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

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22 **Abstract**

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

34 **Introduction**

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

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

54 Individuals of *P. borealis* remain as males for some years. Sex-change occurs in winter
55 and newly transformed females can be identified as primiparous females in the following spring
56 and summer. Primiparous females spawn the following fall. Larvae hatch in spring and

57 reproductive females that survive breeding are then identified as multiparous females.
58 Multiparous and primiparous females can be distinguished by the presence of sternal spines that
59 start disappearing during summer and are definitively lost little time before their first mating
60 (mating occurs few hours/days before spawning - McCrary 1971).

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

75 Despite the economic importance of crustacean fisheries, few analytical methods have been
76 developed for crustacean stock assessments (Smith and Addison 2003) and more specifically for
77 shrimp stocks. Age structured models have been applied for some crustacean stocks (ICES
78 2003), including shrimp (ICES 2001), but in most cases they were found inappropriate because
79 of the uncertainties in aging techniques and the difficulties to track the cohorts after sex-change.

80 Catch-Survey-Analysis (Cadrin 2000; Cadrin et al. 1999) and surplus production models have
81 also been applied (Cadrin et al. 2004; NAFO/ICES 2008) to carry out shrimp assessments. They
82 have the advantage of being simple and rather robust, requiring few data. However, a major
83 limitation is that they do not provide any information on the demographical, and especially sex
84 stock structure which can be considerably altered by commercial harvesting and is essential for
85 fishery management. Consequently, shrimp stock assessments often consist of a descriptive
86 analysis of various indicators and trends (for example commercial catch rates and/or survey
87 abundance indices) through time, sometimes formalized in a traffic light approach (Koeller et al.
88 2000b).

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

100 This paper presents SPAM, a model dedicated to protandric hermaphrodite Pandalids stock
101 assessment, that incorporates (i) a length based submodel for male, (ii) a constant growth model
102 but time varying size at recruitment, (iii) a time varying length at sex-change relationship

103 function and (iv) a stage structure (primiparous/multiparous) submodel for females. Contrary to
104 Fu et al. (2001), a simple two stage structure is used for females whereas the male component
105 relies on a length and age structure. The model is then applied to the exploited *Pandalus borealis*
106 stock of the Gulf of Saint-Lawrence as an illustration showing the relevance of SPAM to assess a
107 commercially harvested shrimp population.

108 **Material and methods**

109 **Population model**

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

116 The population is primarily divided into male and female components. Male component is age
117 (from age 1 to age A) and length (from length class 1 to L) structured. We assume that males are
118 recruited to the population at age 1 at the beginning of spring; they progress from age a to age
119 $a+1$ also at the beginning of spring (Fig. 1). Quantities related to the male component are
120 subscripted with a m , quantities related to the primiparous component are subscripted with *primi*,
121 quantities related to the multiparous component are subscripted with a *multi* and quantities
122 related to the female component (both primiparous and multiparous females) are subscripted
123 with a *fe*.

124 The number of males for a given time step t , a given age a and a given length class l

125 is $N_m(t, a, l)$. The total number of males per time step and length class is denoted by
126 $N_m(t, l) = \sum_a N_m(t, a, l)$, while the total number of males per time step and age is
127 $N_m(t, a) = \sum_l N_m(t, a, l)$. Male can change sex at different length and age following a sex-change
128 at length transition ogive.

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

133 $N_{primi}(t)$ and $N_{multi}(t)$ stands respectively for the number of primiparous and multiparous
134 females at time step t .

135 *Assumptions regarding length-at-age*

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

$$138 \quad (1) \quad \mu_y(t+1) = \mu_y(t) + (L_\infty - \mu_{y,r}) \cdot (1 - \exp^{-K \cdot (\Delta t)})$$

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

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

145 *cv.*

146 *Assumptions regarding sex-change*

147 Quantities related to the sex-change are subscripted with *sex*. Sex-change is assumed to be
148 length dependent. We assume that the sex-change process is completed at the end of winter
149 before the beginning of the new biological year. The proportion of males that change sex in a
150 given year y is modelled by a sigmoid function of length, characterised by two parameters
151 $L_{50_{sex}}(y)$ and R_{sex} (interquartile range). $L_{50_{sex}}(y)$ is assumed to follow a lognormal random walk
152 to account for inter-annual variability in sex-change:

153 (2) $L_{50_{sex}}(y) = L_{50_{sex}}(y-1) \cdot e^{\varepsilon_{sex}(y)}$ with $\varepsilon_{sex}(y) \sim N(0, \sigma_{sex}^2)$

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

155 (3)
$$p(y, l) = \frac{1}{1 + \exp\left(-2 \frac{\log(3)}{R_{sex}} \cdot (l - L_{50_{sex}}(y))\right)}$$

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

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

160 *Survival equations*

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

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

165 $M(y)$ denoting the natural mortality in year y .

166 $F_m(t, l)$, $F_{primi}(t)$ and $F_{multi}(t)$ stand for fishing mortality applied respectively on males of
 167 length l , primiparous and multiparous females at time t . Their calculation is explained in the next
 168 section. Survival is computed with the following equations:

169 (5)
$$\begin{cases} Sr_m(t, l) = e^{-(M(y)+F_m(t, l))\Delta t} \\ Sr_{primi}(t) = e^{-(M(y)+F_{primi}(t))\Delta t} \quad t \in y \\ Sr_{multi}(t) = e^{-(M(y)+F_{multi}(t))\Delta t} \end{cases}$$

170

171 **Fishing activity and survey models**

172 *Fishing mortality and catches*

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

177 (6)
$$s_f(l) = \frac{1}{1 + \exp\left(-2 \frac{\log(3)}{R_f} \cdot (l - L_{50f})\right)}$$

178 Male fishing mortality is equal to:

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

180 Concerning females, it is assumed that selectivity is equal to 1 given that the newly
 181 transformed females reach the sizes that are usually fully recruited to the fishing gear (Shumway

182 et al. 1985). Therefore, primiparous females fishing mortality is equal to:

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

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

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

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

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

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

194 (11)
$$\left\{ \begin{array}{l} C_m(t, l) = N_m(t, l) \cdot \frac{F_m(t, l)}{M + F_m(t, l)} \cdot (1 - \exp(-(M + F_m(t, l)) \cdot \Delta t)) \\ C_m(t) = \sum_l C_m(t, l) \\ C_{primi}(t) = N_{primi}(t) \cdot \frac{F_{primi}(t)}{M + F_{primi}(t)} \cdot (1 - \exp(-(M + F_{primi}(t)) \cdot \Delta t)) \\ C_{multi}(t) = N_{multi}(t) \cdot \frac{F_{multi}(t)}{M + F_{multi}(t)} \cdot (1 - \exp(-(M + F_{multi}(t)) \cdot \Delta t)) \end{array} \right.$$

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

$$\begin{aligned}
 & H_m(y) = \frac{\sum_{t \in y} \sum_a \sum_l C_m(t, a, l)}{\sum_a \sum_l N_m(t_1, a, l)} \\
 & H_{primi}(y) = \frac{\sum_{t \in y} C_{primi}(t)}{N_{primi}(t_1)} \\
 & H_{multi}(y) = \frac{\sum_{t \in y} C_{multi}(t)}{N_{multi}(t_1)}
 \end{aligned}
 \tag{12}$$

198 *Assumptions regarding survey abundance indices*

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

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

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

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

212 **Observation model and likelihood function**

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

215 *Contribution of length-frequency data*

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

$$\begin{aligned}
 & \log L(\text{samp}(t)/\theta) = \sum_t -\frac{1}{2} \cdot \log(v_{\text{samp}}(t,l)) + \log \left(e^{-\frac{1}{2} \frac{(f(t,l) - f_{\text{obs}}(l))^2}{v_{\text{samp}}(t,l)} + 10^{-6}} \right) \\
 & \text{with } v_{\text{samp}}(t,l) = \left((1 - f(t,l)) \cdot f(t,l) + \frac{0.1}{L+2} \right) \cdot \frac{1}{n_{\text{samp}}(t)}
 \end{aligned}
 \tag{15}$$

223 where $n_{\text{samp}}(t)$ is the number of sampled shrimps and $f(t,l) = C_m(t,l) / \sum_{i=1}^L C_m(t,i)$ and

224 $f(t,l) = IA_m(t,l) / \sum_{i=1}^L IA_m(t,i)$ are the expected frequency of length class l estimated by the model

225 for a sample from the commercial fishery and from the scientific survey respectively, and $f_{\text{obs}}(l)$

226 the observed frequency in the sample.

227 *Contribution of total catches and total abundance indices*

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

232 The loglikelihood is given by:

233 (16)

234
$$LogLC(t/\theta) = v_{com} \left[\log \left(\frac{C_{m,obs}(t)}{C_m(t)} \right) - \frac{C_{m,obs}(t)}{C_m(t)} + \log \left(\frac{C_{primi,obs}(t)}{C_{primi}(t)} \right) - \frac{C_{primi,obs}(t)}{C_{primi}(t)} + \log \left(\frac{C_{multi,obs}(t)}{C_{multi}(t)} \right) - \frac{C_{multi,obs}(t)}{C_{multi}(t)} \right]$$

235

236 and

237 (17)
$$LogLIA(t/\theta) = v_{surv} \left[\log \left(\frac{IA_{m,obs}(t)}{IA_m(t)} \right) - \frac{IA_{m,obs}(t)}{IA_m(t)} + \log \left(\frac{IA_{fe,obs}(t)}{IA_{fe}(t)} \right) - \frac{IA_{fe,obs}(t)}{IA_{fe}(t)} \right]$$

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

240 **Parameter estimation**

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

246 *Estimating growth parameters*

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

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

255 (18)
$$\log L_2 P_{samp}(t/\theta_1) = \sum_{l=1}^L \left[f(t,l) \cdot \log \left[\sum_{a=1}^A \lambda_{samp}(t,a) \frac{1}{2 \cdot cv \cdot \mu_a(t)} \exp \left(-\frac{1}{2} \left(\frac{length(l) - \mu_a(t)}{cv \cdot \mu_a(t)} \right)^2 \right) \right] \right]$$

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

- 257 4. Repeat steps 1-3 to θ_1 that maximises

258 (19)
$$\log L_2(\theta_1) = \sum_t (\log L_2 P_{samp}(t/\theta_1))$$

259 *Estimating other parameters*

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

(20)

$$\log L(\theta_2 / \theta_1) = \sum_t \text{Log}L(\text{samp}_{com}(t) / \theta) + \sum_t \text{Log}L(\text{samp}_{surv}(t) / \theta) + \sum_t \text{Log}LC(t / \theta) + \sum_t \text{LogLIA}(t / \theta) \\ + \text{Log}L_{sex}(\theta) + \text{Log}L_M(\theta) + \text{Log}L_f(\theta)$$

265 with:

$$266 \quad (21) \quad \text{Log}L_{sex}(\theta) = -\frac{1}{2 \cdot \sigma_{sex}^2} \sum_y \varepsilon_{sex}^2$$

$$267 \quad (22) \quad \text{Log}L_M(\theta) = -\frac{1}{2 \cdot \sigma_M^2} \sum_y \varepsilon_M^2$$

268 and:

$$269 \quad (23) \quad \text{Log}L_f(\theta) = -\frac{1}{2 \cdot \sigma_f^2} \sum_y \varepsilon_f^2$$

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

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

278 *Description of the fishery*

279 The northern shrimp (*Pandalus borealis*) fishery began in the Gulf of St. Lawrence (Fig. 2) in
280 the 1960s. The exploitation is conducted by trawlers in four shrimp fishing areas (SFA) (DFO
281 2009). In 2008, the Gulf landings reached about 36,000 tons. The Sept-Îles area (SFA 10) is the

282 most productive of the four stocks representing about 41% of the total Gulf catch. The fishery is
283 managed by TAC and the number of fishing licenses is regulated. Fishing season starts on April
284 1st and closes when the TAC is reached or on the 31st of December at the latest. There is no
285 fishing in winter mainly because the ice cover prevents access to fishing grounds.

286 The fishery mainly targets large individuals which are more economically valuable; therefore
287 fishermen allocate a large part of their effort in spring on reproductive females on hatching
288 grounds. On average, females represented 68% of the Sept-Îles fishing area landings between
289 1990 and 2008.

290 Fishers are required to fill out a logbook, indicating the number of hours fished and a
291 dockside monitoring program ensures control over landings. Both log-book and dockside
292 programs have provided very reliable estimates of fishing effort and catches since 1990. The
293 commercial catches are sampled regularly during the fishing season and a bottom trawl survey is
294 conducted each year at the end of summer. The catch sampling program has been running since
295 1982 and the research survey has been conducted since 1990. The total number of shrimp
296 measured each year varies from 8,000 to 18,000 for the commercial sampling as well as for the
297 survey.

298 *Input data*

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

304 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
305 and 23.0 at 4½ y.o. The maximum size is 28.0 mm but few males are found at sizes larger than
306 24 mm. Sex-change occurs after mating (which occurs few hours/day before female spawning),
307 in winter, before they reach the age of 5. Controlled growth experiment studies confirmed this
308 growth pattern (Daoud et al. 2010). Indeed, the authors found that, at 5 °C which is about the
309 bottom temperature of the area, 20.0 mm males are 4 years old.

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

317 *Specific parameters values*

318 Some specific parameters values were fixed for the Sept-Îles case study according to expert
319 knowledge (Tab. 2). We set $v_{com}=v_{surv}=100$ which corresponds to a CV of 10%. We set
320 $\sigma_f = 0.05$ which corresponds to a random walk of coefficient of variation to 5%, given that
321 fishing activity is well known and that catchability is not expected to have changed a lot over the
322 period. Although there is little information on natural mortality inter-annual variability, we
323 choose to fix $\sigma_M = 0.05$, to have equivalent weights between natural and fishing mortality
324 deviations. In the absence of information over sex-change, we choose to let more flexibility to
325 the sex-change random walk and fix $\sigma_{sex} = 0.10$.

326 The model includes 4 male age groups and is fitted over a 19 years data series. Consequently
327 111 parameters should be estimated (24 in phase 1 and 87 in phase 2 - Table 1).

328 **Results**

329 **Fitting observed data**

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

333 The seasonal pattern of landings was captured as well in the fitting (Fig. 5). Each year, a peak
334 of catches is observed in spring that corresponds to the fishery targeting multiparous females
335 which are aggregated on the hatching grounds. The model poorly fits summer catches for the last
336 two years, probably because the estimates rely on only a few data points. More generally, the fits
337 are a bit poorer for the summer season than for the two other fishing seasons since the late
338 1990's, perhaps indicating a change in fishing behaviour over the period. Globally, catches have
339 increased through time over the period (Fig. 5) as a consequence of an increase in TAC (DFO
340 2009).

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

345 **Population numbers**

346 Recruitment at age one (Figs. 7 and 8) estimated by the model is variable with two periods of

347 higher recruitments in early 90's and then in early 2000's. Those strong year classes are
348 especially prominent at 15 mm (2 years old) in the length compositions of the 1992, 1999 and
349 2001 commercial catches (Fig. 3) and at 10 mm (1 year old) in the 1991, 1998 and 2000 survey
350 length compositions (Fig. 4). The abundance of females (primiparous and multiparous) also
351 shows the same trend with however a few years lag (Fig. 9a). The abundance of females has
352 been gradually decreasing for the last four to five years probably due to the decreasing
353 abundance of males estimated from 2003 to 2007. Recruitment seems to be slightly decreasing in
354 latter years, therefore, a decrease in total abundance is expected in the future (the number of
355 males increased in recent year, but it is probably because of a delayed sex-change).

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

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

363 **Natural and fishing mortality rates**

364 The model provides natural and fishing mortality estimates for males and females at each time
365 step (Fig. 9b - male and multiparous female fishing mortality rates are not represented, since they
366 are equal to the primiparous mortality rate multiplied by a constant through time). A high level
367 of both natural and fishing mortality rates at the beginning of the 1990s explains the low
368 abundance of multiparous in the same period. A sudden decrease in natural mortality first,

369 followed by a more limited decrease in fishing mortality with the combination of high
370 recruitment resulted in a period of relatively high female abundance between 1996 and 2001.
371 Similarly, the second peak of female abundance in the 2000's happened after a period of high
372 recruitment, lower fishing mortality, and decreasing natural mortality which continued to
373 decrease till 2006. The recent decrease in the abundance of females is probably due to both an
374 increase in the natural mortality rate estimated for the last two years, and a substantial increase in
375 fishing mortality since 2003.

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

378 **Sex-change**

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

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

390 **Discussion and perspectives**

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

407 The model demonstrates a high inter-annual variability in length at sex-change. Consequently,
408 the numbers of newly transformed females are difficult to predict from one year to the next. We
409 totally agree with Fu et al. (2001) when stating that a better understanding of sex-change would
410 be a valuable improvement for *Pandalus* stocks management, especially for stocks where
411 females are such a large component of the commercial catches. Females represent the spawning
412 population and constitute the main target of the commercial fisheries and thus they need to be

413 effectively managed to prevent stock depletion. Moreover, the results of the model on the yearly
414 variations in size at sex-change will probably help to investigate the process and find relevant
415 explanatory covariables. More specifically, density-dependant influence on the variations in size
416 at sex-change may be investigated in the future, since we observed that periods of high or
417 increasing levels in males abundance correspond to periods with low size at sex-change.

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

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

434 Weights on sex-change (equation 2 - σ_{sex}), natural mortality (equation 4 - σ_M) and year
435 effect random walks (equation 10 - σ_f) were fixed rather arbitrarily. However our objective in

436 this paper was to present an illustrative example. In a formal stock assessment context, those
437 weights should be discussed with experts and adapted to each stock, and sensitivity analysis
438 should be carried out. We think that the model is generic enough to be applied to different
439 *Pandalus* stocks, if reliable data from both scientific survey and commercial fishery are
440 available. Moreover, the model needs reliable fishing effort data to estimate the seasonal pattern
441 in fishing activity.

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

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

455 Finally, the model may be used as an operating model in a management strategy evaluation
456 (MSE) framework (Butterworth and Punt 1999; Punt and Donovan 2007; Sainsbury et al. 2000).
457 MSE aims at assessing the robustness of management options regarding various sources of
458 uncertainty. It relies on an operating model that is able to simulate realistic population dynamics

459 under various scenarios. The model seems to be able to reproduce Pandalid shrimp stock trends
460 and is flexible enough (especially if one adds time varying natural mortality and size at sex-
461 change) to simulate various plausible scenarios of stock evolution.

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556 56.

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	$L_{50sex}(y_0) R_{sex} \varepsilon_{sex}(y_1) \varepsilon_{sex}(y_2) \dots \varepsilon_{sex}(y_{Y-2})$	Y
Natural mortality	$\varepsilon_M(y)$	Y
Initial numbers	First year $N_m(I, a, \cdot) N_{primi}(I) N_{multi}(I)$	A+2
	Yearly recruitment $N_m(y, I, \cdot)$	Y-1
Commercial fishery	Selectivity L_{50f}, R_f	2
	Catchability $q(y_0) \varepsilon_f(y_1) \varepsilon_f(y_2) \dots \varepsilon_{sf}(y_{Y-1})$	Y
	Multiparous targetting $T_{spring, multi}$ for spring	1
Survey	Selectivity $L_{50s} R_s$	2
	Catchability q_s	1

560 **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

562

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

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

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

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

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

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

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

580 **Fig. 7.** Estimated recruitment at age 1.

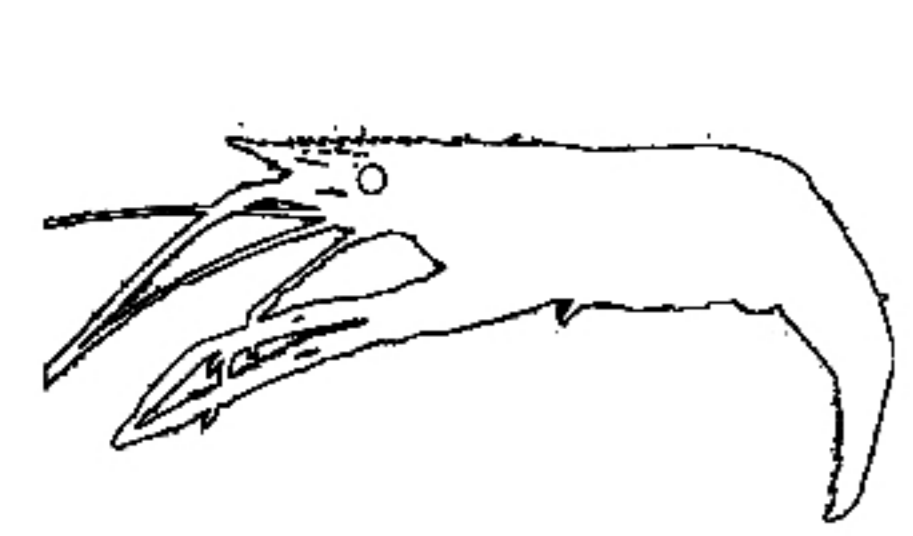
581 **Fig. 8.** Estimated stock recruitment relationships: females in autumn against males of age 1
582 following spring.

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

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

588 **Fig. 10.** Estimated ogive of sex change at length for two extreme years (end of year 1996 and
589 end of year 2007) (left) and evolution of $L50_{sex}(y)$ over the period (right). Vertical dashed lines
590 represent the mean sizes at the period of sex change (Fig. 1) of each male group

591
$$\mu_a = \sum_{y=y_0}^{y_{Y-1}} \mu_a(t_1) / Y \text{ (with } t_1 \text{ spring of year } y)$$



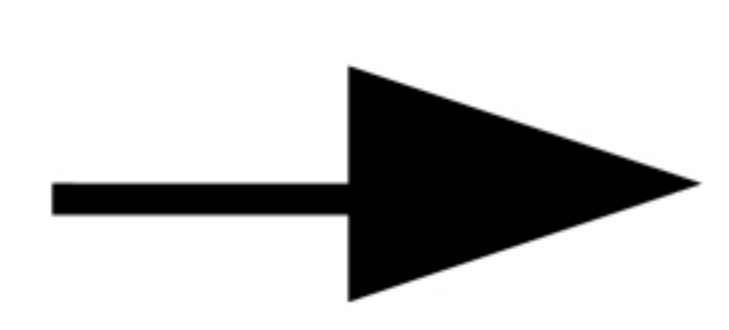
Muliparous female



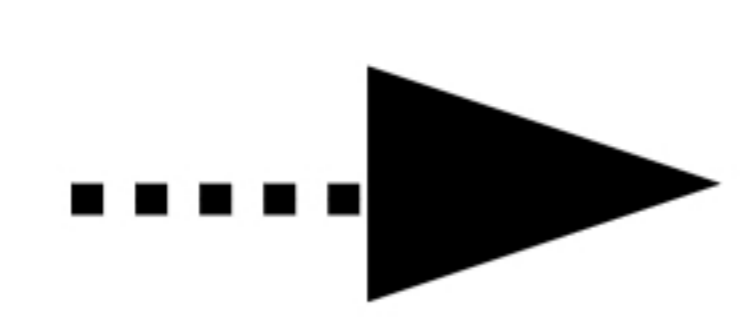
Primiparous female



Male



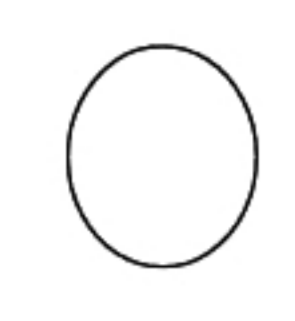
Normal stage transition



Change sex



Change maturity stage



Spawning



Ovigerous



Hatching

1

Age



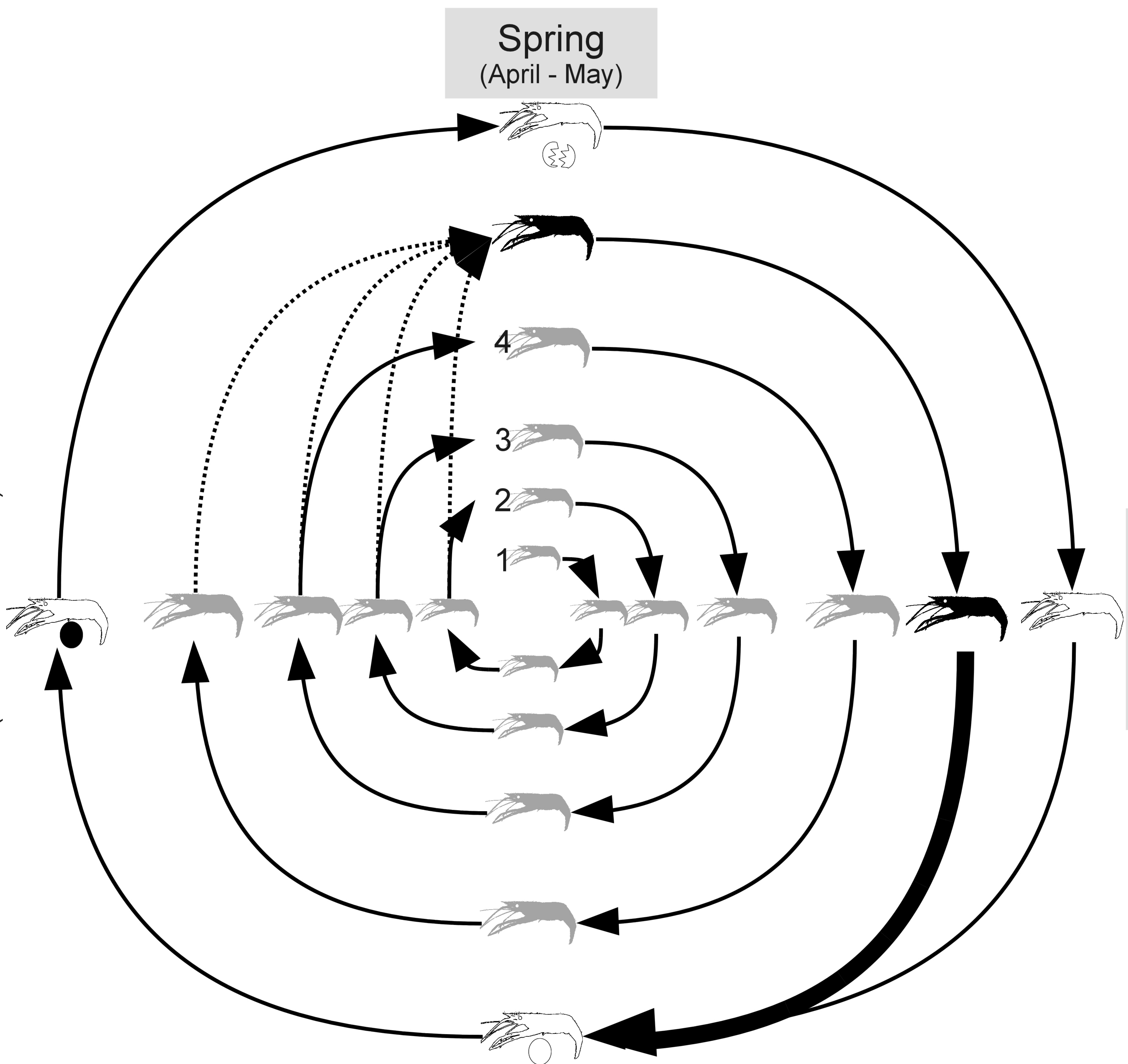
Fishing season

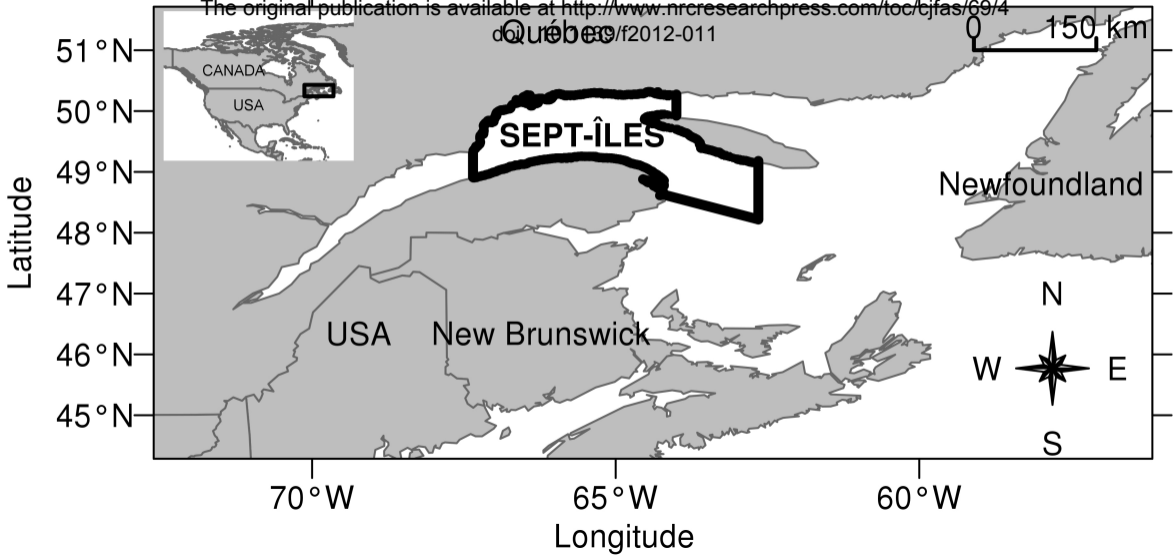
Spring
(April - May)

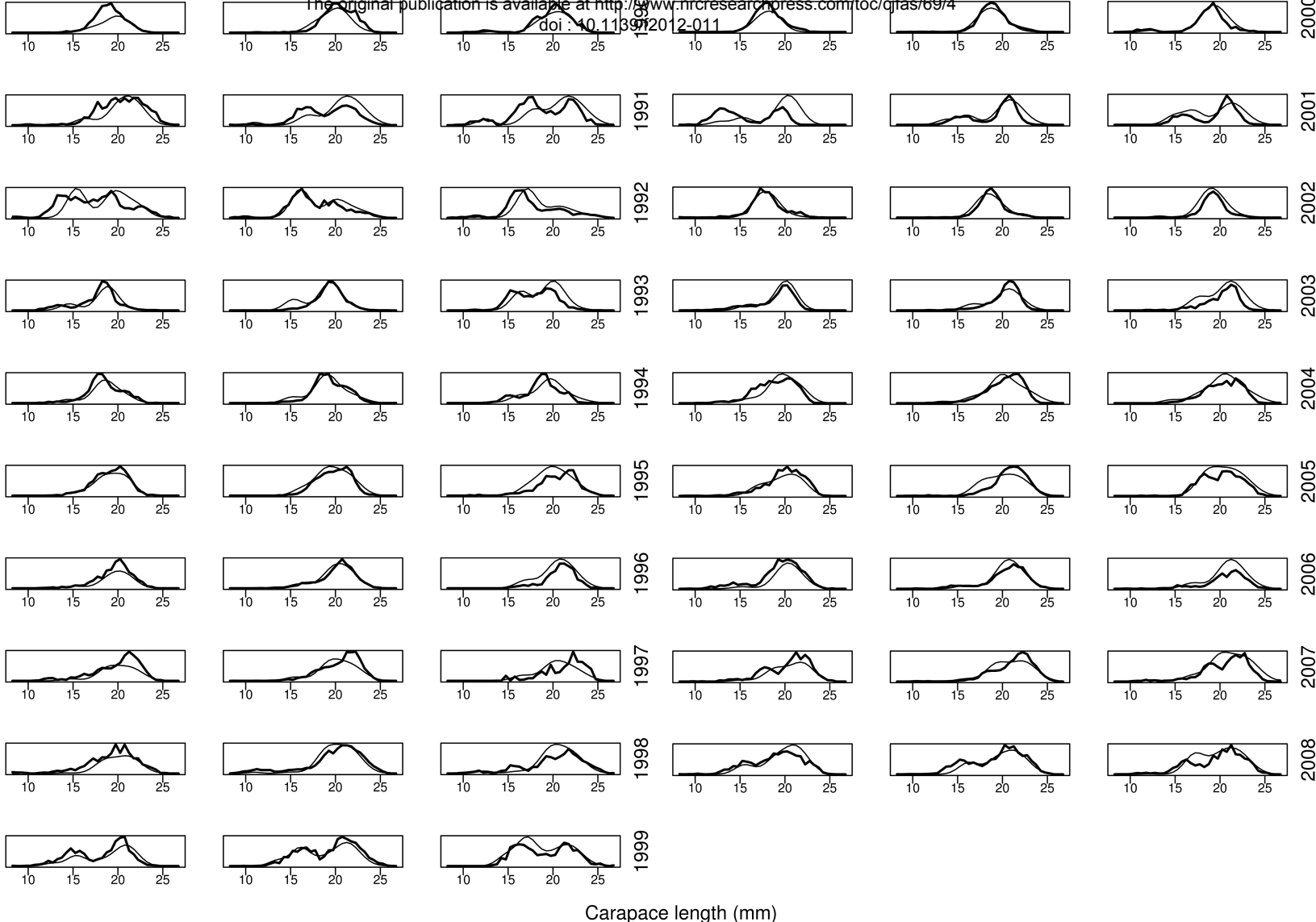
Winter
(December - March)

Summer
(June - August)

Autumn
(September - November)



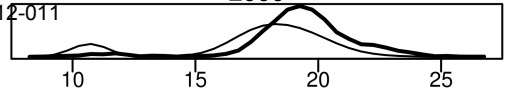
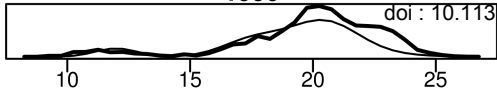




1990

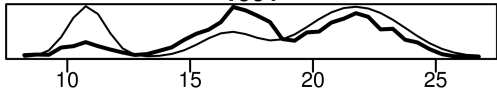
doi: 10.1139/f2012-011

2000



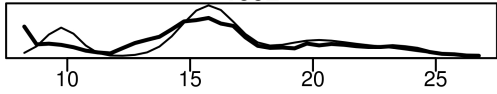
1991

2001



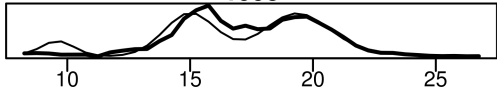
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2002



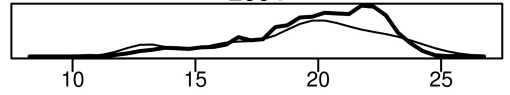
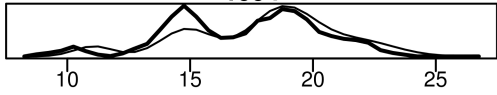
1993

2003



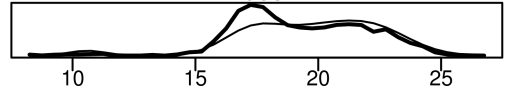
1994

2004



1995

2005



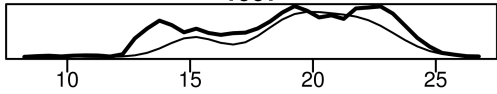
1996

2006



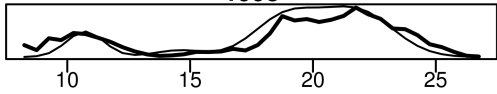
1997

2007



1998

2008

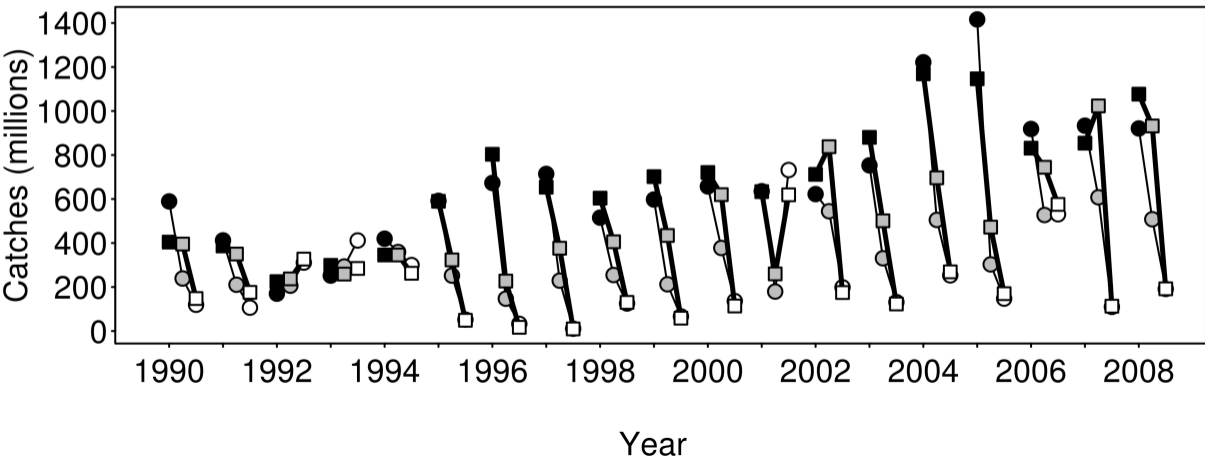


1999



Frequency

Carapace length (mm)



The original publication is available at <http://www.nrcresearchpress.com/doi/10.1139/f2012-011>
doi : 10.1139/f2012-011

Number (billions)

25
20
15
10
5
0

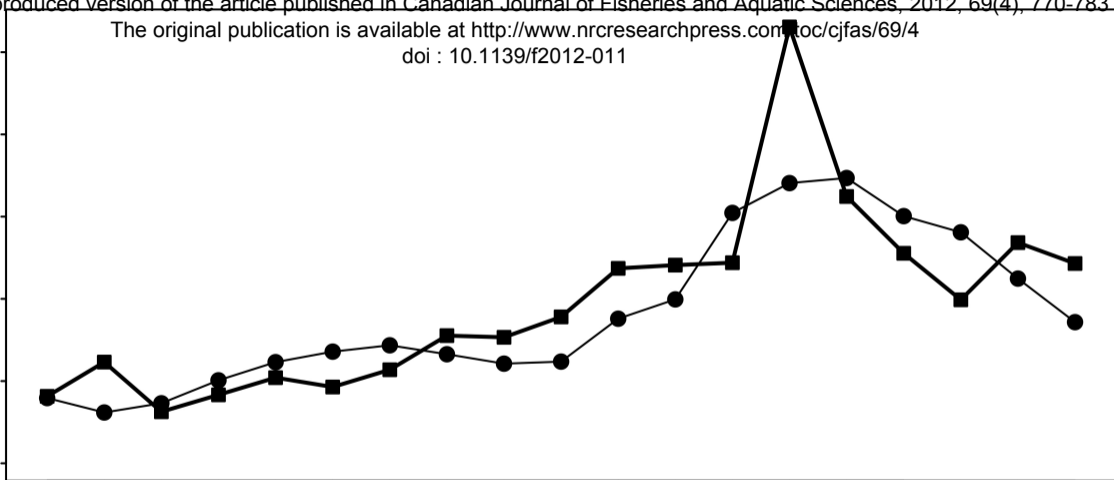
1990

1995

2000

2005

Year



The original publication is available at <http://www.nrcresearchpress.com/toc/cjfas/69/4>
doi : 10.1139/f2012-011

Number (billions)

20
15
10
5
0

1990

1995

2000

2005

Year

