Title: Evaluation of the sensitivity of biological reference points to the spatio-temporal distribution of fishing effort when seasonal migrations are sex-specific.

Author:

Hiroshi Okamura

National Research Institute of Fisheries Science, Fisheries Research Agency, 2-12-4
Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan
okamura@fra.affrc.go.jp

Murdoch K. McAllister

UBC Fisheries Centre, 2202 Main Mall, Vancouver, B.C. V6T 1Z4, Canada
m.mcallister@fisheries.ubc.ca

Momoko Ichinokawa

National Research Institute of Fisheries Science, Fisheries Research Agency, 2-12-4
Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan
ichimomo@fra.affrc.go.jp

Lynne Yamanaka

Pacific Biological Station, 3190 Hammond Bay Rd, Nanaimo, BC V9T 6N7, Canada
Lynne.Yamanaka@dfo-mpo.gc.ca

Kendra Holt

Pacific Biological Station, 3190 Hammond Bay Rd, Nanaimo, BC V9T 6N7, Canada
Kendra.Holt@dfo-mpo.gc.ca

Corresponding author:

Hiroshi Okamura (email: okamura@fra.affrc.go.jp, tel: +81-45-788-7645, address:
National Research Institute of Fisheries Science, Fisheries Research Agency, 2-12-4
Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan)

ABSTRACT

Offshore lingcod (*Ophiodon elongatus*) in British Columbia (B.C.) make seasonal migrations that differ by sex: in winter most adult males aggregate in shallow water and most adult females aggregate in deep water, while in summer both sexes distribute equally in deep and shallow water. We developed a semi-age structured delay-difference model that accommodates sex-, and age/depth-specific seasonal migration and examined the sensitivity of biological reference points for B.C. offshore lingcod to migration pattern and the allocation of fishing effort across seasons and depths. When a migration pattern with a homogeneous distribution of males and females in shallow and deep water throughout the year was assumed, the estimated maximum sustainable yield (MSY), biomass at MSY (B_{MSY}), and percent spawning per recruitment at MSY ($\%SPR_{MSY}$) were robust to changes in effort allocation. However, when a migration pattern that assumed a winter distribution of 95% of adult males in shallow water and 95% of adult females in deep water was used, the estimated MSY, B_{MSY} , and $\%SPR_{MSY}$ were markedly sensitive to changes in effort allocation. These results suggest that incorporating sex-, age/depth-, and season-specific structuring in stock assessment models could enable improved evaluations of management options for B.C. lingcod and other species with sex- and season-specific migrations.

Keywords: Biological reference point; delay-difference model; *Ophiodon elongates*; sex-specific migration

1. Introduction

The distribution and movement of fish are important components for conservation and fisheries or ecosystem management (Walters and Martell, 2004). Because fish often use spatially and temporally different habitats, the efficacy and efficiency of conservation measures and management tools can depend on the types of spatial and temporal restrictions placed on fishing effort. For example, marine protected areas, the restriction of fishing seasons, and modifications and/or bans of certain types of fishing gear are important fishery management tools that act by changing the intensity and distribution of fishing effort (Hilborn and Walters, 1992; Pauly et al., 2002; Roberts et al., 2005). However, relatively few quantitative assessments of the effects of spatial and temporal management tools on fish populations and biologically-based reference points have been conducted. To properly evaluate the potential impacts of spatial and temporal management on dynamic fish populations, an appropriately structured mathematical model describing fish population dynamics is essential (Punt et al., 2000).

One of the most important quantities in fisheries management is maximum sustainable yield (MSY), which has been criticized in the past (Larkin, 1977), but recently reevaluated (Mace, 2001; Punt and Smith, 2001) and is still widely used as a principal biological reference point (Hilborn and Hilborn, 2012). Seasonal movements of different components of an exploited fish population, e.g., by age and sex, can cause spatio-temporal variation in the population's vulnerability to exploitation when fishing effort has seasonal and spatial structuring (Sampson and Scott, 2011). Incorrect assumptions about such spatio-temporal movements in a stock assessment may lead to biased estimation of reference points (Carruthers et al., 2011; Taylor et al., 2011). Thus,

there is a need to develop tools to quantitatively evaluate the impacts of different spatial and temporal management options on MSY-based reference points.

British Columbia's (B.C.) offshore lingcod (*Ophiodon elongatus*) stocks, which are an important component of commercial and recreational fisheries on Canada's west coast, provide an interesting case study with which to examine the effect of spatial and temporal management tools on fisheries reference points. Lingcod are generally considered a non-migratory species because they do not move long distances. They do however make seasonal migrations each year to and from the spawning grounds, with males and females displaying different migration patterns (Cass et al., 1990; Martell et al., 2000). Spawning closures by depth and season have been used as a management tool for lingcod populations in B.C., as well as Pacific United States (US) fisheries jurisdictions, since the 1930's.

We develop a population dynamics model that incorporates sex-specific spatial and temporal lingcod movement and examines the impacts of differing vulnerability patterns by sex and age on biological reference points such as MSY using B.C. offshore lingcod data. First, we specify a population dynamics model that explicitly accounts for spatial movement patterns by lingcod and their multiple fisheries with differing ages at recruitment. The sensitivity of biological reference points to the spatio-temporal distribution of fishing effort is then evaluated using deterministic and stochastic predictions from the population dynamics model. The deterministic evaluation shows how the biological reference points change depending on movement patterns and the stochastic simulation provides information on the effect of uncertainty in the estimation of biological reference points and robustness of results of the deterministic evaluation.

2. Methods

2.1. Lingcod off British Columbia

B.C. offshore lingcod stocks are assessed and managed as four separate areas based on the Department of Fisheries and Oceans Canada (DFO) Statistical Areas: 3C, 3D, 5AB, and 5CDE (King et al., 2012). Tagging studies in British Columbia have shown that once lingcod reach maturity, they tend to stay close to their natal area. One study on the outer coast of Vancouver Island (Area 3C) found that 95% of tagged fish were recovered within 10 km of the tagging location, and that only a few individuals migrated beyond 50 km (Cass et al., 1990). While tagging studies have shown that adult migration is likely small, more work is needed to examine the stock assessment assumption that each management area in B.C. is a separate stock. In this paper, we treat the population in each area as independent and focus on Area 3C which covers the southwest coast of Vancouver Island, B.C. and is the most important fishing region.

B.C. lingcod are caught by multiple fisheries (commercial trawl and hook and line, and recreation hook and line). Commercial fishing for lingcod began before the 1900s (King et al., 2012), but the available catch statistics in Area 3C date from 1927. The commercial trawl and hook & line landings were similar and low before 1950. Since the 1960s, trawl landings have dominated (Fig. 1). Trawl landings increased from the 1950s and peaked at about 3,400 metric tonnes (mt) in 1985. Trawl catches remained high in the early 1980s, and then dropped gradually to less than 500 mt. Hook & line landings peaked at 295 mt in 1957 and then dropped to less than 100 mt. Records of recreational hook and line catches are not available for years prior to 1983 but are considered low and increased from 0 mt in 1927 to 7 mt in 1983 (King et al., 2012). After 1983,

available records have not shown any clear trend and are less than 20 mt (King et al., 2012).

These three fisheries target different depth distributions, and as a result, have been subject to different seasonal closures over time. At present, the commercial and recreational hook & line lingcod fishery is closed annually from November 15 to April 1 for the protection of male lingcod guarding nests. Commercial trawl fisheries are allowed to target lingcod during winter months because they typically occur at greater depths than nest sites.

Maturity ogives and weight at age curves by sex were inferred from the fishery sample data (King et al., 2012). The logistic curves were fitted to each maturity status dataset by sex and the von Bertalanffy growth curves and the allometry curves were fitted to each length at age and weight-length dataset by sex. The maturity curves were discretized to the probability of maturity at age by sex and the weight at age curves were transformed to the linear model to get the coefficients needed for the delay-difference model (Hilborn and Walters, 1992; Quinn and Deriso, 1999; and see Appendix).

Cass et al. (1990) noted that between May and September, both male and female lingcod are captured on nearshore trawling grounds in British Columbia. During the winter, trawl catches of male lingcod drop steeply as individuals begin to aggregate inshore in October. Females spend a shorter amount of time on the spawning grounds and are more likely to be caught by trawl fisheries in the winter than males. Available biological samples from B.C. bottom trawl fisheries (1977-2011) show that during the winter months (October 1 - March 30), in depths greater than 50 m and 120 m, more than 80% and 95%, respectively, are females. The long history of winter closures for B.C. lingcod fisheries precludes the collection of sufficient data to show a

corresponding increase in male sex-ratios at shallow depths (< 50 m); however, fishery samples from southeast Alaska have shown this pattern (Gordon, 1994).

We prepared two movement patterns to evaluate the sensitivity of biological reference points to the spatio-temporal distribution of fishing effort (Table 1). In this study, season consists of summer and winter, and depth consists of shallow (< 50 m) and deep (≥ 50 m). The first pattern (Pattern 1) whose components in the matrix are all 0.5 is adopted as a reference pattern and has no spatial effect, i.e., different fishing effort allocations are expected to have no effect on biological reference points. The second pattern (Pattern 2) describes a migration where in winter most adult males aggregate in shallow water and most adult females aggregate in deep water, while in summer both sexes distribute equally among deep and shallow water. Male and female juvenile lingcod distribute in only shallow water in both seasons in Pattern 2. While the values in this pattern are hypothetical, they represent the general pattern that has been observed for lingcod populations (Cass et al., 1990; Gordon, 1994; Martell et al., 2000).

2.2. Population dynamics model

The population dynamics model of lingcod is described in the Appendix and is based on a delay-difference model (Deriso, 1980; Schnute, 1985, 1987; Hilborn and Walters, 1992; Quinn and Deriso, 1999). To allow for heterogeneous effects, we developed a spatially-explicit semi-age-structured delay-difference model. The delay-difference model is an intermediate model between biomass dynamic models, such as a production model, and fully age-structured models, such as virtual population analysis and statistical catch-at-age models, and has moderate data requirements. The population dynamics model consists of two age groups: the first one has ages between $k_{\min}$ and $k_{\max}$

– 1, and the second one has ages equal to and greater than $k_{\max}$. $k_{\min}$ is the youngest age among ages at recruitment by different fisheries and the age of full maturation, while $k_{\max}$ is the oldest age among them. The population dynamics with ages between $k_{\min}$ and $k_{\max} - 1$ is described by a fully age-structured model, while the population dynamics with ages equal to and greater than $k_{\max}$ is described by an ordinary delay-difference model (Appendix). The population is assumed to have been at its pre-exploitation equilibrium at the start of the available catch time series in 1927.

Catch time series in Area 3C from 1927 to 2012 was used in the model. B.C. offshore lingcod are caught by multiple fisheries (commercial trawl, commercial hook and line, and recreational hook and line) that have different ages at recruitment and seasonal openings (Appendix). The catch data was disaggregated by different fisheries, season (summer/winter), and depth (< 50 m/ ≥ 50 m). The knife-edged ages at recruitment for each fishery assumed in the model were determined by evaluating the catch-at-age data of B.C. lingcod in the commercial trawl (12 years between 1977 and 2006) and commercial hook and line fisheries (1989, 1991), and average body size of lingcod in the recreational hook and line fisheries (Leaman and McFarlane, 1997; King et al., 2012). Where age frequencies were available, they were pooled for decadal periods and the first age with non-negligible frequency (i.e., $> 20\%$ of the average non-negative age frequency) was taken as the recruitment age. The very low average round weight (1.6 kg) observed for recreationally caught offshore lingcod prior to 1999 (Leaman and McFarlane, 1997) suggested a very low age at recruitment (i.e., about 1 year) for years up to 1998. Due to the implementation of a 65 cm minimum size limit for recreationally caught Area 3C lingcod in 1999, the age of recruitment to the recreational fishery was set at 4 years for 1999 and after.

Survival is a product of ratios of survivors by natural mortality and fishing mortality. The component related to fishing mortality uses information on maturity status and sex-dependent vertical movement by fish (Table 1 and see the equation of $S_{a,t}^g$ in Appendix).

The reproduction function is given by the Beverton-Holt function, although the Ricker function is used as a sensitivity test. Because reproduction of B.C. lingcod occurs between summer and winter, the spawning biomass is the mature female component that has been reduced by natural and fishing mortality in summer (Eq. (A.4) in Appendix). The parameters of the stock-recruitment function are obtained as functions of steepness, which is the ratio of recruitment at 20% of the unexploited biomass to recruitment in the unfished state, and the initial biomass B_0 (Forrest et al., 2010).

The assumed biological parameters other than the movement pattern are listed in Table A1 of the Appendix. The steepness parameter was assumed to be 0.8 corresponding to the value for lingcod used in King et al. (2012).

MSY is estimated by finding constant fishing mortality to maximize catch under equilibrium. For simplicity, we assumed that fishing mortality, except in the trawl fishery, is zero when estimating MSY, because the proportion of trawl landings in the catch is substantial (76% ~ 94% for recent 10 years, Fig. 1). The results will not change substantially even if more detail on the actual fishing operations is modeled (e.g., maintaining constant relative fishing mortality rates between the fisheries).

2.3. Sensitivity of biological reference points to different distributions of fishing effort

First, we examined the sensitivity of biological reference points to the distribution of

fishing effort among seasons and depth bins using deterministic models. The distribution of fishing effort is defined by weighting values between 0 and 1 for season and depth. w_S is the effort allocation for season. When $w_S = 0$, 100 percent of effort is allocated to summer. When $w_S = 1$, 100 percent of effort is allocated to winter. w_D is the effort allocation for depth. When $w_D = 0$, 100 percent of effort is allocated to shallow waters (less than 50 m). When $w_D = 1$, 100 percent of effort is allocated to deep waters (equal to and greater than 50 m). Assuming that the steepness parameter is 0.8 and the initial biomass B_0 is 50,000 (King et al., 2012), we examined how MSY, B_{MSY} (Biomass at MSY), and $\%SPR_{MSY}$ (SPR = Spawning Per Recruitment and $\%SPR_{MSY} = SPR$ with constant fishing at the MSY level divided by SPR without fishing; Mace and Sissenwine, 1993) changed when w_S and w_D were changed. The weighting values were changed by the interval of 0.1.

Second, we examined the sensitivity of biological reference points to different movement patterns and effort allocation using stochastic models. The stochastic calculation is based on a Monte Carlo simulation. Relative indices of abundance of lingcod in Area 3C all showed high levels of interannual variability and have not yet been disaggregated by season and depth (King et al., 2012). The only available time series data used in the model were catch series for the different fisheries. We used initial biomass (B_0) and steepness (h) as Monte Carlo-drawn input parameters. We assumed that B_0 has the uniform distribution $U[5000, 200000]$ with increment of 100 and h has the uniform distribution $U[0.5, 0.9]$ with increment of 0.1. This procedure could be considered a Bayesian approach in which the likelihood function has a value of 0 if negative estimated biomasses are present and has a value of 1 otherwise (Dick and MacCall, 2011). The grid approximation method was used for calculating the posterior

distribution of B_0 and h (Gelman et al., 2004). All catch data from the three fisheries (Fig. 1) were used to estimate B_0 and h . The posterior distributions of MSY and B_{MSY} were calculated using the corresponding posterior probability on B_0 and h . MSY/B_{MSY} is estimated under a single fishery with the same age at recruitment as the trawl fishery. We drew 1,000,000 values from the posterior probability of B_0 and h and calculated posterior medians and credible intervals of MSY and B_{MSY} by sex. The following four model scenarios were used:

SC1. Pattern 1 as a movement pattern & $w_S = 0.5$ & $w_D = 1.0$

SC2. Pattern 2 as a movement pattern & $w_S = 0.5$ & $w_D = 1.0$

SC3. Pattern 2 as a movement pattern & $w_S = 1.0$ & $w_D = 0.2$

SC4. Pattern 2 as a movement pattern & $w_S = 1.0$ & $w_D = 0.0$

The effort allocation values of first two scenarios correspond to the recent catch distribution of the trawl fishery, which has, on average, almost equal amounts of catch taken in summer and winter and no (or very few) catches taken in depths less than 50 m over the last 10 years. The third and fourth scenarios have the same movement pattern as scenario 2, but the values of effort allocation are different. The effort allocations of scenarios 3 and 4 are based on the values that gave the highest MSY and the highest $\%SPR_{MSY}$ in the deterministic run, respectively.

3. Results

As expected, using Pattern 1 in deterministic model runs, MSY , B_{MSY} (scaled to B_0), and $\%SPR_{MSY}$ did not change very much ($CV < 5\%$) as expected when w_S and w_D were changed from 0 to 1 (Fig. 2). Because Pattern 1 has a uniform probability distribution

on vertical movement, all quantities are insensitive to the effort allocation of depth. MSY values when $w_S = 1$ (winter) are slightly larger than those when $w_S = 0$ (summer) because reproduction occurs between summer and winter, which means fishing in winter allows higher catches.

Using Pattern 2 in deterministic model runs, MSY, B_{MSY} , and $\%SPR_{MSY}$ changed greatly ($CV = 5 \sim 20\%$) and nonlinearly when w_S and w_D were changed from 0 to 1 (Fig. 2). The standard deviations of MSY were 15.3 for Pattern 1 and 118.3 for Pattern 2 so that the ranges of MSY for Pattern 1 and Pattern 2 were 1,700–1,748 mt and 1,138–1,815 mt, respectively. The magnitude of changes in B_{MSY} for Pattern 2 was also larger than for Pattern 1 and the degree of difference was similar to MSY (the ratio of standard deviations for B_{MSY} of Pattern 1 and Pattern 2 was 8.1 while that for MSY was 7.7). The values of $\%SPR_{MSY}$ varied considerably and increased in a linear fashion diagonally from the lower left to the upper right (the right panel of Fig. 2c). The maximum value of $\%SPR_{MSY}$ at the upper-right corner was 0.72 and the minimum value at the left corner was 0.27.

Fig. 3 provides the medians, 5%-iles, and 95%-iles of sex-specific MSY and B_{MSY} in stochastic model runs. Total values (both sexes combined) are fairly sensitive to the different scenarios, and the values for males and females are markedly different between the scenarios. Between scenarios 1 and 2, MSYs and B_{MSY} s for females were similar, while B_{MSY} for males of scenario 2 was larger than scenario 1 and MSY for males of scenario 2 was smaller than scenario 1. Scenarios 3 and 4 had considerably larger B_{MSY} for females and smaller B_{MSY} for males. MSYs for males in scenarios 3 and 4 were larger than scenario 2, but MSYs for females were larger for scenario 3 and smaller for scenario 4. Scenario 3 had the highest MSY among scenarios with Pattern 2. MSY was

sensitive to different effort scenarios for Pattern 2 with the MSY ranging from about 3,165 to 3,685 mt for scenarios 4 and 3, respectively. B_{MSY} was similarly sensitive with values ranging from 50,418 to 64,683 mt for scenarios 3 and 4.

We conducted sensitivity tests using different stock-recruitment curves (Ricker). The results were not different qualitatively and the general trends were similar (not shown here).

4. Discussion

Deterministic model runs showed MSY-related parameters changed markedly and nonlinearly when sex-specific seasonal migrations and different seasonal and depth-specific fishing practices were modeled (i.e., using Pattern 2). It is well known that reference points are sensitive to changes in selectivity. When the w_S and w_D parameters were changed under Pattern 2, this was analogous to changing the sex and age-specific selectivity of the fishing gear, even though it was not modeled as such.

Ignoring movement effects (i.e., using Pattern 1), $\%SPR_{MSY}$ was consistently about 35% across the full range of allocations of fishing effort to different depths and seasons. This value is close to that commonly recommended in fisheries management as a proxy of B_{MSY} (Mace and Sissenwine, 1991; Brodziak, 2002). However, taking fish movement into account (Pattern 2), $\%SPR_{MSY}$ fluctuated greatly and increased with increasing concentration of effort in the winter and in shallower depths, i.e., approximately diagonally from the lower left to the upper right (Fig. 2). Using Pattern 2, there are few females in the shallow water in winter. Thus the upper-right effort allocation using Pattern 2 gives protection to spawning biomass and the existence of an untouched

female population leads to higher spawning biomass at equilibrium. This indicates that the value of $\%SPR_{MSY}$ is sensitive to the fish's behavior and effort allocation by season and depth so that the fishing rate $F_{\%SPR}$, which is commonly used for fisheries management, could be less reliable as a surrogate of F_{MSY} unless spatial and temporal movement by sex is suitably considered in the model.

We caution however that some important behavioral attributes of lingcod were ignored in the analysis that could have substantial impacts on the results for this species. Mature male lingcod remain over nests to guard eggs in the winter whereas mature females retreat quickly to deep water following spawning (Cass et al., 1990). Male lingcod are known to aggressively guard fertilized eggs against egg predation from a variety of fish and invertebrate species and forego foraging for up to seven weeks following spawning (Low and Beamish, 1978; Withler et al., 2004). Thus, while managing lingcod fisheries using the effort distribution from the upper right corner of Fig. 2 (fishing occurs in winter at shallow depths) combined with Pattern 2 may protect spawning biomass in the short-term by protecting females, it is unknown how it would affect overall reproductive success. Our results could therefore change significantly if the relationship between mature male biomass and reproductive success were more realistically represented in our model. The current ban on hook and line-fishing for lingcod in winter months in B.C. was intended to protect nest guarding mature males (King et al., 2012), thus current lingcod fishery management actually acts to avoid the effort distribution from the upper right corner of Fig. 2. Should this winter fishery be reopened and permitted to capture nest guarding males, this could result in accelerated mortality rates for nest guarding males and poorer survival of eggs when nest guarding males are removed by exploitation. We do not suggest using the study's current results

for management as further work is needed to account for the potential reduction in egg survival in scenarios in which fishing in shallower depths during the winter was permitted.

In stochastic model runs, both B_{MSY} and MSY were considerably different among scenarios (Fig. 3). The optimum effort allocation in the deterministic run (i.e., the star mark in Fig. 2) combined with Pattern 2 (SC3 in Fig. 3) gave the highest MSYs for both sexes among scenarios. Using scenario 4, which used the upper-right effort allocation in Fig. 2, resulted in a B_{MSY} for females that was considerably higher than other scenarios. This result occurs for the same reason as the higher $\%SPR_{MSY}$ seen for the upper-right effort allocation in Fig. 2, i.e., automatic protection of spawning biomass. On the other hand, B_{MSY} for males was considerably lower in scenario 4 than scenario 2, which used the same Pattern 2, while MSY for males was higher in scenario 4 than in scenario 2 (Fig. 3). Given that these breakdowns by sex for both MSY and B_{MSY} are markedly different among scenarios, the proportion of males and females in catch could impact population dynamics. These results highlight that for species such as lingcod that have sex-specific seasonal migration patterns, records of sex ratio in landings are important information to support fisheries assessment and management. In such cases, careful effort allocation and/or gear selectivity measures that take sex effects into account could improve yields without compromising the productive capacity of the stock. In addition, more detailed information on sex-specific seasonal movement could lead to more efficient fisheries management by helping to improve the parameterization of spatially-structured stock assessment and management models. Tagging studies could provide the movement information that would be required (Punt et al., 2000).

The robustness from the sensitivity analyses using a different stock-recruitment curve

indicates that the sensitivity of biological reference points to sex- and season-specific migrations may apply to a broad range of parameters and model structures. In this study, only catch was used as time series data. If there were standardized catch rate data (Maunder and Punt, 2004), we could have assessed impacts on biological reference points under different scenarios of fish movement and fishing effort allocation with greater precision than in the current analysis.

We used a grid approximation method for calculating posterior distributions of parameters in the stochastic runs. If there were catch rate data, a more flexible model such as the state-space model (Millar and Meyer, 2000), could be used and a more advanced technique for Bayesian integration like the Sampling-Importance Resampling method (McAllister and Ianelli, 1997) and Markov chain Monte Carlo method (Gelman et al., 2004) would be needed.

The delay-difference model has fewer parameters than a fully age-structured model and thus faster calculations are expected when using the delay-difference model. When there are fewer data available, we could still estimate parameters by the delay-difference model. This is the case especially when there are multiple fisheries. Having a model with fewer estimated parameters like the delay-difference model but has the flexibility to include different fisheries with different median ages of recruitment is an advantage over the simpler delay-difference model which assumes only one age at recruitment that equals the median age at maturity.

The delay-difference model has a potential advantage over a fully age-structured model when it comes to modeling seasonal and spatial movements of different age and sex groups due to its more compact formulation. Again, fewer parameters need to be estimated in the delay-difference model than the age structured model when it comes to

modeling sex-, season-, and age-specific movements. The application of more compact yet biologically detailed models such as the delay-difference model could enable an improved empirical and statistical basis for the evaluation of fine-scale spatio-temporal management of multiple fisheries. The progressive improvements in the design of fishing gear, vessel monitoring systems and fish population sampling methods (e.g., Block et al., 2005; Taylor et al., 2011) may help to facilitate such refinements in fisheries assessment and evaluations of management options.

Acknowledgements

The research in this paper was supported by the NSERC funded Canadian Fisheries Research Network and JST, CREST. The authors thank all participants of the Selectivity Workshop (CAPAM) held in La Jolla in March, 2013, Jackie King, Tom Carruthers, Carl Walters, Mark Maunder, and two anonymous reviewers for their helpful suggestions and discussions. Robert Flemming, Kate Rutherford and Brian Krishna are thanked for providing data used in the analyses.

Appendix.

Suppose that each fishery i ($i = 1, \dots, n$) has the specific age at 50% vulnerability, k_i . The minimum ages at 50% vulnerability in all the fisheries is $k_{\min} = \min(k_{\text{mat}}, \min_i k_i)$. $k_{\max} = \max(k_{\text{mat}}, \max_i k_i)$ where k_{mat} = age of full maturation. Now we have $k_{\min} = 1$ and $k_{\max} = 9$ for outside lingcod in Area 3C. The biomass B_t in year t can then be written as follows:

$$\begin{aligned}
B_t^g &= \sum_{a=k_{\min}}^{\infty} N_{a,t}^g w_a^g \\
&= \sum_{a=k_{\max}}^{\infty} N_{a,t}^g w_a^g + \sum_{a=k_{\min}}^{k_{\max}-1} N_{a,t}^g w_a^g \\
&= B_{[k_{\max}, \infty], t}^g + B_{[k_{\min}, k_{\max}-1], t}^g
\end{aligned} \tag{A.1}$$

where g is gender ($g = 0$: male, 1 : female), a is age, N is population size (number), and w is weight. $B_{[k_{\max}, \infty], t}^g$ is the biomass for age ranging from $k_{\max}$ to infinity, year t , and gender g , and $B_{[k_{\min}, k_{\max}-1], t}^g$ is the biomass for age ranging from $k_{\min}$ to $k_{\max} - 1$, year t , and sex g ,

Using the derivation of the delay-difference model, the first component of Eq. (A.1) is:

$$\begin{aligned}
B_{[k_{\max}, \infty], t}^g &= \sum_{a=k_{\max}}^{\infty} N_{a,t}^g w_a^g \\
&= \sum_{a=k_{\max}+1}^{\infty} S_{a-1, t-1}^g N_{a-1, t-1}^g (\alpha^g + \rho^g w_{a-1}^g) + N_{k_{\max}, t}^g w_{k_{\max}}^g \\
&= S_{[k_{\max}, \infty], t-1}^g \left(\alpha^g N_{[k_{\max}, \infty], t-1}^g + \rho^g B_{[k_{\max}, \infty], t-1}^g \right) + N_{k_{\max}, t}^g w_{k_{\max}}^g
\end{aligned} \tag{A.2}$$

where $S_{[k_{\max}, \infty], t}^g = S_0^g \prod_{s=0}^1 \left(1 - \sum_{d=0}^1 \sum_{m=0}^1 p_m^{g,d,s} \phi_{[k_{\max}, \infty], m}^g U_{[k_{\max}, \infty], t}^{g,d,s} \right)$ (s is season ($s = 0$: winter, 1 : summer), and d is depth ($d = 0$: less than 50m, 1 : equal to and greater than 50m)) is the survival rate,

$S_0^g = \exp(-M^g)$ is the natural survival rate where M^g is the natural mortality coefficient by gender g ,

$p_m^{g,d,s}$ is a movement matrix component (Table 1) by gender g , depth d , season s , and

400 maturity status m ($m=0$: immature, $m=1$: mature),

401 $\phi_{a,m}^g$ is the proportion of individuals for age a , maturity status m , and gender g

402 ($\phi_{a,1}^g = 1 - \phi_{a,0}^g$),

403 $U_{[k_{\max},\infty],t}^{g,d,s} = \sum_{i=1}^n C_{i,t}^{g,d,s} / B_{[k_i,\infty],t}^{g,d,s}$ (i : fishery) is the fishing rate for age ranging from

404 $k_{\max}$ to infinity, year t , gender g , depth d , and season s ,

405 $C_{i,t}^{g,d,s} = C_{i,t}^{d,s} \frac{B_{[k_i,\infty],t}^{g,d,s}}{\sum_{g=0}^1 B_{[k_i,\infty],t}^{g,d,s}}$ is the catch for age i , year t , gender g , depth d , and season s ,

406 $N_{[k_{\max},\infty],t}^{g,d,0} = \sum_{m=0}^1 p_m^{g,d,0} \phi_{[k_{\max},\infty],m}^g N_{[k_{\max},\infty],t}^g$,

407 $B_{[k_{\max},\infty],t}^{g,d,0} = \sum_{m=0}^1 p_m^{g,d,0} \phi_{[k_{\max},\infty],m}^g B_{[k_{\max},\infty],t}^g$,

408 $N_{[k_{\max},\infty],t}^{g,d,1} (S_0^g)^{0.5} \left(1 - \sum_{d=0}^1 \sum_{m=0}^1 p_m^{g,d,0} \phi_{[k_{\max},\infty],m}^g U_{[k_{\max},\infty],t}^{g,d,0} \right) \times$

409 $\sum_{m=0}^1 p_m^{g,d,1} \phi_{[k_{\max},\infty],m}^g N_{[k_{\max},\infty],t}^g$,

410 $B_{[k_{\max},\infty],t}^{g,d,1} =$

411 $(S_0^g)^{0.5} \left(1 - \sum_{d=0}^1 \sum_{m=0}^1 p_m^{g,d,0} \phi_{[k_{\max},\infty],m}^g U_{[k_{\max},\infty],t}^{g,d,0} \right) \sum_{m=0}^1 p_m^{g,d,1} \phi_{[k_{\max},\infty],m}^g B_{[k_{\max},\infty],t}^g$,

412 $N_{k_{\max},t}^g = S_{k_{\max}-1,t-1}^g N_{k_{\max}-1,t-1}^g$,

$w_{k_{\max}}^g = w_{k_{\min}}^g + \frac{1 - (\rho^g)^{k_{\max}-k_{\min}}}{1 - \rho^g} \{ \alpha^g + (\rho^g - 1) w_{k_{\min}}^g \}.$

413 $N_{[k_{\max},\infty],t}^g$ is distributed to each depth d in a specific season s through the movement

414 pattern $p_m^{g,d,s} \phi_{[k_{\max},\infty],m}^g$.

415 The second term of Eq. (A.1) is

$$B_{[k_{\min},k_{\max}-1],t}^g = \sum_{a=k_{\min}}^{k_{\max}-1} N_{a,t}^g w_a^g$$

$$= \sum_{a=k_{\min}+1}^{k_{\max}-1} S_{a-1,t-1}^g N_{a-1,t-1}^g (\alpha^g + \rho^g w_{a-1}^g) + N_{k_{\min},t}^g w_{k_{\min}}^g$$

$$= \sum_{a=k_{\min}+1}^{k_{\max}-1} S_{a-1,t-1}^g (\alpha^g N_{a-1,t-1}^g + \rho^g B_{a-1,t-1}^g) + N_{k_{\min},t}^g w_{k_{\min}}^g \quad (\text{A.3})$$

$$\text{where } S_{a,t}^g = S_0^g \prod_{s=0}^1 (1 - \sum_{d=0}^1 \sum_{m=0}^1 p_m^{g,d,s} \phi_{a,m}^g U_{a,t}^{g,d,s}),$$

$$U_{a,t}^{g,d,s} = \sum_{i=1}^n I(k_i \leq a) C_{i,t}^{g,d,s} / B_{[k_i,\infty],t}^{g,d,s} \quad (i: \text{fishery}), \quad C_{i,t}^{g,d,s} = C_{i,t}^{d,s} \frac{B_{[k_i,\infty],t}^{g,d,s}}{\sum_{g=0}^1 B_{[k_i,\infty],t}^{g,d,s}},$$

$$N_{a,t}^{g,d,0} = \sum_{m=0}^1 p_m^{g,d,0} \phi_{a,m}^g N_{a,t}^g,$$

$$B_{a,t}^{g,d,0} = \sum_{m=0}^1 p_m^{g,d,0} \phi_{a,m}^g B_{a,t}^g,$$

$$N_{a,t}^{g,d,1} = (S_0^g)^{0.5} (1 - \sum_{d=0}^1 \sum_{m=0}^1 p_m^{g,d,0} \phi_{a,m}^g U_{a,t}^{g,d,0}) \sum_{m=0}^1 p_m^{g,d,1} \phi_{a,m}^g N_{a,t}^g,$$

$$B_{a,t}^{g,d,1} = (S_0^g)^{0.5} (1 - \sum_{d=0}^1 \sum_{m=0}^1 p_m^{g,d,0} \phi_{a,m}^g U_{a,t}^{g,d,0}) \sum_{m=0}^1 p_m^{g,d,1} \phi_{a,m}^g B_{a,t}^g,$$

$$N_{k_{\min},t}^g = 0.5 R_t = 0.5 F(B'_t),$$

where F is a stock–recruitment function such as the Beverton-Holt or the Ricker and B'_t

is the escapement of mature female population in year t ,

$$\begin{aligned} B'_t &= \sum_{a=k_{\text{mat}}}^{\infty} B_{a,t}^{1,d,0} (S_0^1)^{0.5} \prod_{s=0}^1 \left(1 - \sum_{d=0}^1 p_1^{1,d,s} \phi_{a,1}^1 U_{a,t}^{1,d,s} \right) \\ &= B_{[k_{\max},\infty],t}^{1,d,0} (S_0^1)^{0.5} \prod_{s=0}^1 \left(1 - \sum_{d=0}^1 p_1^{1,d,s} \phi_{a,1}^1 U_{[k_{\max},\infty],t}^{1,d,s} \right) \\ &\quad + \sum_{a=k_{\text{mat}}}^{k_{\max}-1} B_{a,t}^{1,d,0} (S_0^1)^{0.5} \prod_{s=0}^1 \left(1 - \sum_{d=0}^1 p_1^{1,d,s} \phi_{a,1}^1 U_{a,t}^{1,d,s} \right). \end{aligned}$$

$$\quad \quad \quad (\text{A.4})$$

426

427

428 References

429

430 Block, B.A., Teo, S., Walli, A., Boustany, A., Farwell, C., Dewar, H., Weng, K. Williams,
 431 T., 2005. Electronic tagging and population structure of Atlantic bluefin tuna.
 432 Nature 434, 1121–1127.

433 Brodziak, J., 2002. In search of optimal harvest rates for west coast groundfish. N. Am.
 434 J. Fish. Manage. 22, 258–271.

435 Cass, A.J., Beamish, R.J., McFarlane, G.A., 1990. Lingcod (*Ophiodon elongatus*). Can.
 436 Spec. Pub. Fish. Aquat. Sci. 109, 40pp.

437 Carruthers, T.R., McAllister, M.K., Taylor, N.G., 2011. Spatial surplus production
 438 modeling of Atlantic tunas and billfish. Ecol. Appl. 21, 2734–2755.

439 Deriso, R.B., 1980. Harvesting strategies and parameter estimation for an age-structured
 440 model. Can. J. Fish. Aquat. Sci. 37, 268–282.

441 Dick, E.J., MacCall, A.D., 2011. Depletion-based stock reduction analysis: a
 442 catch-based method for determining sustainable yields for data-poor fish stocks.
 443 Fish. Res. 110, 331–341.

444 Forrest, R.E., McAllister, M.K., Dorn, M.W., Martell, S.J.D., Stanley, R.D. 2010.
 445 Hierarchical Bayesian estimation of recruitment parameters and reference points
 446 for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the
 447 stock-recruitment function. Can. J. Fish. Aquat. Sci. 67, 1611–1634.

448 Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis –
 449 Second Edition. Chapman & Hall, New York.

450 Gordon, D.A., 1994. Lingcod fishery and fishery monitoring in Southeast Alaska.
 451 Alsk. Fish. Res. Bull. 1, 140–152.

452 Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice,
 453 Dynamics and Uncertainty. Chapman and Hall, New York.

454 Hilborn, R., Hilborn U., 2012. Overfishing: What Everyone Needs to Know. Oxford
 455 University Press, UK.

456 King, J.R., McAllister, M., Holt, K.R., Starr, P.J., 2012. Lingcod (*Ophiodon elongatus*)
 457 stock assessment and yield advice for outside stocks in British Columbia. DFO
 458 Can. Sci. Advis. Sec. Res. Doc. 2011/124. 177 p.

459 Larkin, P.A., 1977. An epitaph for the concept of maximum sustainable yield. T. Am.
 460 Fish. Soc. 106, 1–11.

461 Leaman, B.M., McFarlane, G.A., 1997. Lingcod stock assessment and recommended
 462 yield options for 1998. Can. St. Assess. Sec. Res. Doc., 97/131.

463 Low, C.J., Beamish, R.J., 1978. A study of the nesting behaviour of lingcod (*Ophiodon*
 464 *elongates*) in the Strait of Georgia, British Columbia. Fish. Mar. Serv. Tech. Rep.
 465 843, 27pp.

466 Mace, P.M., 2001. A new role for MSY in single-species and ecosystem approaches to
 467 fisheries stock assessment and management. Fish Fish. 2, 2–32.

468 Mace, P.M., Sissenwine, M.P., 1993. How much spawning per recruit is enough? In S.J.
 469 Smith, J.J. Hunt, D. Rivard [ed.] Risk evaluation and biological reference points
 470 for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120, 101–118.

471 Martell, S.J.D., Walters, C.J., Wallace, S.S., 2000. The use of marine protected areas for
 472 conservation of lingcod (*Ophiodon elongatus*). B. Mar. Sci. 66, 729–743.

473 Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of
 474 recent approaches. Fish. Res. 70, 141–159.

475 McAllister, M.K., Ianelli, J.N., 1997. Bayesian stock assessment using catch-age data
 476 and the sampling–importance resampling algorithm. Can. J. Fish. Aquat. Sci. 54,
 477 284–300.

478 Millar, R., Meyer, R., 2000. Bayesian state-space modeling of age-structured data:
 479 fitting a model is just the beginning. *Can. J. Fish. Aquat. Sci.* 57, 43–50.

480 Pauly, D., Christensen, V., Guenette, S., Pitcher, T.J., Sumaila, R., Walters, C.J., Watson,
 481 R., Zelller, D., 2002. Towards sustainability in world fisheries. *Nature* 418,
 482 689–695.

483 Punt, A.E., Smith, A.D.M., 2001. The gospel of maximum sustainable yield in fisheries
 484 management: birth, crucifixion and reincarnation. In: *Conservation of Exploited*
 485 *Species* (eds J.D. Reynolds, G.M. Mace, K.R. Redford and J.R. Robinson),
 486 Cambridge University Press, UK.

487 Punt, A.E., Pribac, F., Walker, T.I., Taylor, B.L., Prince, J.D., 2000. Stock assessment of
 488 school shark, *Galeorhinus galeus*, based on a spatially explicit population
 489 dynamics model. *Mar. Freshw. Res.* 51, 205–220.

490 Quinn, T.J., Deriso, R.B., 1999. *Quantitative Fish Dynamics*. Oxford University Press,
 491 New York.

492 Roberts, C.M., Hawkins, J.P., and Gell, F.R., 2005. The role of marine reserves in
 493 achieving sustainable fisheries. *Phil. Trans. R. Soc. B* 360, 123–132.

494 Sampson, D.B., Scott, R.D., 2011. A spatial model for fishery age-selection at the
 495 population level. *Can. J. Fish. Aquat. Sci.* 68, 1077–1086.

496 Schnute, J., 1985. A general theory for analysis of catch and effort data. *Can. J. Fish.*
 497 *Aquat. Sci.* 42, 414–429.

498 Schnute, J., 1987. A general fishery model for a size-structured fish population. *Can. J.*
 499 *Fish. Aquat. Sci.* 44, 924–940.

500 Taylor, N.G., McAllister, M.K., Lawson, G. L., Carruthers, T., Block, B. A., 2011.
 501 Atlantic bluefin tuna: a novel multistock spatial model for assessment population
 502 biomass. *PLOS ONE* 6 (12), 1–10.

503 Walters, C.J., Martell, S.J.D., 2004. Fisheries Ecology and Management. Princeton
504 University Press, New Jersey.

505 Withler, R.E., King, J.R., Marliave, J.B., Beaith, B., Li, S., Supernault, K.J., Miller,
506 K.M., 2004. Polygamous mating and high levels of genetic variation in lingcod,
507 *Ophiodon elongates*, of the Strait of Georgia, British Columbia. Environ. Biol.
508 Fishes 69, 345–357.

509

510

511 Figure captions

512 Figure 1. The catch time series for offshore B.C. lingcod. C. Hook&Line = commercial
513 hook and line fishery, and R. Hook&Line = recreational hook and line fishery.

514

515 Figure 2. MSY, B_{MSY} (scaled to B_0), and %SPR at MSY for different effort allocations
516 using Pattern 1 and Pattern 2. ★ shows the position with the highest MSY.

517

518 Figure 3. Posterior distributions of MSY and B_{MSY} by sex. SC1: Pattern 1, $w_S=0.5$,
519 $w_D=1.0$, SC 2: Pattern 2, $w_S=0.5$, $w_D=1.0$, SC 3: Pattern 2, $w_S=1.0$, $w_D=0.2$, and SC
520 4: Pattern 2, $w_S=1.0$, $w_D=0.0$. Black circles are posterior medians and the bars are
521 90% credible intervals.

522

Table 1. Hypothetical movement pattern. The values denote the proportion of fish inhabiting the deep water ($\geq 50\text{m}$).

a) Pattern 1			b) Pattern 2		
Sex	Summer	Winter	Sex	Summer	Winter
<u>Immature</u>			<u>Immature</u>		
Male	0.50	0.50	Male	0.00	0.00
Female	0.50	0.50	Female	0.00	0.00
<u>Mature</u>			<u>Mature</u>		
Male	0.50	0.50	Male	0.50	0.05
Female	0.50	0.50	Female	0.50	0.95

Table A1. Parameters used in the delay-difference model

Parameters	Description	Value	Unit	Source
steepness (h)	$R(0.2B_0)/R(B_0)$	0.800	-	King et al. (2012)
natural mortality (M)	male	0.193	year ⁻¹	King et al. (2012)
	female	0.193	year ⁻¹	
α	Ford-Brody growth model intercept parameter,	0.00087	-	inferred in this study
	Ford-Brody growth model intercept parameter,	0.00114	-	
ρ	Ford-Brody growth model trend parameter, male	0.873	-	inferred in this study
	Ford-Brody growth model trend parameter, female	0.931	-	
k_r	age at recruitment for recreational fishery	1 (1927~1998),	years	guesstimated
		4 (1999~2012)		
k_h	age at recruitment for hook & line fishery	3	years	estimated from catch at age data
k_t	age at recruitment for trawl fishery	3 (1927~1994),	years	estimated from catch at age data
		4 (1995~2003),		
		5 (2004~2012)		
k_m	age at full maturation	9	years	inferred in this study
w_k	weight at kmin, male	0.00054	tons	King et al. (2012)
	weight at kmin, female	0.00059	tons	

b) Maturity proportion

age	Male	Female
1	0.04	0.05
2	0.14	0.14
3	0.37	0.31
4	0.68	0.56
5	0.89	0.78
6	0.97	0.91
7	0.99	0.97
8	1.00	0.99
9	1.00	1.00

Fig. 1

a) MSY (mt)

b) B_{MSY}

c) %SPR_{MSY}

Fig.2

a) $MSY/Male$

b) $B_{MSY}/Male$

c) $MSY/Female$

d) $B_{MSY}/Female$

Fig. 3