groups (but recruitment) in first time step $\mu_a(t_0)$	A-1
Sex-change	$L_{50sex}(y_0)\ R_{sex}\ \varepsilon_{sex}(y_1)\ \varepsilon_{sex}(y_2)\ldots\varepsilon_{sex}(y_{Y-2})$	Y
Natural mortality	$\varepsilon_M(y)$	Y
Initial numbers	First year $N_m(1,a,.)\ N_{primi}(1)\ N_{multi}(1)$	A+2
	Yearly recruitment $N_m(y,1,.)$	Y-1
Commercial fishery	Selectivity L_{50f}, R_f	2
	Catchability $q(y_0)\ \varepsilon_f(y_1)\ \varepsilon_f(y_2)\ldots\varepsilon_{sf}(y_{Y-1})$	Y
	Multiparous targetting $T_{spring,multi}$ for spring	1
Survey	Selectivity $L_{50s}\ R_s$	2
	Catchability q_s	1

Table 2. Fixed parameters' values for the Sept-Îles case study

Parameters	Value
A	4
L	38
y_0	1990
Y	19
L_∞	28
v_{com}	100
v_{surv}	100
σ_f	0.05
σ_M	0.05
σ_{sex}	0.1

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Fig. 1. Illustration of the life cycle of a protandric hermaphrodite *Pandalus* species and model time-steps (winter, spring, summer autumn) Arrows represent (age or stage or sex) transitions occurring instantaneously between two successive time-steps.

Fig. 2. Sept-Îles stock location in the Gulf of Saint-Lawrence.

Fig. 3a. Observed (normal lines) and estimated (bold lines) length-composition of male commercial catches per season and per year from 1990 to 1999. Scales on Y axis cannot be compared between seasons and years.

Fig. 3b. Observed (normal lines) and estimated (bold lines) length-composition of male commercial catches per season and per year from 2000 to 2008. Scales on Y axis cannot be compared between seasons and years.

Fig. 4. Observed (normal lines) and estimated (bold lines) male length-composition of survey catches. Scales on Y axis cannot be compared between years.

Fig. 5. Observed (bold solid line and squares) and estimated (solid line and circles) total commercial catches per season (spring: black point, summer: grey point, fall: white point) and year.

Fig. 6. Observed (bold line and squares) and estimated (normal line and circles) total survey abundances per year

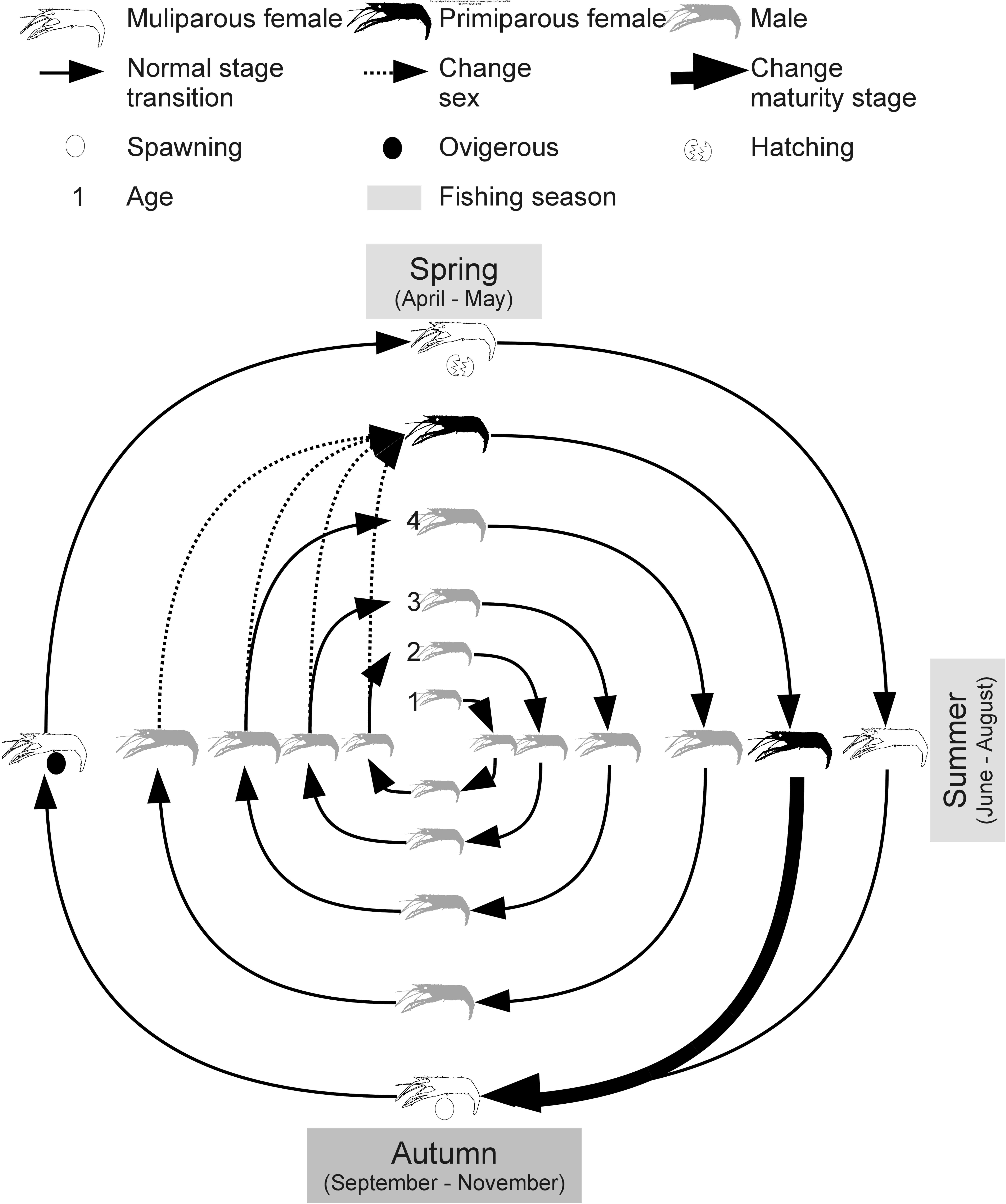
Fig. 7. Estimated recruitment at age 1.

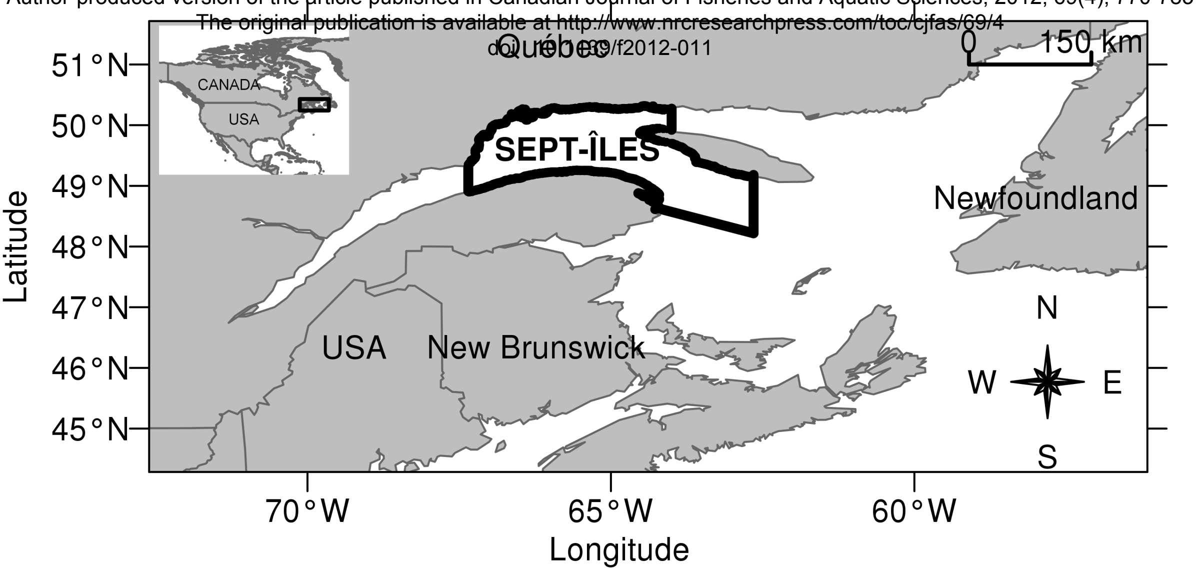
Fig. 8. Estimated stock recruitment relationships: females in autumn against males of age 1 following spring.

Fig. 9. a) Estimated population numbers obtained from the assessment model : numbers for males (ages 2 to 4), primiparous and multiparous females at the beginning of spring, i.e. before

the fishing season and b) estimated natural mortality (dotted line) and spring fishing mortality of primiparous females (multiparous mortality is equal to the primiparous mortality multiplied by the targeting factor – solid line).

Fig. 10. Estimated ogive of sex change at length for two extreme years (end of year 1996 and end of year 2007) (left) and evolution of $L50_{sex}(y)$ over the period (right). Vertical dashed lines represent the mean sizes at the period of sex change (Fig. 1) of each male group $\mu_a = \sum_{y=y_0}^{y_{Y-1}} \mu_a(t_1)/Y$ (with t_1 spring of year y)


Muliparous female
Primiparous female
Male
Normal stage transition
Change sex
Change maturity stage
Spawning
Ovigerous
Hatching
1 Age
Fishing season
Spring
(April - May)
Summer
(June - August)
Autumn
(September - November)
Winter
(December - March)
1
2
3
4


Québec
0
150 km
51°N
50°N
49°N
48°N
47°N
46°N
45°N
Latitude
CANADA
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SEPT-ÎLES
Newfoundland
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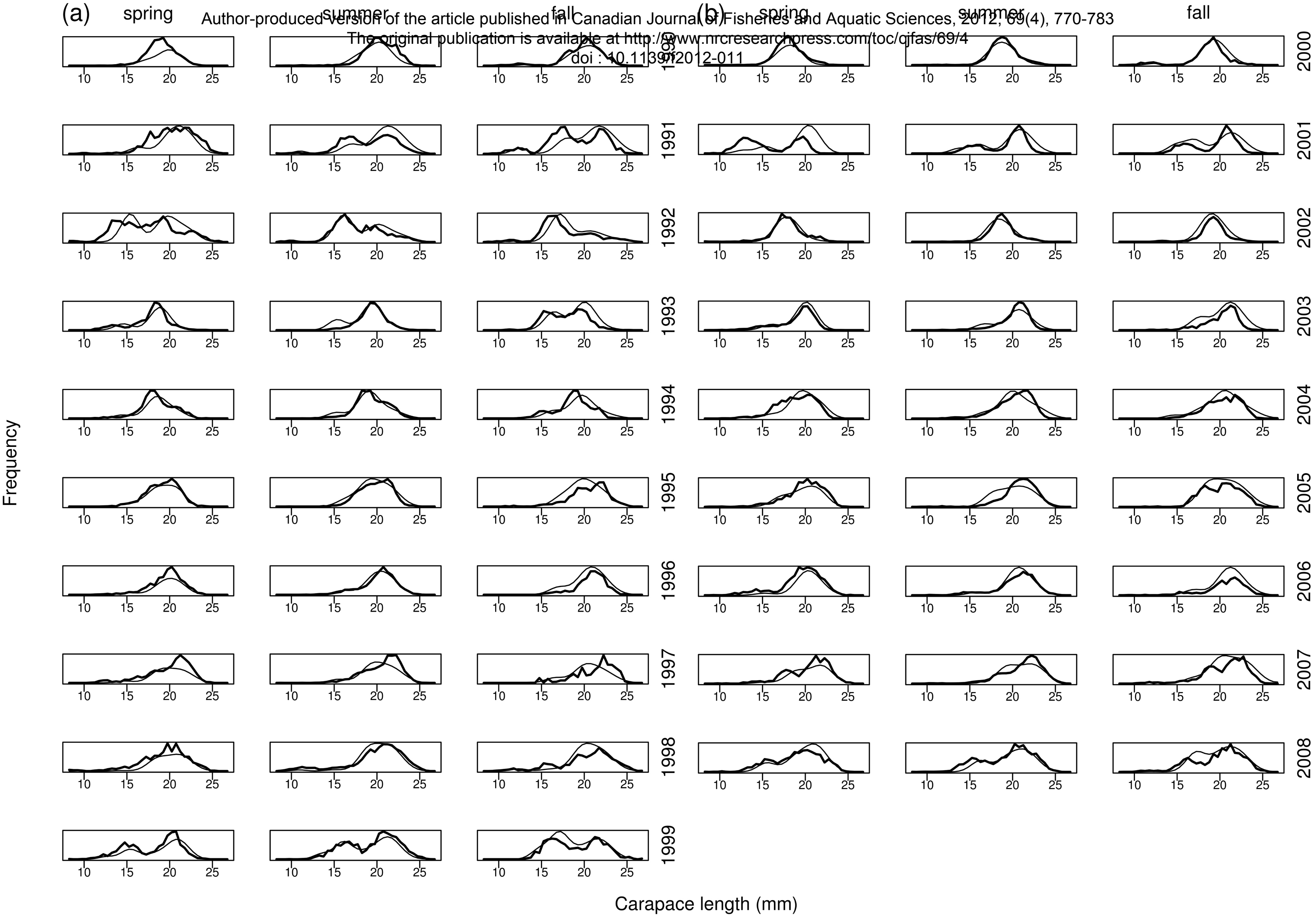
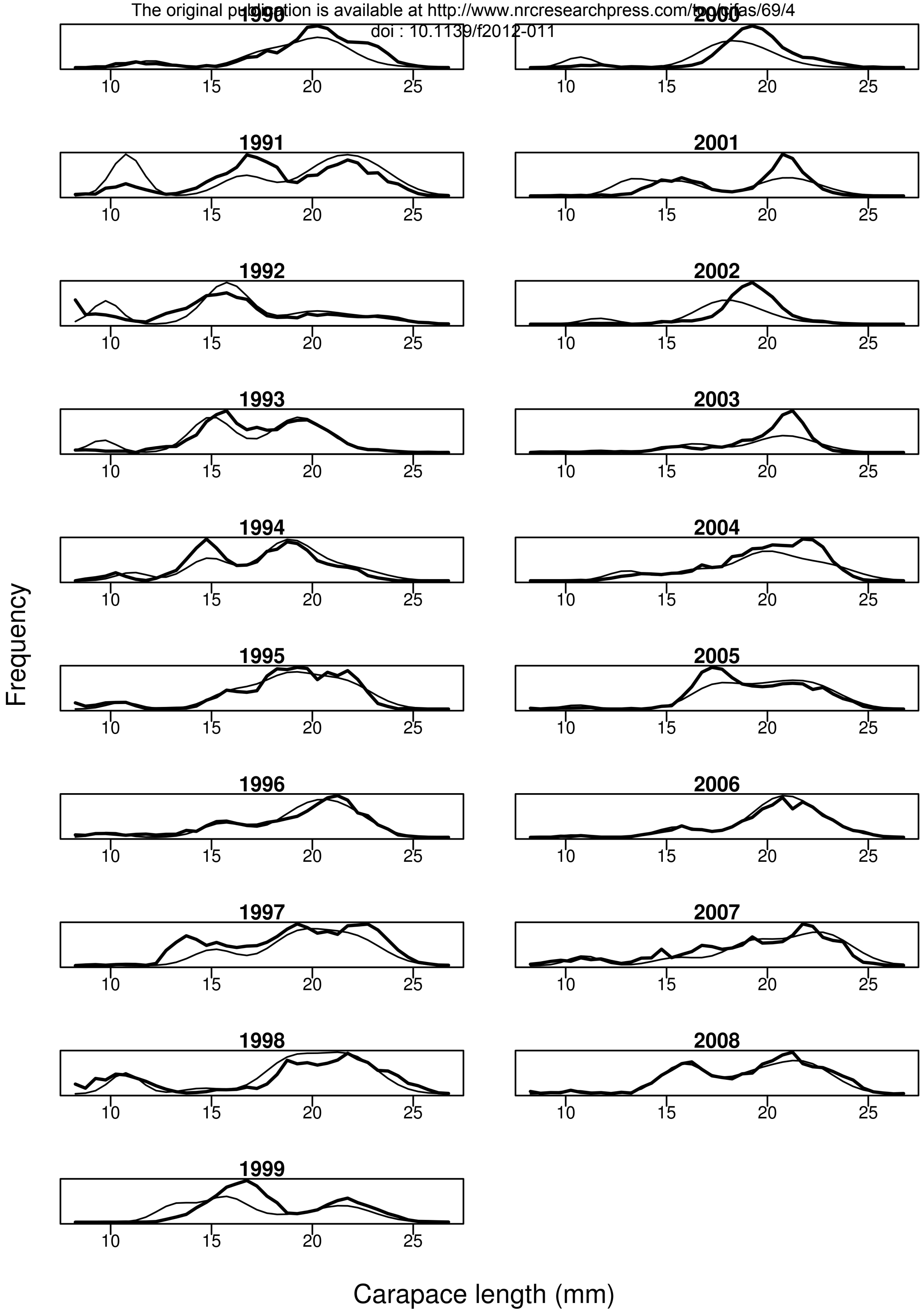
E
S
USA
New Brunswick
70°W
65°W
60°W
Longitude


(a)
spring
summer
fall
(b)
spring
summer
fall
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
10
15
20
25
Frequency
Carapace length (mm)


1990
2000
1991
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10
15
20
25
Frequency
Carapace length (mm)

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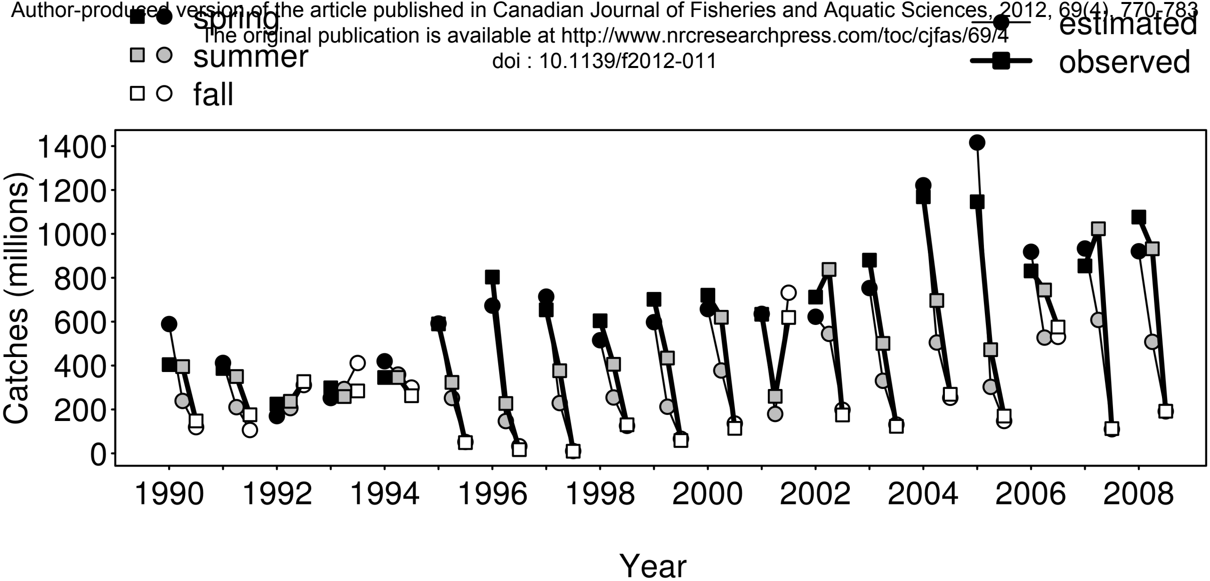
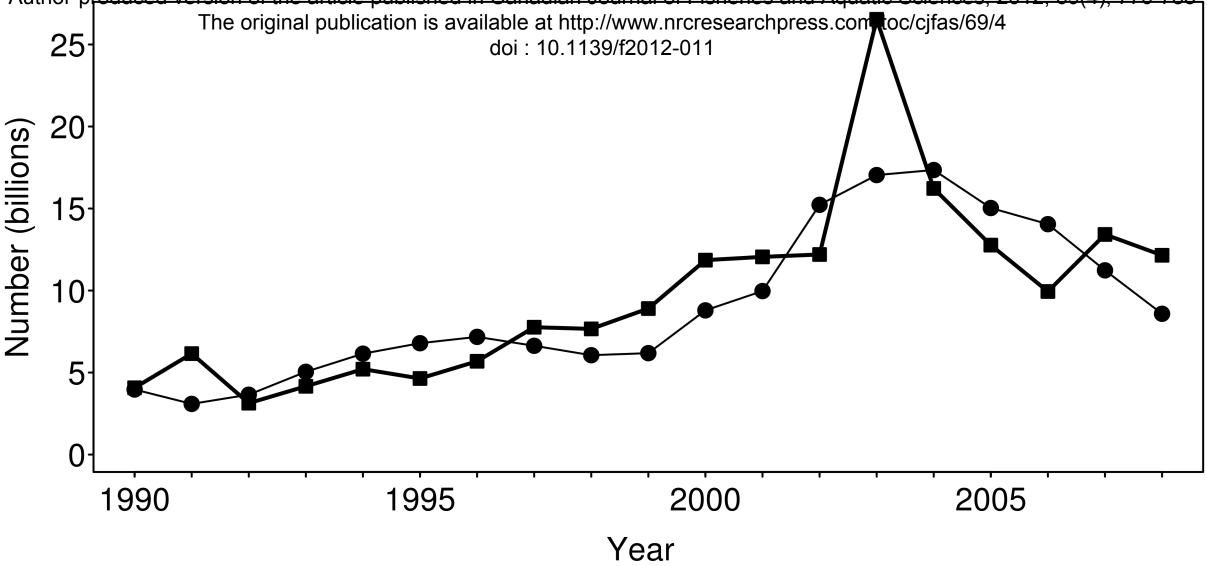
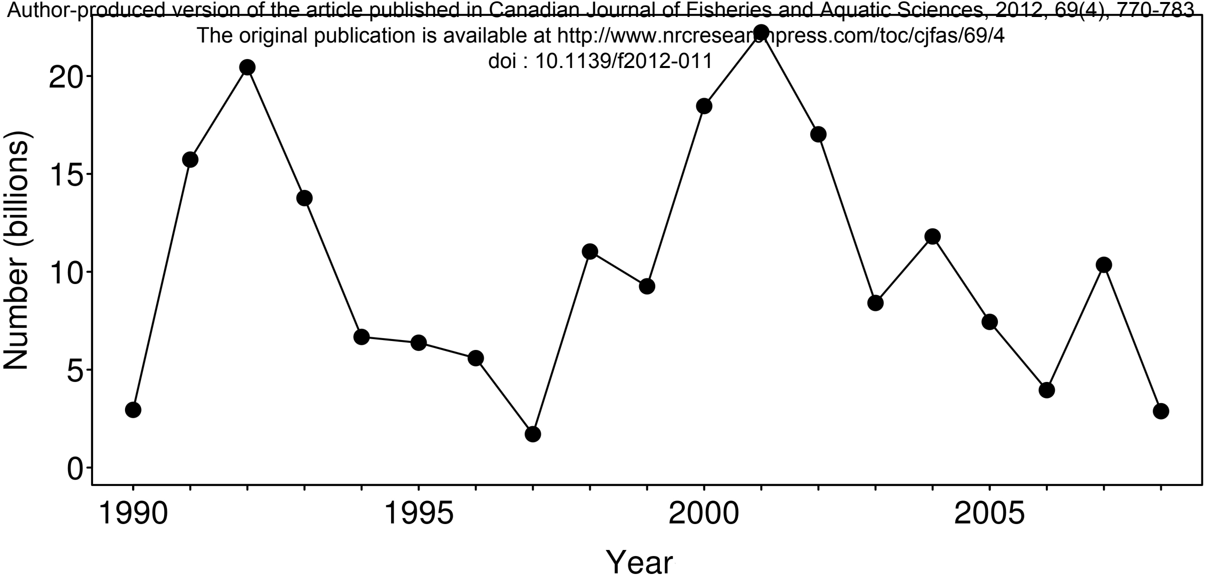
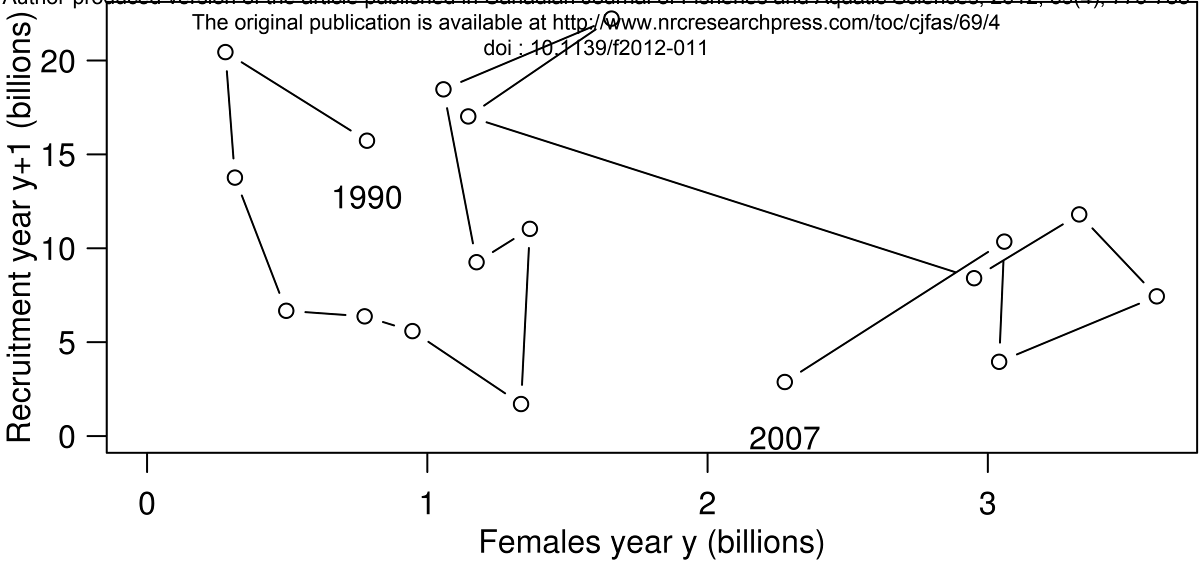



Number (billions)
0
5
10
15
20
25
1990
1995
2000
2005
Year


20
15
10
5
0
Number (billions)
1990
1995
2000
2005
Year


Recruitment year y+1 (billions)
20
15
10
5
0
1990
2007
0
1
2
3
Females year y (billions)

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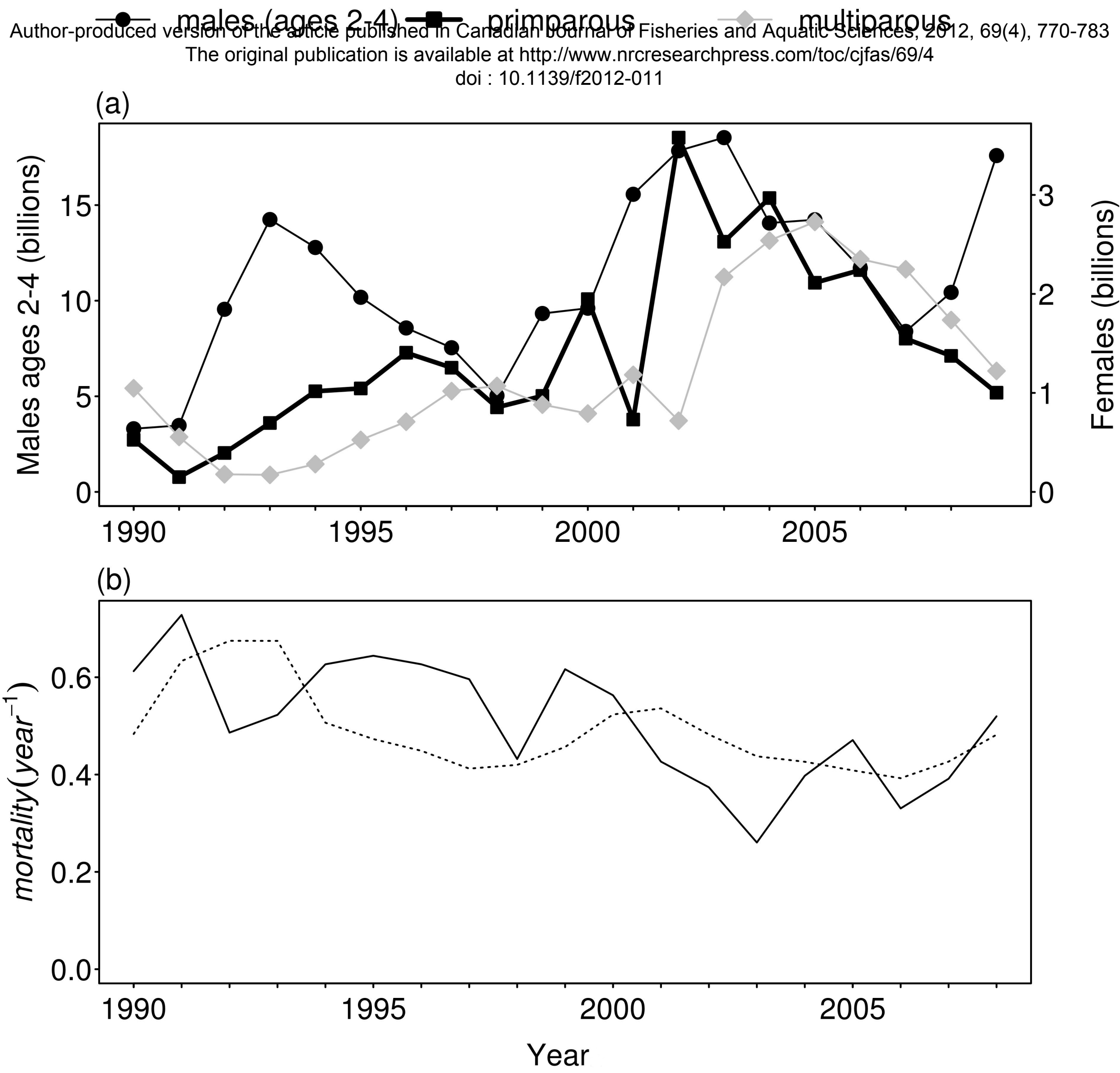

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