

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

Hilaire Drouineau, Louise Savard, Mathieu Desgagnés, and Daniel Duplisea

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 (Sex-Structured *Pandalus* Assessment Model), 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 and 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 (Québec, Canada) as an illustrative example of the utility of the approach.

Résumé : Malgré l'importance économique des pêches aux crevettes *Pandalus*, peu d'outils ont été mis au point pour en évaluer les stocks, car les modèles d'évaluation courants ne sont pas appropriés à cause des caractéristiques biologiques particulières des espèces de *Pandalus*. Dans ce contexte, nous proposons SPAM (Sex-Structured *Pandalus* Assessment Model — modèle d'évaluation des *Pandalus* structuré en fonction du sexe), un modèle servant à évaluer les stocks de pandalidés hermaphrodites protandriques. Les pandalidés sont difficiles à évaluer parce que les signaux qui affectent le changement de sexe, la taille lors de recrutement et la variabilité de la mortalité restent mal connus et caractérisés. La structure inédite de notre modèle permet de décrire adéquatement la variabilité de la mortalité naturelle en fonction des stades et du temps, de même que la variabilité dans la taille au moment du changement de sexe et lors du recrutement. Le modèle fournit les résultats des modèles traditionnels d'évaluation des stocks, tels que les estimations de la mortalité due à la pêche et le nombre d'individus, mais il donne en plus des estimations des mortalités naturelles annuelles. Nous appliquons le modèle au stock exploité de crevettes *Pandalus borealis* de Sept-Îles (Québec, Canada) comme exemple pour illustrer l'utilité de la méthodologie.

[Traduit par la Rédaction]

Introduction

Shrimp fisheries are becoming more and more important throughout the world. According to the Food and Agriculture Organization of the United Nations (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 (Food and Agriculture Organization of the United Nations 2009). A Pandalidae, *Pandalus borealis*, is the second most important exploited shrimp species globally, accounting for 12.3% of the global shrimp catches (Food and Agriculture Organization of the United Nations 2009).

Shrimp of the genus *Pandalus* are exploited in the North Atlantic and the North Pacific oceans mainly by trawl fisheries targeting 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; Berkeley 1931; 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 that 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 cer-

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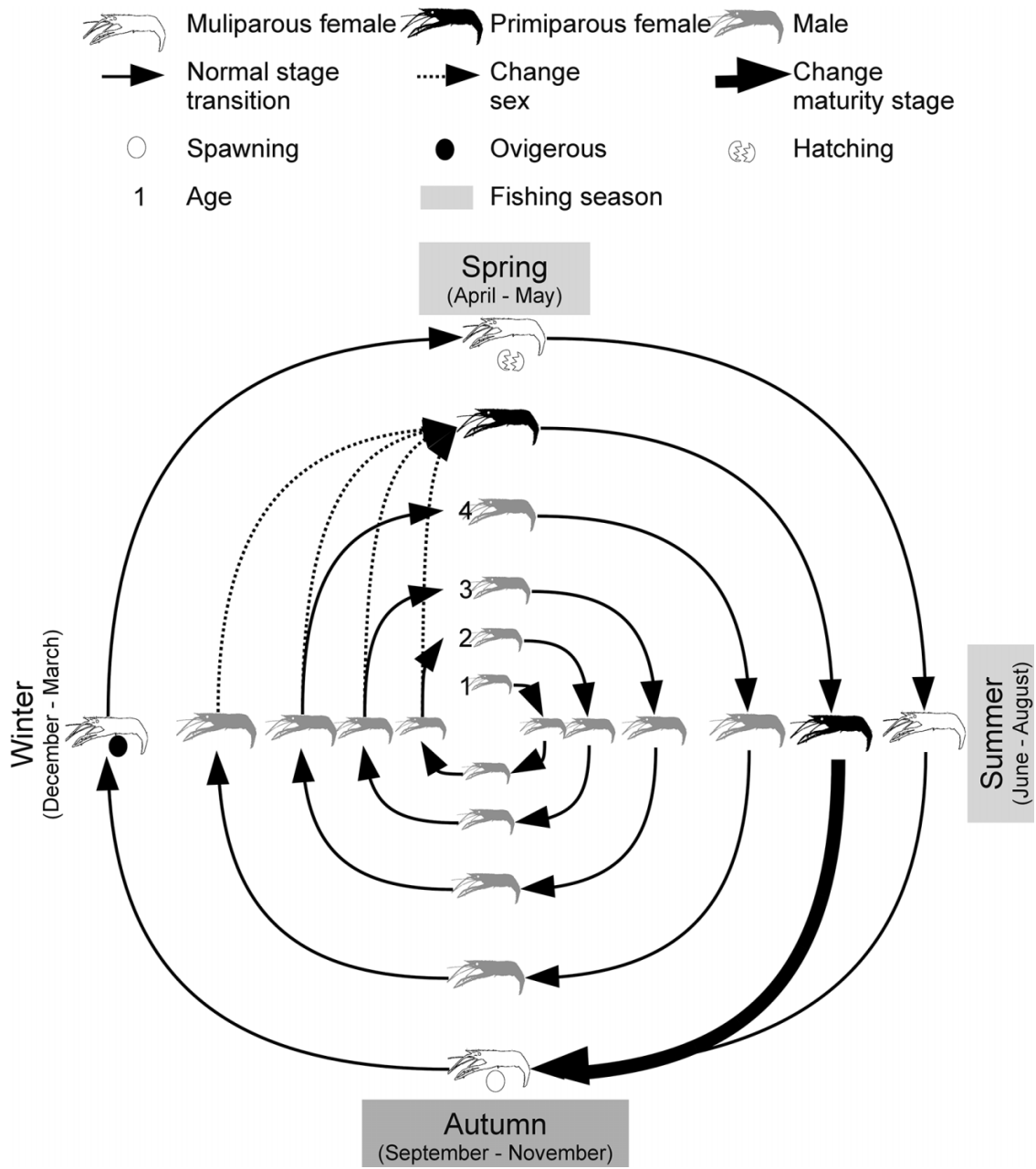
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Fig. 1. Illustration of the life cycle of a protandric hermaphrodite *Pandalus* species and model time steps (winter, spring, summer, autumn). Arrows represent (age or stage or sex) transitions occurring instantaneously between two successive time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



tain 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 shortly before their first mating (mating occurs few hours or 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 techni-

ques are often used, but this technique is more difficult to apply to shrimps because of frequent moulting, small size of the individuals, and the generally high 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 (International Council for the Exploration of the Sea 2003), including shrimp (International Council for the Exploration of the Sea 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; North Atlantic Fisheries Organization / International Council for the Exploration of the Sea 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, 2010) and age–length-structured (Fournier et al. 1998; Quinn et al. 1998; Frøysa 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, these kinds 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 (Sex-Structured *Pandalus* Assessment Model), 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 St. Lawrence

as an illustration showing the relevance of SPAM to assess a commercially harvested shrimp population.

Materials 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-structured (from age 1 to age A) and length-structured (from length class 1 to L). 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 “m”, quantities related to the primiparous component are subscripted with “primi”, quantities related to the multiparous component are subscripted with “multi”, and quantities related to the female component (both primiparous and multiparous females) are subscripted with “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 $N_m(t, ., l) = \sum_a N_m(t, a, l)$, while the total number of males per time step and age is $N_m(t, a, .) = \sum_l N_m(t, a, l)$. Males can change sex at different lengths and ages 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. $N_{\text{primi}}(t)$ and $N_{\text{multi}}(t)$ 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

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

where $\mu_{y,r}$ is the size at recruitment (size at age 1 at the beginning of spring) of the year class, and Δt is 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, characterized by two parameters: $L_{50_{\text{sex}}}(y)$ and R_{sex} (interquartile range). $L_{50_{\text{sex}}}(y)$ is assumed to follow a lognormal random walk to account for interannual variability in sex change:

$$(2) \quad L_{50_{\text{sex}}}(y) = L_{50_{\text{sex}}}(y-1) \cdot \exp[\varepsilon_{\text{sex}}(y)] \\ \text{with } \varepsilon_{\text{sex}}(y) \sim N(0, \sigma_{\text{sex}}^2)$$

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

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

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 that in year $Y-1$.

Survival equations

Survival (S_r) 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 interannual variability:

$$(4) \quad M(y) = M \cdot \exp[\varepsilon_M(y)] \quad \text{with } \varepsilon_M(y) \sim N(0, \sigma_M^2)$$

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

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

$$(5) \quad S_{rm}(t, l) = \exp\{-[M(y) + F_m(t, l)]\Delta t\} \\ S_{r\text{primi}}(t) = \exp\{-[M(y) + F_{\text{primi}}(t)]\Delta t\} \\ S_{r\text{multi}}(t) = \exp\{-[M(y) + F_{\text{multi}}(t)]\Delta t\}$$

where $t \in y$.

Fishing activity and survey models

Fishing mortality and catches

Quantities related to the commercial fishery are subscripted with an “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, characterized by two parameters, L_{50_f} and R_f (interquartile range):

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

Male fishing mortality is equal to

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

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

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

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 $T_{\text{spring, multi}}$ is thus introduced into the calculation of multiparous female fishing mortality in spring to describe this interaction:

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

Year effect is assumed to follow a random walk to avoid unrealistic interannual variations:

$$(10) \quad q_f(y) = q_f(y-1) \cdot \exp[\varepsilon_f(y)] \quad \text{with } \varepsilon_f(y) \sim N(0, \sigma_f^2)$$

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

$$(11) \quad C_m(t, l) = N_m(t, l) \cdot \frac{F_m(t, l)}{M + F_m(t, l)} \\ \times \left(1 - \exp\{-[M + F_m(t, l)] \cdot \Delta t\} \right) \\ C_m(t) = \sum_l C_m(t, l) \\ C_{\text{primi}}(t) = N_{\text{primi}}(t) \cdot \frac{F_{\text{primi}}(t)}{M + F_{\text{primi}}(t)} \\ \times \left(1 - \exp\{-[M + F_{\text{primi}}(t)] \cdot \Delta t\} \right) \\ C_{\text{multi}}(t) = N_{\text{multi}}(t) \cdot \frac{F_{\text{multi}}(t)}{M + F_{\text{multi}}(t)} \\ \times \left(1 - \exp\{-[M + F_{\text{multi}}(t)] \cdot \Delta t\} \right)$$

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:

$$(12) \quad H_m(y) = \frac{\sum_{t \in y} \sum_a \sum_l C_m(t, a, l)}{\sum_a \sum_l N_m(t_1, a, l)}$$

$$H_{\text{primi}}(y) = \frac{\sum_{t \in y} C_{\text{primi}}(t)}{N_{\text{primi}}(t_1)}$$

$$H_{\text{multi}}(y) = \frac{\sum_{t \in y} C_{\text{multi}}(t)}{N_{\text{multi}}(t_1)}$$

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, characterized by two parameters L_{50s} and R_s (interquartile range), to model selectivity for males. Therefore, $s_s(l)$ is given by

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

Selectivity is assumed to be equal to 1 for the females,

$$(15) \quad \text{LogL} [\text{samp}(t)|\theta] = \sum_l -\frac{1}{2} \cdot \log [v_{\text{samp}}(t, l)] + \log \left(\exp \left\{ -\frac{1}{2} \cdot \frac{[f(t, l) - f_{\text{obs}}(l)]^2}{v_{\text{samp}}(t, l)} \right\} + 10^{-6} \right)$$

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

where $n_{\text{samp}}(t)$ is the number of sampled shrimps, and

$$f(t, l) = C_m(t, l) / \sum_{i=1}^L C_m(t, l)$$

and

$$f(t, l) = \text{IA}_m(t, l) / \sum_{i=1}^L \text{IA}_m(t, l)$$

are the expected frequencies of length class l estimated by the model for a sample from the commercial fishery and from the scientific survey, respectively, and $f_{\text{obs}}(l)$ is the observed frequency in the sample.

$$(16) \quad \text{LogL } C(t|\theta) = v_{\text{com}} \left\{ \log \left[\frac{C_{m,\text{obs}}(t)}{C_m(t)} \right] - \frac{C_{m,\text{obs}}(t)}{C_m(t)} + \log \left[\frac{C_{\text{primi},\text{obs}}(t)}{C_{\text{primi}}(t)} \right] - \frac{C_{\text{primi},\text{obs}}(t)}{C_{\text{primi}}(t)} + \log \left[\frac{C_{\text{multi},\text{obs}}(t)}{C_{\text{multi}}(t)} \right] - \frac{C_{\text{multi},\text{obs}}(t)}{C_{\text{multi}}(t)} \right\}$$

and

$$(17) \quad \text{LogL } \text{IA}(t|\theta) = v_{\text{surv}} \left\{ \log \left[\frac{\text{IA}_{m,\text{obs}}(t)}{\text{IA}_m(t)} \right] - \frac{\text{IA}_{m,\text{obs}}(t)}{\text{IA}_m(t)} + \log \left[\frac{\text{IA}_{\text{fe},\text{obs}}(t)}{\text{IA}_{\text{fe}}(t)} \right] - \frac{\text{IA}_{\text{fe},\text{obs}}(t)}{\text{IA}_{\text{fe}}(t)} \right\}$$

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

$$(14) \quad \text{IA}_m(t, l) = s_s(l) \cdot q_s \cdot N_m(t, l)$$

$$\text{IA}_{\text{fe}} = q_s \cdot [N_{\text{primi}}(t) + N_{\text{multi}}(t)]$$

Observation model and likelihood function

The model is fitted by maximizing a likelihood function that 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 log-likelihood of a sample “samp” is

Contribution of total catches and total abundance indices

Total commercial catches per time step ($C_m(t)$, $C_{\text{primi}}(t)$, $C_{\text{multi}}(t)$) and total survey abundance indices per time step ($\text{IA}_m(t, l)$, $\text{IA}_{\text{fe}}(t)$) 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 (Frøysa et al. 2002; Haddon 2001).

The log-likelihood is given by

ν_{com} and ν_{surv} are equal to the inverse of the square root of the CV of the distributions (McCullagh and Nelder 1989).

Parameter estimation

A large number of parameters have to be estimated (Table 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 $\theta_1 = [K, \text{CV}, \mu_{1,r}, \dots, \mu_{Y,r}, \mu_2(t_0), \dots, \mu_A(t_0)]$ 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}).

$$(18) \quad \text{LogL}_2 P_{\text{samp}}(t|\theta_1) = \sum_{l=1}^L \left[f(t, l) \cdot \log \left(\sum_{a=1}^A \lambda_{\text{samp}}(t, a) \frac{1}{2 \cdot \text{CV} \cdot \mu_a(t)} \exp \left\{ -\frac{1}{2} \left[\frac{\text{length}(l) - \mu_a(t)}{\text{CV} \cdot \mu_a(t)} \right]^2 \right\} \right) \right]$$

with $\lambda_{\text{samp}}(t, a)$ estimated for each sample by an Expectation Maximization algorithm. (4) Repeat steps 1–3 to θ_1 that maximizes

$$(19) \quad \text{LogL}_2(\theta_1) = \sum_t [\text{LogL}_2 P_{\text{samp}}(t|\theta_1)]$$

Estimating other parameters

Given θ_1 , other parameters are estimated by maximizing the log-likelihood that is a function of five components: (i) the length composition of commercial and survey catches (eq. 15), (ii) the total commercial catches (eq. 16), (iii) the total abundance from survey (eq. 17), (iv) assumption regarding the random walk of $L_{50\text{sex}}$, and (v) assumption regarding the random walk of the year effect q_t :

$$(20) \quad \begin{aligned} \text{LogL}(\theta_2|\theta_1) = & \sum_t \text{LogL}[\text{samp}_{\text{com}}(t)|\theta] \\ & + \sum_t \text{LogL}[\text{samp}_{\text{surv}}(t)|\theta] \\ & + \sum_t \text{LogL} C(t|\theta) \\ & + \sum_t \text{LogL IA}(t|\theta) + \text{LogL}_{\text{sex}}(\theta) \\ & + \text{LogL}_M(\theta) + \text{LogL}_f(\theta) \end{aligned}$$

with

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

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

and

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

Following Drouineau et al. (2010), the log-likelihood is maximized using an evolutionary algorithm (Schwefel 1995)

Estimating growth parameters

The following procedure is used to estimate the log-likelihood $\text{LogL}_2(\theta_1)$: (1) given θ_1 , mean size-at-age $\mu_a(t)$ is computed for each age group and each time step (eq. 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 log-likelihood 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:

that provides a starting point to a quasi-Newton algorithm provided in the autodif library of AD Model Builder (AD Model Builder, <http://www.otter-rsch.com/>). The evolutionary algorithm is a stochastic algorithm that is relevant to explore highly dimensional objective functions and that 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) (Fisheries and Oceans Canada 2009). In 2008, the Gulf landings reached about 36 000 tonnes. 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 total allowable catch (TAC), and the number of fishing licenses is regulated. Fishing season starts on 1 April and closes when the TAC is reached or on 31 December at the latest. There is no fishing in winter mainly because the ice cover prevents access to fishing grounds.

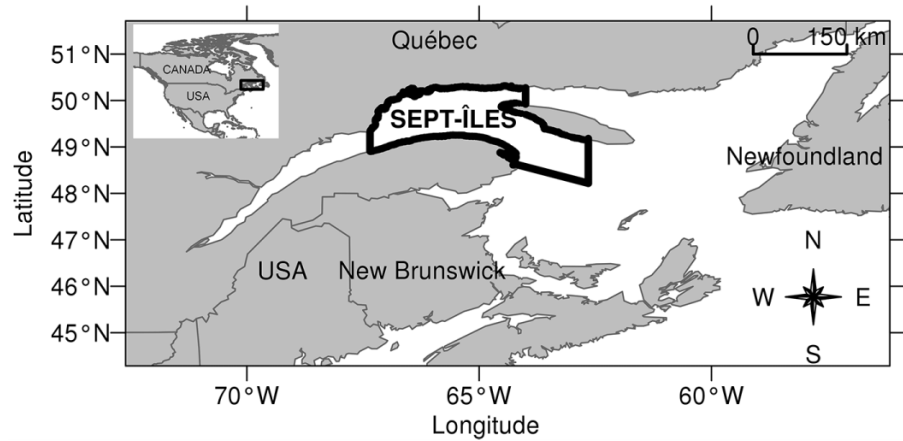
The fishery mainly targets large individuals, which are more economically valuable; therefore, fishermen allocate a large part of their effort in spring on reproductive females on hatching grounds. On average, females represented 68% of the Sept-Îles fishing area landings between 1990 and 2008.

Fishers are required to fill out a logbook, indicating the number of hours fished, and a dockside monitoring program ensures control over landings. Both logbook 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 8000 to 18 000 for the commercial sampling as well as for the survey.

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

Type of parameter	Parameter	No. 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 $N_m(1,a,\cdot), N_{primi}(1), N_{multi}(1)$	$A + 2$
	Yearly recruitment $N_m(y,1,\cdot)$	$Y - 1$
Commercial fishery	Selectivity L_{50}, R_f	2
	Catchability $q(y_0), \varepsilon_f(y_1), \varepsilon_f(y_2), \dots, \varepsilon_{sf}(y_{Y-1})$	Y
	Multiparous targeting $T_{spring,multi}$ for spring	1
Survey	Selectivity L_{50s}, R_s	2
	Catchability q_s	1

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



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 years old and measure between 8.0 and 12.0 mm. They are between 12.0 and 16.0 mm at 2½ years old, 16.0 and 19.0 mm at 3½ years old, and 19.0 and 23.0 mm at 4½ years old. 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 or 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 lowest 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 parameter values

Some specific parameter values were fixed for the Sept-Îles case study according to expert knowledge (Table 2). We set $\nu_{com} = \nu_{surv} = 100$, which corresponds to a CV of 10%. We set $\sigma_f = 0.05$, which corresponds to a random walk of CV of 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 interannual 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 $\sigma_{sex} = 0.10$.

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

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

The model includes four male age groups and is fitted over a 19-year 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 (Figs. 3a, 3b, and 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 that are aggregated on the hatching grounds. The model poorly fits summer catches for the last 2 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 1990s, 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 (Fisheries and Oceans Canada 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 (Fisheries and Oceans Canada 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 1 (Figs. 7 and 8) estimated by the model is variable, with two periods of higher recruitments in early 1990s and then in early 2000s. 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 4–5 years, probably because of the de-

creasing 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 years, 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 females 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 2000s 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 2 years and a substantial increase in fishing mortality since 2003.

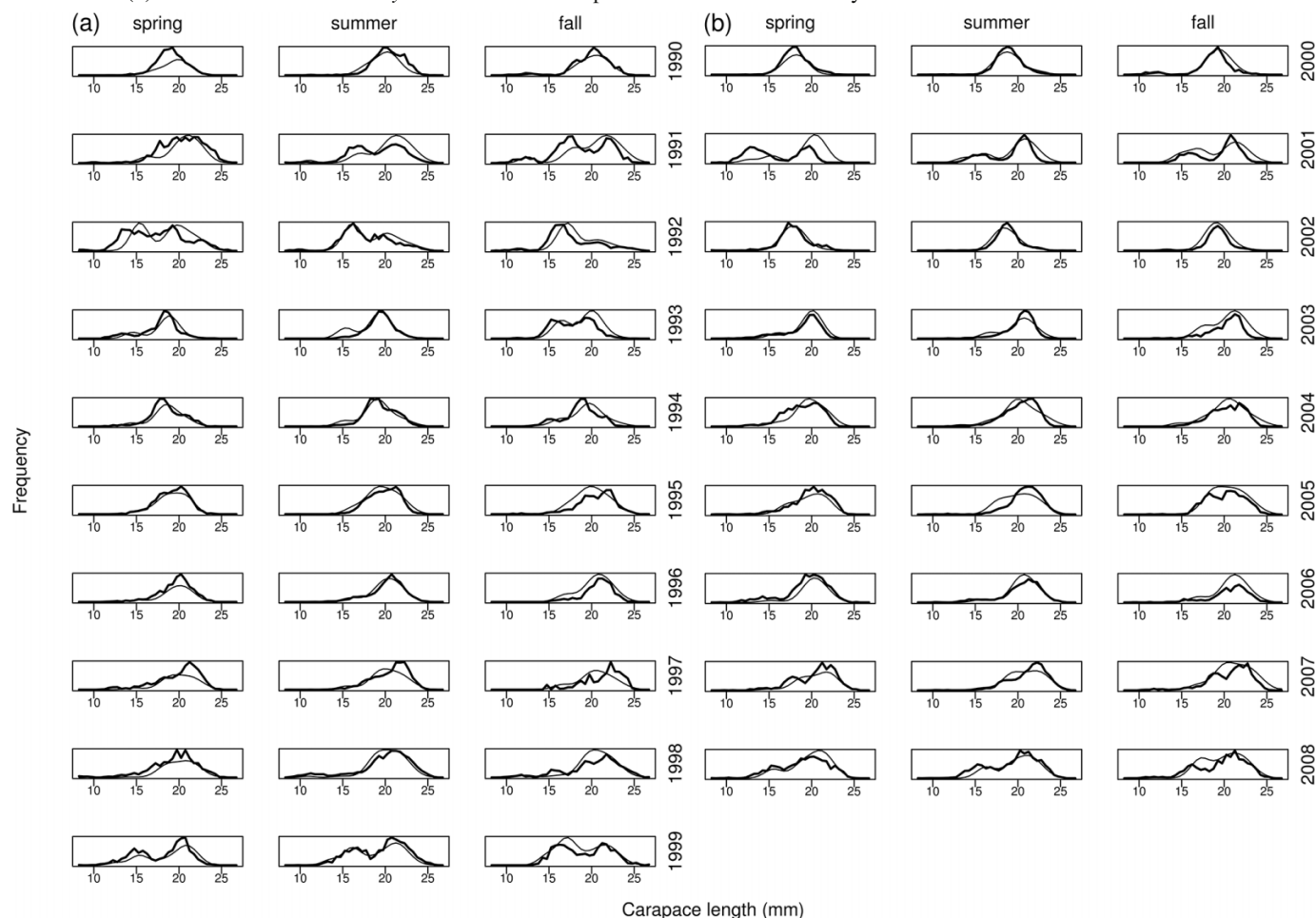
Year effects do not exhibit strong variations through the period; however, a model with a constant year effect was rejected by the Akaike information criterion (Akaike 1973).

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 (Fisheries and Oceans Canada 2009).

Fig. 3. Observed (thin lines) and estimated (bold lines) length composition of male commercial catches per season and per year from (a) 1990 to 1999 and (b) 2000 to 2008. Scales on y axes cannot be compared between seasons and years.



Discussion

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, species that changes sex and for whom aging after the sex change is difficult, if not impossible. Our model is a sex-structured model with a length-based sub-model for males and a simple stage-structured submodel for females. To characterize 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 provides 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 multi-

parous females, which can be distinguished by morphological differences.

The model demonstrates a high interannual 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 male 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

Fig. 4. Observed (thin lines) and estimated (bold lines) male length composition of survey catches. Scales on y axes cannot be compared between years.

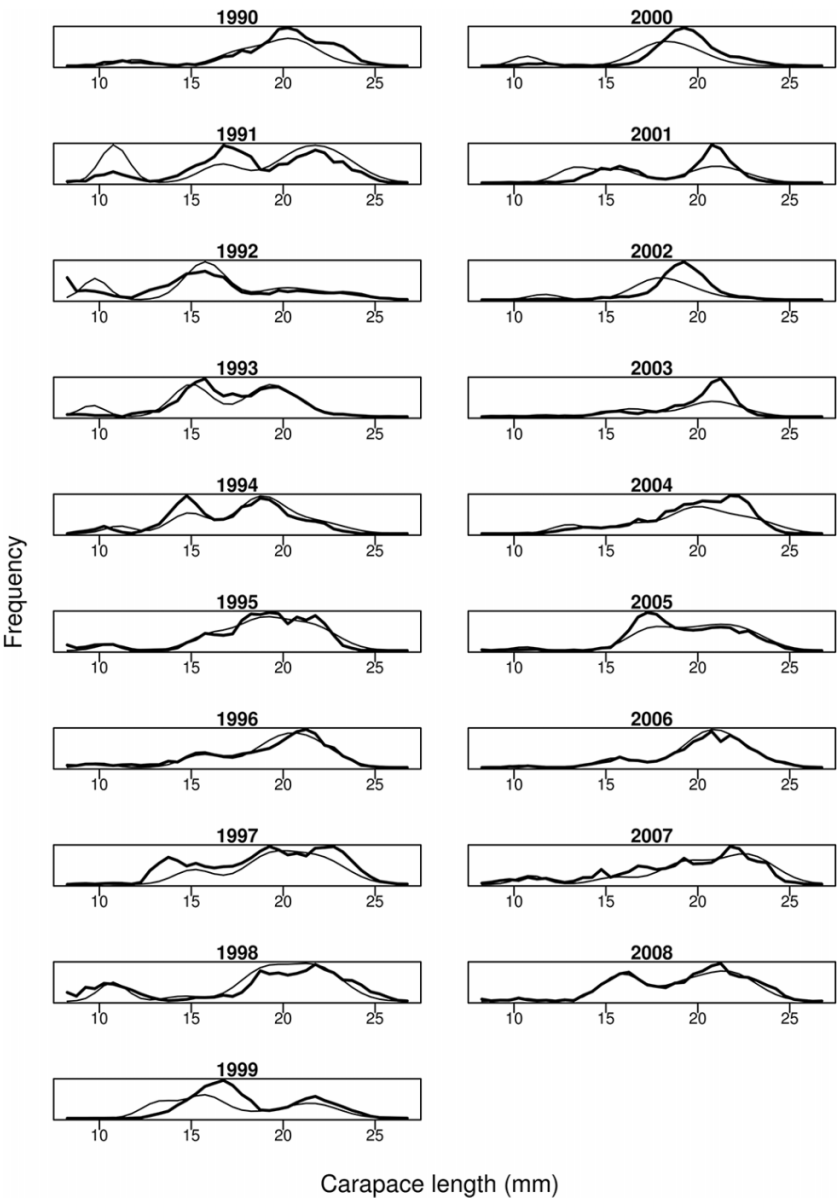


Fig. 5. Observed (bold solid line and squares) and estimated (thin solid line and circles) total commercial catches per season (spring: black symbols; summer: grey symbols; fall: open symbols) and year.

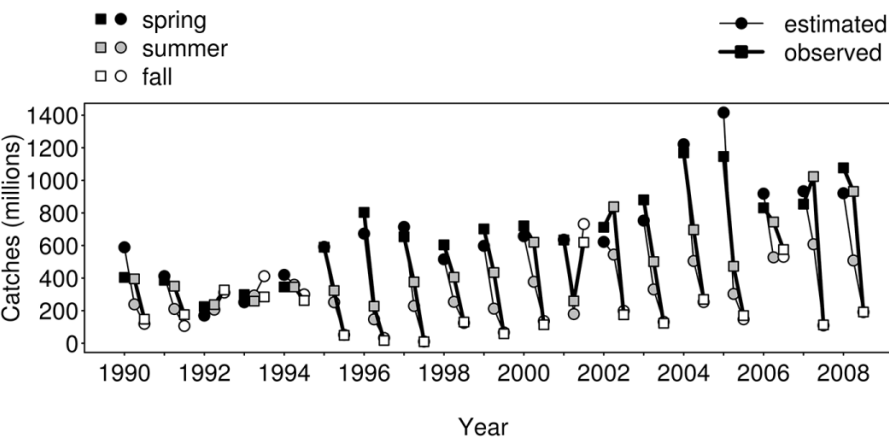


Fig. 6. Observed (bold line and squares) and estimated (thin line and circles) total survey abundances per year.

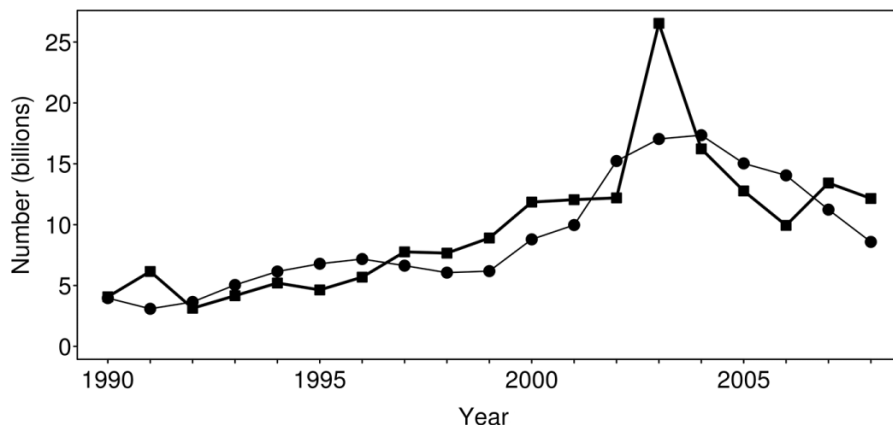


Fig. 7. Estimated recruitment at age 1.

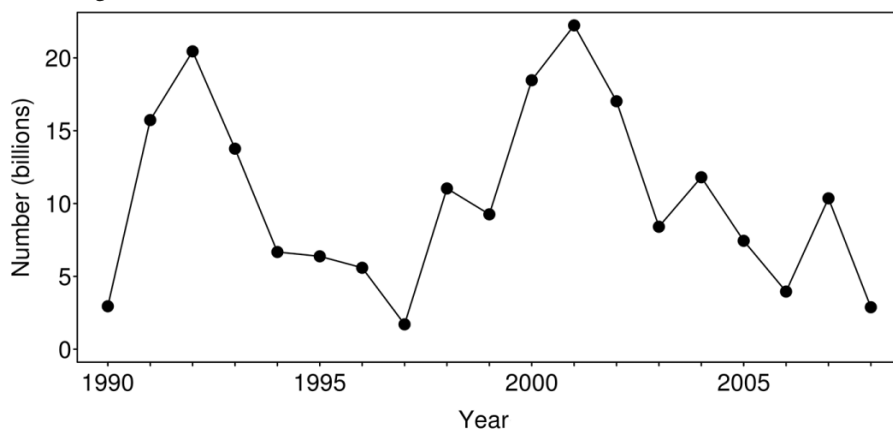
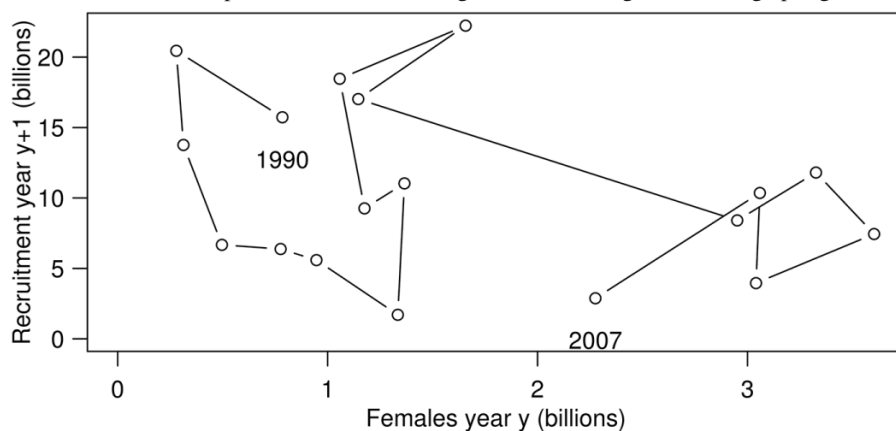


Fig. 8. Estimated stock–recruitment relationships: females in autumn against males of age 1 following spring.



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 Atlantic cod (*Gadus morhua*) and redfish (*Sebastes* spp.), which have decreased substantially in many of the northwest Atlantic shrimp fishing areas. Consequently, it may prove necessary in the future to de-

scribe 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 that are consistent with existing knowledge on the species and the stock (Fisheries and Oceans Canada 2009).

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). (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, indicated by a solid line).

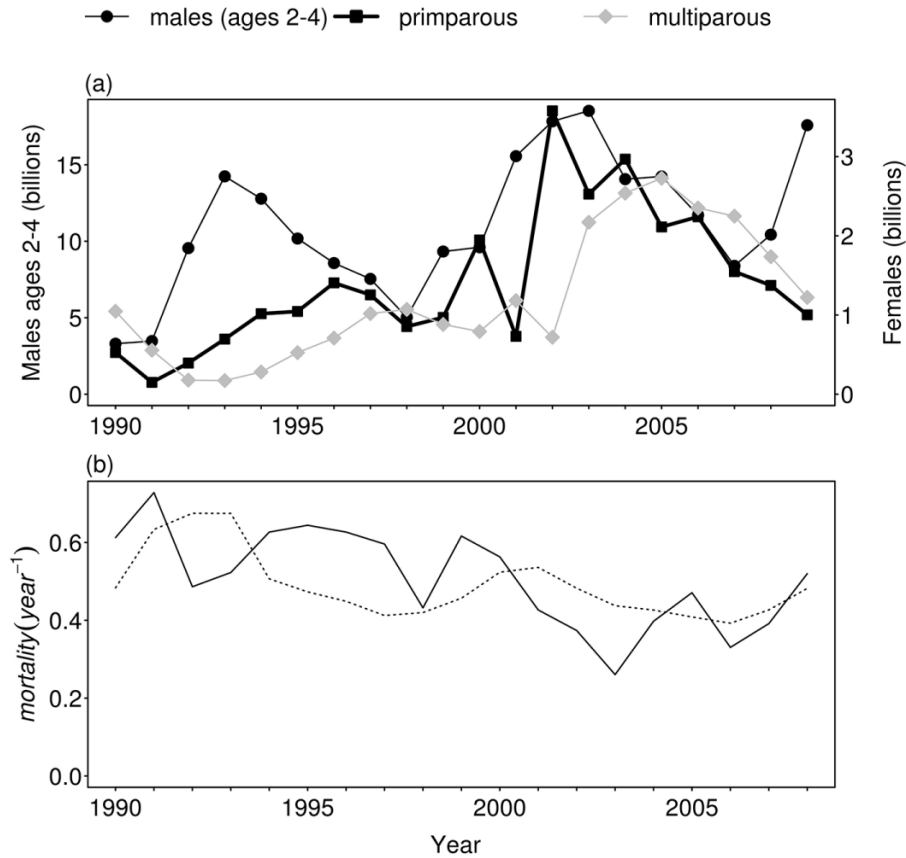
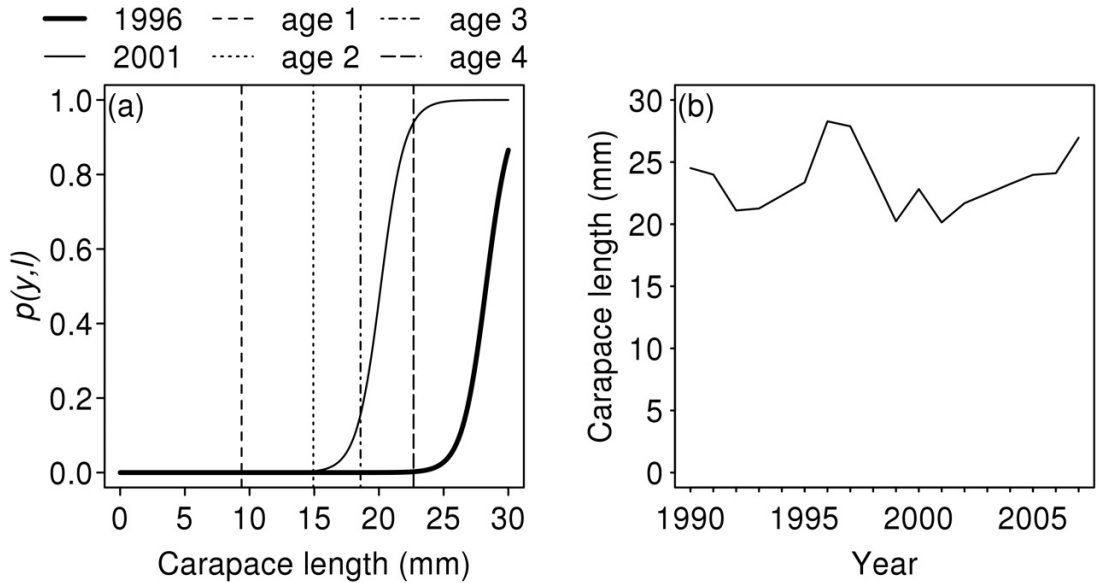


Fig. 10. Estimated ogive of sex change-at-length for two extreme years (end of year 1996 and end of year 2007; left) and evolution of $L_{50_{\text{sex}}}(y)$ over the period (right). Vertical dashed lines represent the mean sizes at the period of sex change of each male group $\mu_a = \sum_{y=y_0}^{y-1} \mu_a(t_1)/Y$ (with t_1 representing the spring of year y).



Weights on sex change (eq. 2; σ_{sex}), natural mortality (eq. 4; σ_M), and year effect random walks (eq. 10; σ_t) 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 (Catch–Survey–Analysis), 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 (Fisheries and Oceans Canada 2009) confirming a present high abundance level compared with the early 1990s. However, short- or medium-term projections are possible with SPAM, and consequently, managers may detect more quickly variations in abundance and adapt management measures (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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References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In 2nd International Symposium on Information Theory. Edited by B.N. Petrov and F. Csaki. Akademiai Kiado, Budapest, Hungary. pp. 267–281.

Bergström, B.I. 2000. The biology of *Pandalus*. Adv. Mar. Biol. **38**: 55–245. doi:10.1016/S0065-2881(00)38003-8.

Berkeley, A.A. 1931. The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. Fish. **6**(1): 79–163. doi:10.1139/f31-006.

Butterworth, D., and Punt, A. 1999. Experiences in the evaluation and implementation of management procedures. ICES J. Mar. Sci. **56**(6): 985–998. doi:10.1006/jmsc.1999.0532.

Cadrin, S.X. 2000. Evaluating two assessment methods for Gulf of Maine northern shrimp based on simulations. J. Northwest Atl. Fish. Sci. **27**: 119–132. doi:10.2960/J.v27.a11.

Cadrin, S.X., Clark, S.H., Schick, D.F., Armstrong, M.P., McCarron, D., and Smith, B. 1999. Application of catch–survey models to the northern shrimp fishery in the Gulf of Maine. N. Am. J. Fish. Manage. **19**(2): 551–568. doi:10.1577/1548-8675(1999)019<0551:AOCSTMT>2.0.CO;2.

Cadrin, S.X., Boutillier, J.A., and Idoine, J.S. 2004. A hierarchical approach to determining reference points for *Pandalid* shrimp. Can. J. Fish. Aquat. Sci. **61**(8): 1373–1391. doi:10.1139/f04-133.

Charnov, E.L., and Skuladottir, U. 2000. Dimensionless invariants for the optimal size (age) of sex change. Evol. Ecol. Res. **2**(8): 1067–1071.

Daoud, D., Lambert, Y., Audet, C., and Chabot, D. 2010. Size and temperature-dependent variations in intermolt duration and size increment at molt of northern shrimp, *Pandalus borealis*. Mar. Biol. (Berl.), **157**(12): 2655–2666. doi:10.1007/s00227-010-1526-1.

Drouineau, H., Mahévas, S., Bertignac, M., and Fertin, A. 2008. Assessing the impact of discretisation assumptions in a length-structured population growth model. Fish. Res. **91**(2–3): 160–167. doi:10.1016/j.fishres.2007.11.017.

Drouineau, H., Mahévas, S., and Bertignac, M. 2010. A length-structured spatially explicit model for estimating hake growth and migration rates. ICES J. Mar. Sci. **67**(8): 1697–1709. doi:10.1093/icesjms/fsq042.

Fisheries and Oceans Canada. 2009. Assessment of shrimp stocks in the Estuary and Gulf of St. Lawrence in 2008. DFO Can. Sci. Advis. Sec., Sci. Advis. Rep. 2009/001.

Food and Agriculture Organization of the United Nations. 2009. FAO Yearbook. Fishery Statistics 2008, I1013/T, Food and Agriculture Organization of the United Nations. Rome, Italy.

Fournier, D.A., Sibert, J.R., Majkowski, J., and Hampton, H. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Can. J. Fish. Aquat. Sci. **47**(2): 301–317. doi:10.1139/f90-032.

Fournier, D.A., Hampton, J., and Sibert, J.R. 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock-assessment, with application to South Pacific albacore, *Thunnus alalunga*. Can. J. Fish. Aquat. Sci. **55**(9): 2105–2116. doi:10.1139/f98-100.

Frøysa, K.G., Bogstad, B., and Skagen, D.W. 2002. Fleksibest — an age–length structured fish stock assessment model. Fish. Res. **55** (1–3): 87–101. doi:10.1016/S0165-7836(01)00307-1.

Fu, C., Quinn, T.J., II, and Shirley, T.C. 2001. The role of sex change, growth and mortality in *Pandalus* population dynamics and management. ICES J. Mar. Sci. **58**(3): 607–621. doi:10.1006/jmsc.2001.1050.

Haddon, M. 2001. Modelling and quantitative methods in fisheries. 2nd ed. Chapman & Hall, London, UK.

Hvingel, C., and Savard, L. 1997. Northern shrimp research in the North Atlantic — state of the art and future research strategy. TemaNord, **1997**: 592.

International Council for the Exploration of the Sea. 2001. Report of the *Pandalus* assessment working group, ICES CM 2001/ACFM:04, ICES, Copenhagen, Denmark.

International Council for the Exploration of the Sea. 2003. Report of the Working Group on *Nephrops* stocks, ICES CM 2003/ACFM:18, ICES, Copenhagen, Denmark.

- Koeller, P., Mohn, R., and Etter, M. 2000a. Density dependent sex change in northern shrimp, *Pandalus borealis*, on the Scotian Shelf. J. Northwest Atl. Fish. Sci. **27**: 107–118. doi:10.2960/J.v27.a10.
- Koeller, P., Savard, L., Parsons, D.G., and Fu, C. 2000b. A precautionary approach to assessment and management of shrimp stocks in the northwest Atlantic. J. Northwest Atl. Fish. Sci. **27**: 235–246. doi:10.2960/J.v27.a20.
- Koeller, P.A., Covey, M., and King, M. 2003. Is size at sex transition an indicator of growth or abundance in pandalid shrimp? Fish. Res. **65**(1–3): 217–230. doi:10.1016/j.fishres.2003.09.016.
- Mauder, M.N., and Watters, G.M. 2003. A-SCALA: un analisis estadístico de captura a talla estructurado por edad para la evaluación de las poblaciones de atunes en el océano pacífico oriental. Bull. I-ATCC, **22**(5): 531–581.
- McCrary, J.A. 1971. Sternal spines as a characteristic for differentiating between females of some pandalidae. J. Fish. Res. Board Can. **28**(1): 98–100. doi:10.1139/f71-014.
- McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. Chapman & Hall, London, UK.
- North Atlantic Fisheries Organization / International Council for the Exploration of the Sea. 2008. Report of the NAFO/ICES *Pandalus* Assessment Group, NAFO SCS Doc. 08/25;ICES CM 2008/ACOM:11, NAFO/ICES, Copenhagen, Denmark.
- Ouellet, P., Savard, L., and Larouche, P. 2007. Spring oceanographic conditions and northern shrimp *Pandalus borealis* recruitment success in the north-western Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. **339**: 229–241. doi:10.3354/meps339229.
- Ouellet, P., Fuentes-Yaco, C., Savard, L., Platt, T., Sathyendranath, S., Koeller, P., Orr, D., and Siegfstad, H. 2011. Ocean surface characteristics influence recruitment variability of populations of northern shrimp (*Pandalus borealis*) in the Northwest Atlantic. ICES J. Mar. Sci. **68**(4): 737–744. doi:10.1093/icesjms/fsq174.
- Punt, A.E. 2003. The performance of a size-structured stock assessment method in face of spatial heterogeneity in growth. Fish. Res. **65**(1–3): 391–409. doi:10.1016/j.fishres.2003.09.028.
- Punt, A.E., and Donovan, G.P. 2007. Developing management procedures that are robust to uncertainty: lessons from the International Whaling Commission. ICES J. Mar. Sci. **64**(4): 603–612. doi:10.1093/icesjms/fsm035.
- Quinn, T.J., Turnbull, C.T., and Fu, C. 1998. A length-based model for hard-to-age invertebrate populations. Proc. Symp. Fishery Stock Assess. Models 21st Cent. Alaska Sea Grant College Program, Fairbanks, Alaska. pp. 531–556.
- Sainsbury, K., Punt, A., and Smith, A. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. ICES J. Mar. Sci. **57**(3): 731–741. doi:10.1006/jmsc.2000.0737.
- Schwefel, H.P. 1995. Evolution and optimum seeking. Wiley & Sons, New York.
- Shumway, S.E., Perkins, H.C., Shick, D.F., and Stickney, A.P. 1985. Synopsis of biological data of the pink shrimp, *Pandalus borealis*, (Krøyer 1838), FAO Fisheries Synopsis No. 44. National Oceanic and Atmospheric Administration Technical Report of the National Marine Fisheries Services 30, Seattle, Washington.
- Smith, M.T., and Addison, J.T. 2003. Methods for stock assessment of crustacean fisheries. Fish. Res. **65**(1–3): 231–256. doi:10.1016/j.fishres.2003.09.017.
- Wieland, K. 2004. Length at sex transition in northern shrimp (*Pandalus borealis*) off West Greenland in relation to changes in temperature and stock size. Fish. Res. **69**(1): 49–56. doi:10.1016/j.fishres.2004.04.003.