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Exploring the effect of sampling, protogyny, and larval advection on stock estimates subject to no-take closures in a spatially complex coral reef line fishery on the Great Barrier Reef, Australia

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Abstract: Simulation is used to evaluate the ability of a two-region age-structured assessment model to provide accurate and precise estimates of stock status, i.e. the ratio of female spawning biomass to unfished female spawning biomass, for coral trout, *Plectropomus leopardus*, on the Great Barrier Reef (GBR), Australia. The model used to generate the simulated data used by the assessment model is a spatially complex age- and sex-structured population dynamics model that captures the protogynous nature of coral trout. Stock status is under-estimated (negatively biased), with the extent of negative bias related to mis-specification of the breeding strategy of the target fish stock, the impact of the amount of larval connectivity among reefs, including reefs in fished areas and closures, as well as exploitation rates. The estimates of stock status were less negatively biased when fishery-independent index and age- length-composition data were available from closed areas. The results will inform the development of management strategies for coral trout in the GBR, and highlight the importance of basing evaluations of estimation and management performance on operating models that capture ecologically-important processes such as metapopulation dynamics and protogynous life history.

Keywords: coral trout, fishery-independent sampling, simulation, closed areas, two-region assessment model

Introduction

The effectiveness of marine spatial closures as a conservation management tool is well documented (e.g., Lauck et al. 1998; Mangel 2000; Halpern, 2003; McCook et al. 2010). Many claims have been made that closing parts of the range of a fish stock can benefit the part that remains open to fishing, through adult ‘spill-over’ (Abesamis et al. 2006) or larval ‘subsidy’ (Hilborn et al. 2004). However, the conditions for such benefits can be quite specific (Armstrong 2007) and determined by the degree to which the stock is able to move between the areas open and closed to fishing. In fact, spatial closures are often implemented for management purposes with the understanding that there is at least some impediment to movement in the species being managed, for them to offer protection from fishing (Field et al. 2006).

This impediment or “viscosity” in movement may present a problem for assessing a stock that is partially found in a marine closure, because most assessment methods assume that the entire stock is subject to the same fishing mortality rate (Punt et al. 2015), and the consequences of violating this assumption can be biased or highly imprecise estimates of biomass. This is especially true if the assessment relies strongly on fishery-dependent data (Field et al. 2006).

In general, assessment of stocks that are partially found in spatial closures can be addressed relatively easily when the species is sedentary, or there are very high levels of mixing. For the former case, the assessment relates only to the biomass in the area open to fishing, whereas in the latter case, it relates to the biomass in areas that are open and closed combined. The difficulty comes when a stock has intermediate amounts of mixing, or mixing that is density-dependent, such as for populations structured as a metapopulation (Smedbol et al. 2002; Kritzer and Sale 2004; Little et al. 2010). Metapopulations characterize many coral reef fish species (Mapstone et al. 2008), where migration occurs during the larval stages, but not for the established or settled adult component. Such dynamics could allow fish within spatial closures to subsidize areas open to fishing (Little et al. 2007).

Metapopulation dynamics are starting to be considered in stock assessment (Cadrin and Secor 2009; Punt et al. 2015), and spatial closures present a particular challenge to estimating stock status (Punt et al. 2015). However, spatial closures offer the opportunity as a potential source of data and information on the unexploited component of the stock (McGilliard et al. 2011; Babcock and MacCall 2011). More accurate estimates of biomass might be obtained by using data from within an area closed to fishing (Pincin and Wilberg 2012).

We show results from a simulation study of fisheries stock assessment performed on a coral reef metapopulation subject to a system of spatial no-take areas. The species of interest is coral trout (*Plectropomus leopardus*), the principal target species of the Queensland (Australia) Coral Reef Fin Fish Fishery (CRFFF), which operates within the Australian (federally) managed Great Barrier Reef Marine Park. The Park is managed for biodiversity conservation using a series of no-take zones. We simulated data collection from a structured line survey that samples catch rates, and age- and length-frequencies from a subset of reefs, either inside the no-take closed areas, or outside of them using an operating model developed for the CRFFF. These simulated data were then analyzed to provide estimates of stock status, the ratio of female spawning biomass to unfished female spawning biomass, across all areas. We explored estimation performance under a range of conditions, including various configurations of spatial closures and levels of larval advection from locally-spawned reefs.

Materials and methods

Operating model

ELFSim (the Effects of Line Fishing Simulator: Mapstone et al. 2004, 2008; Little et al. 2007, 2009a) was used as the operating model to generate data for input into the assessment

model. ELFSim models the population dynamics, harvest, and management of coral trout on more than 3,000 individual reefs on the Great Barrier Reef that are connected through larval dispersal. It operates stochastically using monthly time steps, with each simulation consisting of two parts: initialization and projection.

Initialization operates historically, and is used to derive a credible distribution of age-structure and biomass of coral trout on individual reefs by 2012. Starting from an assumed year in which harvest began (1965), individual reef sub-populations are conditioned on historical commercial, charter, and recreational catches; the selectivity of the gear in catching fish of different sizes; the biological characteristics of coral trout; and the physical characteristics of the individual reefs. Reef sub-populations are then projected from 2012 to 2035 by simulating harvest using an agent-based model of fishing vessel dynamics, subject to management constraints including spatial closures, minimum fish size, gear limits, and catch controls implemented with individual transferable quotas (ITQs, Little et al. 2009b). In the simulations reported here, we implemented three scenarios involving different levels of TAC: (a) 1,300 t, which represented the actual TAC for coral trout that has been in place since 2004, (b) a TAC that is 50% larger than this (1,950t), and (c) a TAC that is 50% smaller than this (650t).

A simulated line fishing survey vessel was implemented using the agent-based model (Little et al. 2016). The survey vessel was chosen randomly at the start of a projection from the commercial vessels characterized in ELFSim, to reflect that scientific surveys for the GBR use commercial vessels. That vessel collected data from a sample of 30 reefs in September of each projection year in an attempt to mimic the patterns of previous surveys (Little et al. 2016). These reefs were selected randomly at the start of each replicate projection, but stratified regionally (Mapstone et al. 2004), based on a probability proportional to the historical commercial catch rates experienced on the reef prior to 2012, when the projections began, but with a 10% chance each reef selected had never experienced commercial fishing. Two scenarios for this survey were simulated based on obtaining samples from: (i) reefs open to fishing; and (ii) reefs closed to fishing (Table 1).

The simulated survey on each sampled reef randomly sampled 100 fish from an age-based selectivity-weighted age distribution. The age for each of the sampled fish was determined ignoring aging error. However, variability of length-at-age was added to the associated length measurement, in the form of a normal deviate, $N(0, \sigma_l^2)$, where the variability in the length measurement, σ_l was set to 6.17 cm (Little et al. 2007, page 228). This had the effect of smoothing the frequencies across length bins, because each age class in ELFSim has only a single associated length.

Assessment model

The stock assessment model used in this study is based on the model (see Appendix) developed for cabezon *Scorpaenichthys marmoratus* (Cope et al. 2003). It aggregates biomass across reefs into two sub-populations (equivalent to regions): an unfished (protected) and a fished portion, and represents a greater simplification of the operating model than the assessment model developed for coral trout in 2014 (Leigh et al. 2014).

The assessment model was applied annually. Two abundance indices were simulated in each year during the projection period to represent how fisheries data could be collected from a fishery with no-take areas. The first index was a fleet-wide standardized catch-rate index, computed from the aggregate catch and effort data of the commercial fleet by applying a General Linear Model with factors for month, vessel, one-degree resolution spatial grid, and year. The second index of abundance was based on the catch rate data collected during the structured line survey.

The two sub-populations in the assessment model had different time-series of exploitation rate, but were linked through a common stock-recruitment relationship, which allocates a constant proportion (r_p) of the recruitment to each sub-population, p , such that recruitment for each sub-population in each year is:

$$R_{p,t} = \frac{r_p 4h R_0 S_t}{S_0(1-h) + (5h-1)S_t} e^{x_t - \sigma_r^2/2} \quad (1)$$

where x_t is the estimated recruitment deviation for year t , ($x_t \sim N(0; \sigma_r^2)$), R_0 is the total number of age-0 animals at unfished equilibrium, S_0 is the number of spawners at unfished equilibrium in both sub-populations combined, S_t is the number of spawners in both populations combined at time t , h is the steepness parameter that controls the degree of compensation, and σ_r is the (assumed) standard deviation of log-recruitment (Appendix).

The differences between the operating and the assessment models are summarized in Table 2. One of the main differences is that the operating model represents the coral trout population as protogynous (Figure 1a), i.e. all fish are born females, but change sex as they grow, which is represented in the operating model using a logistic equation (Mapstone et al. 2004, Little et al. 2007). In contrast, half of each age-class is assumed to be female in the assessment model. An implication of this difference is that total spawner weight per recruit at unfished equilibrium is 19% greater in the operating model than the assessment model (Figure 1b). This difference was considered in the results by deriving a comparable summary spawning stock biomass from the assessment model based on the age distribution, and the proportion of females at age that occurs in the operating model.

Assessments were conducted annually on each of 10 projected replicates from 2012 to 2035, which was thought to balance the time it takes for the operating model to run with the expected replication needed to demonstrate differences among the scenarios. Most models converged with a negative log-likelihood of about 1,000. Model results (<10%) were omitted for assessments with a negative log-likelihood greater than 10,000.

Assessment output was not used to change the TAC in the operating model because we sought to determine the accuracy with which the assessment model could estimate stock status, and changing exploitation rates as a function of the outputs from the assessment model was deemed likely to confound or complicate the results, and also no control rule existed in the fishery that could use the estimates from the assessment.

We were interested in the effect on the stock assessment estimates of using the simulated structured line survey to collect data from areas closed to fishing. Consequently, we conducted analyses in which the line survey collected catch-rate, age and length information from reefs open to fishing as well as analyses where the line survey collected data from reefs closed to fishing only (Table 1).

Simulations also examined different operating model conditions. First, the amount of larval connectivity, or self-seeding (ss) among reefs, was varied at two levels in the operating model: 1.0, and 0.1. Self-seeding (ss) equal to 1.0 meant that all of the larvae spawned on a reef remained there, whereas self-seeding equal to 0.1 meant that 10% of the larvae spawned on a reef remained there, with the remaining being advected based on a migration matrix (note however, that with 10% self-seeding, some of the remaining 90% of larvae advected return to their native reef due to the hydrodynamics associated with that reef captured in the migration matrix; each reef however is technically different; Mapstone et al. 2004).

Second, the amount of closures in the operating model was varied at two levels corresponding to 21% and 41% of coral trout habitat, measured as reef perimeter, in the marine park (Table 1). This represented roughly the amount of closed coral trout habitat

before and after the Representative Areas Program (RAP) was implemented in 2002, which increased the amount of no-take marine reserve coverage (Fernandes et al. 2005). The amount of area assumed to be closed in the assessment model was set to correspond to level in the operating model.

The results of the simulations were summarized by the errors associated with estimation of the ratio of the female spawning biomass to the unfished level in each year of each simulation replicate.

Results

The effect of a fishing survey in area closures

Figure 2 shows that the assessment model estimates stock status at about 50%, whereas stock status in the operating model is around 70-80% when the simulated line survey collects data only from the reefs in which the fishery operates. The estimated stock status in each projection year varied little across the replicate simulations, except at the start of the projections when relatively low amounts of simulated data resulted in highly variable estimates of spawning biomass. The estimates of stock status are more accurate, but more variable across the replicates, when the line survey collects data from reefs closed to fishing (Figure 3).

Sensitivity of estimation performance to the structure of the operating model

The data points in Figure 4 represent stock status as a function of operating model biomass for each projection year and replicate, and across a range of TACs and assuming survey sampling in closed areas only. Perfect estimation in Figure 4 would be points on the 1:1 line. In general, there was a strong correlation between the operating model biomass and the estimated biomass across all larval advection and closure scenarios.

The estimates of stock status were generally negatively biased (i.e. they are below the 1:1 line; Figure 4). However, the bias differed among larval advection and closure scenarios, as represented by the slopes of the lines through the respective panels in Figure 4. Specifically, under the lesser self-seeding scenario $ss = 0.1$, when larvae were shared among reefs, and the metapopulation behaved more closely to a single stock, the bias was proportional to the underlying actual stock status, and largest at high actual stock size (bottom panels, Figure 4). For example, the estimated stock status was approximately 81% of the actual stock status (0.70 / 0.87 and 0.71 / 0.88) when the operating model stock status was high (large blue points, bottom panels, Figure 4), and declined to 73% (0.52 / 0.71 and 0.53 / 0.72) when the operating model stock status was low (large grey points, bottom panels, Figure 4).

In contrast, the pattern was reversed, and the estimates of stock status were more accurate when self-seeding was such that reefs are independent of each other, $ss = 1.0$, (and hence the larvae stay on the reef on which they were spawned), (top panels, Figure 4), especially when the operating model stock status was high. For example, the estimated stock status was between 92% and 98% of the actual stock status (0.81 / 0.82 and 0.75 / 0.81) when the operating model stock status was high (large blue points, top panels, Figure 4). However, as the operating model stock status declined, the negative bias increased, such that the estimated stock status ranged between 72% and 74% (0.48 / 0.67 and 0.49 / 0.66) of the actual stock status (large grey points, top panels, Figure 4).

The issue was complicated by the fact that the various scenarios represent different portions of the metapopulation that are closed to fishing. In the left panels of Figure 4, 21% of the coral trout habitat was assumed to be closed to fishing, while on the right panels, 41% was assumed to be closed. The amount of closure had little effect on the negative bias when $ss=0.1$ and reefs are highly connected as seen in comparing the two lower panels of Figure 4. In contrast, there was a marked effect of closures on the bias of stock status when recruitment

to a reef was more independent of that to other reefs ($ss = 1.0$; top panels, Figure 4). In this case, the bias became increasingly negative as stock status in the operating model declined under the lower closure scenario of 21% (top left panel, Figure 4). The effect was reduced when the amount of closures was increased so that the estimated bias was more constant with respect to underlying actual stock status, but still negative (top right panel, Figure 4).

Discussion

Closures that restrict fishing and other extractive activities within their boundaries have been proposed for a range of purposes, including conserving the habitat and species within them, as well as increasing the biomass and thus yield from fishing activities outside of them. While closures have been seen to achieve conservation objectives inside closure boundaries (e.g. Lester et al. 2009), the ability to achieve fishery objectives outside of them is less apparent (e.g. Mangel 1998) because fish move. Movement complicates fisheries management because animals may cross jurisdictional and spatial management boundaries. It also poses a problem for conservation management, because putatively protected stocks become vulnerable when animals move outside of the closure. Even if animals do not move between open and closed areas, implementing marine reserves challenges fisheries management partly because it changes the portion of the fishery that is open, and partly because it does not reduce fishing effort. Thus, marine closures will often displace effort, and increase fishing mortality elsewhere, as in the case in the operating model (Mapstone et al. 2004).

When there is no mixing, the population in the open and closed areas can be considered separately. This is represented by the scenario in which $ss = 1.0$ in the operating model. However, the assessment model produced biased estimates of stock status owing in part to the fact that spawning biomass used to calculate recruitment in the stock recruitment function is scaled-up from individual reefs and pooled, with the extent of bias dependent on the amount of area closed to fishing (pre-RAP vs RAP closures).

In addition, another main cause of bias was the difference in how female mature biomass was defined in the assessment and operating models. Specifically, the assessment model assumed more of the large, older fish were female, while the operating model assumed fish were born female but became male as they grew (protogyny). Even though we corrected for any apparent differences in the output statistic, this difference would still result in fishing mortality having a greater impact on the number of females in the assessment model, and contribute to the negative bias. When more of the stock was exposed to fishing (Figure 4, top left panel), and under lower fishing mortality (large blue point), the assessment model would have estimated more females survived than in reality (in the operating model), resulting in greater productivity, and relatively higher estimated stock status. Increasing the amount of closures, and protecting more of the larger older part of the population, increased the negative bias of the assessment model as the assessment model estimated much fewer females were affected under reduced fishing pressure (Figure 4, top right panel, large blue point).

When the reefs are connected through larval mixing (e.g. $ss = 0.1$), larval subsidy, the process of larvae spilling over from the closed areas to the open areas, would be expected to increase the actual (operating model) biomass across both open and closed areas (Little et al. 2007), thus potentially leading to higher actual stock status in the lower panels of Figure 4 than in the upper panels (Little et al. 2007). At the same time, the assessment model, which did not consider this, estimated relatively lower stock estimates from the assessment model (Figure 4, bottom panels) compared to more restricted larval mixing (Figure 4 top panels), especially when the fishing pressure was low (blue points).

The assessment model used to account for closures is a robust, but biased way of dealing with spatial heterogeneity. Similar assessment models have also shown to be biased when

they are mis-matched compared to the underlying dynamics (e.g. Punt et al. 2016). Our results indicate similar effects when life-history characteristics are mis-matched. Mixing has also been shown to bias estimates of management-related quantities from assessment models in previous studies. For example, McGilliard et al. (2015) showed that a mixed stock subject to closures resulted in negatively biased estimates from a single stock perspective, and positively biased estimates when separate assessments for the open and closed areas are combined. Mixing can confound life history parameters such as natural mortality (Williams et al. 2010), with movement rates (Garrison et al. 2011; McGilliard et al. 2015).

Sampling from the closed areas improved estimation performance. This was not surprising given that this provided the assessment model, which included two regions/populations, data from trend and demographics on one in which data was limited. Nevertheless, the exercise shows how fishing data from no-take areas can be used to manage the stocks outside of them.

Overall, the results of this study contribute to further understanding of assessment models applied to support fisheries management. The ideal would be that the estimates of stock status are unbiased and precise, or at least that any bias was independent of the features of the operating model such as the extent of mixing, exploitation rate, and closures. However, our results suggest that the extent of bias in estimates of stock status depend on all of these factors. Moreover, the estimates of stock status are still biased when the assessment model is close to capturing the structure of the operating model (i.e. $ss=1.0$).

The cause of this bias was confounded between reproductive strategies, scaling-up from individual reefs, and life history (protogyny) assumptions that varied between the operating model and assessment model. As a first attempt at estimating the coral trout population using a simple off-the-shelf assessment model, the results stress the potential implications of trying to estimate the state of a stock without explicitly using an assessment model developed for such stocks. However, even a highly-specific coral trout assessment model (Leigh et al. 2014) still resulted in bias estimates (Little et al. 2016), although in this case with positive, over-estimated results. With an operating model that includes over 3,000 individual populations, each of which may be connected to the others and subject to different levels of exploitation, it is infeasible to conduct assessments by reef or even collect monitoring data from each reef. However, it is still necessary to provide management advice, recognizing that some reefs will be more depleted than intended and others less so, no matter what management strategy is applied. The lessons learned as part of this study will help to assist managers as they identify candidate management strategies, including harvest control rules, for testing and eventual adoption for this complex fishery.

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- 408

409 Table 1. Factors considered in the operating model scenarios. Simulations were undertaken
410 for all combinations of factors.
411

Factor	Level
Location of line fishing survey	Open areas only; closed areas
Extent of larval self-seeding	ss = 1; ss = 0.1
TAC	1,300t; 1,950t; 650t
Level of closure	Pre-RAP (21% of the GBR); RAP (41% of the GBR)

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Table 2 Key differences between operating and assessment models.

Model feature	Operating model	Assessment model
Spawning	Larvae are spawned on a reef based on the amount of habitat it contains.	Spawning and recruitment are combined by sub-population.
Movement	Based on the self-seeding (<i>ss</i>) parameter, larvae that are not ‘self seeded’ from each reef are pooled and then advected according to a connectivity or migration matrix.	No movement between sub-populations
Recruitment	The number of 1-year old recruits is determined for each reef by a Ricker stock recruitment function based on the number of larvae self-seeded, and advected from other reefs. $h = 0.5$	A single Beverton-Holt stock-recruitment relationship combining the spawning biomass from both sub-populations. Resulting recruitment is partitioned to sub-populations according to a fixed proportion. $h = 0.5$
Spawning definition	biomass Mature females. Protogynous: Fish are born female, but the proportion of females declines with age (Figure 1a).	Mature females. Females comprise 50% of population (Figure 1a).

(a)

(b)

Figure 1 (a) The constant proportion of females at length assumed in the assessment model (CAB) and the protogynous assumption for the proportion of females in the operating model (ELFSim). (b) Weight (kg) at age of mature female-per-recruit of coral trout at equilibrium under zero fishing mortality defined by the assessment model (CAB) and the operating model (ELFSim).

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432 Figure 2. Average spawning biomass (mature females) across project replicates, relative to
433 pre-exploitation equilibrium values, for the operating model (black) $\pm$ SD (grey) and the
434 associated estimates (blue $\pm$ SD) when the annual survey only samples in the areas open to
435 fishing. Top panels represent scenarios where self-seeding (ss) is 1.0, and bottom panels
436 where it is 0.1. Left panels represent scenarios where the no-take areas totaled 21% of the
437 coral trout habitat (pre-RAP closures), and right panels 41% of coral trout habitat (RAP
438 closures).

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Figure 3. Average spawning biomass (mature females) relative to pre-exploitation equilibrium values for the operating model (black) $\pm$ SD (grey) and the associated estimates (blue $\pm$ SD) when the annual survey only samples in the areas closed to fishing. Top panels represent scenarios where self-seeding (ss) is 1.0, and bottom panels where it is 0.1. Left panels represent scenarios where the no-take areas totaled 21% of the coral trout habitat (pre-RAP closures), and right panels 41% of coral trout habitat (RAP closures).

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465 Figure 4. Estimated stock status from the assessment model, corrected for the difference in
466 definition of spawning biomass, as a function of stock status in the operating model, when
467 there are annual survey only samples in the areas closed to fishing, for two levels of self-
468 seeding in the operating model ($ss = 0.1$; $ss = 1.0$) and two levels of closures (pre-RAP,
469 RAP). Black points: TAC = 1,300t; blue points: TAC = 650t; grey points: TAC = 1,950t.
470 Large points represent the mean, with their corresponding values ($\pm$ st. dev). Red lines
471 represent the fitted regression lines to the data points $\pm$ 95% confidence interval. Top panels
472 represent scenarios where self-seeding (ss) is 1.0, and bottom panels where it is 0.1. Left
473 panels represent scenarios where the no-take areas totaled 21% of the coral trout habitat (pre-
474 RAP closures), and right panels 41% of coral trout habitat (RAP closures).
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Appendix A: The assessment method

The stock assessment is based on a multi-component population dynamics model (where “component” for the purposes of this paper is whether the animal in the component are in areas open or closed to fishing). The catches are removed for each of several fleets (commercial, charters and recreational), and recruitment is governed by a Beverton-Holt stock-recruitment relationship in which spawning biomass is the total (over all components) female spawning biomass, i.e. density-dependence is a function of total female spawning biomass rather than component-specific female spawning biomass.

A.1 Basic dynamics

The numbers of animals by component, age, and year are given by:

$$N_{y,a}^c = \begin{cases} R_{c,y} & \text{if } a = 0 \\ (N_{y-1,a-1}^c e^{-M/2} - C_{y-1,a-1}^c) e^{-M/2} & \text{if } 1 \leq a < x \\ (N_{y-1,x}^c e^{-M/2} - C_{y-1,x}^c) e^{-M/2} + (N_{y-1,x-1}^c e^{-M/2} - C_{y-1,x-1}^c) e^{-M/2} & \text{if } a = x \end{cases} \quad (1)$$

where $N_{y,a}^s$ is the number of animals of age a in component c at the start of year y , M is the instantaneous rate of natural mortality (assumed to be independent of age, component and time), x is the plus-group age (set to 18y), $R_{c,y}$ is the recruitment to component c during year y :

$$R_{c,y} = \frac{p_c 4h R_0 S_y}{(1-h)S_0 + (5h-1)S_y} e^{\varepsilon_y - \sigma_R^2/2} \quad \varepsilon_y \sim N(0; \sigma_R^2) \quad (2)$$

R_0 is the (total over components) recruitment corresponding to unfished equilibrium, p_c is the proportion of the total recruitment that recruits to component c , S_y is the spawning biomass during year y :

$$S_y = \sum_c \sum_{a=1}^x f_a w_a N_{y,a}^c \quad (3)$$

S_0 is the spawning biomass corresponding to unfished equilibrium, f_a is the proportion of animals of age a that are mature, w_a is the mass of an animal of age a at the start of the year, h is the “steepness” of the stock-recruitment relationship (the proportion of R_0 when $S_y = 0.2 S_0$; set to 0.5), σ_R is the standard deviation of the recruitment residuals (set to 0.7), and $C_{y,a}^c$ is the total (over fleet) catch of animals of age a in component c at the start of year y .

A.2 Catches and selectivity

The catches in numbers are computed from the catches in mass, i.e.:

$$C_{y,a}^c = \sum_{g \in \mathcal{G}} \frac{\tilde{C}_y^g}{V_y^g} S_a^g N_{y,a}^c e^{-M/2} \quad (4)$$

where $\tilde{C}_y^g$ is catch in mass by fleet g during year y , $c \in \mathcal{G}$ indicates the components that are subject to exploitation by fleet g , V_y^g is the vulnerable biomass for fleet g during year y :

$$V_y^g = \sum_{c \in g} \sum_a w_{a+1.2} S_a^g N_{y,a}^c e^{-M/2} \quad (5)$$

where $w_{a+1/2}$ is the mass of an animal of age a in the middle of the year, and S_a^g is the selectivity of fleet g on animals of age a .

A.3 Initial conditions

The initial conditions (year 1965) correspond to a population at unexploited equilibrium.

A.4 Selectivity and growth

Selectivity is assumed to be a function of length, i.e. for fleet g :

$$S_L^g = \left(1 + \exp[-\ell \ln 19 (\bar{L}_L - L_{50}^g) / \delta^g]\right)^{-1} \quad (6)$$

where $\bar{L}_L$ is the mid-point of size-class L , L_{50}^g is the length corresponding to 0.5 selectivity for fleet g , and δ^g determines the width of the selectivity pattern for fleet g . Selectivity-at-age by fleet is computed from selectivity-at-length by fleet, taking account of the length-at-age relationship and the variation in length-at-age, i.e.:

$$S_a^g = \sum_{L=1}^{n_L} S_L^g \phi_{a,L} \quad \phi_{a,L} = \int_{\bar{L}_L - \Delta L/2}^{\bar{L}_L + \Delta L/2} \frac{1}{\sqrt{2\pi}\sigma_a} e^{-(\ell - L_{a+1/2})^2 / (2\sigma_a^2)} d\ell \quad (7)$$

where $\phi_{a,L}$ is the proportion of animals of age a that it is in size-class L , n_L is the number of size-classes (10), ΔL is the width of each size-class (70mm), L_a is the expected length of an animal of age a , i.e.:

$$L_a = \ell_\infty + (L_0 - \ell_\infty) e^{-\kappa a} \quad (8)$$

ℓ_∞ is the asymptotic size, κ is the growth rate parameter, σ_a is the standard deviation of the length-at-age for animals of age a , i.e.:

$$\sigma_a = [CV_{\min} + (CV_{\max} - CV_{\min}) \frac{a-1}{x-1}] L_a \quad (9)$$

$CV_{\min}$ and $CV_{\max}$ is the coefficients of variation of length-at-age for ages 0 and x .

A.5 Likelihood function

The estimable parameters of the model are unfished recruitment (R_0), the parameters of the logistic selectivity function, and the recruitment residuals for years 1984 onward. The remaining parameters are pre-specified (Table A.1). The information that can be used for parameter estimation are index data, size-composition data and age-composition data, in addition to a penalty on the extent to which the recruitment residuals can vary among years.

The contribution of the catch-rate and survey indices to the negative of the logarithm of the likelihood function is:

$$L_1 = \frac{1}{2(\sigma_y')^2} \sum_y \left(\ell \ln I_y - \ell \ln \hat{I}_y \right)^2 \quad (10)$$

where I_y is the index of abundance for year y (standardized CPUE or survey CPUE), $\hat{I}_y$ is the model-estimate corresponding to I_y :

$$\hat{I}_y = \sum_{a=0}^x w_a S_a^* (N_{y,c}^{c(*)} - C_{y,c}^{c(*)}) e^{-M/2} \quad (11)$$

* denotes the fleet corresponding to the index, $c(*)$ the component from which the data are collected (areas open or closed to fishing), and σ_y^I is the pre-specified standard error of the logarithm of I_y .

The contribution of the size-composition information to the negative of the logarithm of the likelihood function is based on the assumptions that (a) the data are obtained from a gear that has the same selectivity as the fishery fleets, and (b) the sampling process is multinomial, i.e.:

$$L_2 = \sum_y \sum_{L=1}^{n_L} \tilde{N}_y^{\text{Len}} \rho_{y,L}^* \ell n(\hat{\rho}_{y,L}^* / \rho_{y,L}^*) \quad (12)$$

where $\tilde{N}_y^{\text{Len}}$ is the effective sample size for the size-composition data for year y , $\rho_{y,L}^*$ is the observed proportion of the catch during year y that is in size-class L , * denotes the fleet from which size-composition data are collected, and $\hat{\rho}_{y,L}^*$ the model-estimate of the proportion of the catch during year y that is in size-class L :

$$\hat{\rho}_{y,L}^* = \sum_a C_{y,a}^{c(*)} \phi_{a,L} / \sum_{L'} \sum_a C_{y,a'}^{c(*)} \phi_{a',L'} \quad (13)$$

The contribution of the age-composition information to the negative of the logarithm of the likelihood function is based on the assumptions that (a) the data are obtained from a gear that has the same selectivity as the fishery fleets, and (b) the sampling process is multinomial, i.e.:

$$L_3 = \sum_y \sum_{a=0}^x \tilde{N}_y^{\text{Age}} \rho_{y,a}^* \ell n(\hat{\rho}_{y,a}^* / \rho_{y,a}^*) \quad (14)$$

where $\tilde{N}_y^{\text{Age}}$ is the effective sample size for the age-composition data for year y , $\rho_{y,a}^*$ is the observed proportion of the catch during year y that is in age-class a , * denotes the fleet from which age-composition data are collected, and $\hat{\rho}_{y,a}^*$ the model-estimate of the proportion of the catch during year y that is in age-class a :

$$\hat{\rho}_{y,a}^* = C_{y,a}^{c(*)} / \sum_{a'} C_{y,a'}^{c(*)} \quad (15)$$

The penalty imposed on the recruitment deviations is:

$$P_1 = \frac{1}{2\sigma_R^2} \sum_y \mathcal{E}_y^2 \quad (16)$$

94 Table A.1 Parameters of the assessment model and how they are treated.

Parameter		Value used (or estimated)
<i>General</i>		
Natural mortality, M		0.45yr ⁻¹
Maturity-at-age, f_a		Fig A.1(a)
Plus-group, x		18 yr
<i>Recruitment-related</i>		
Unfished recruitment, R_0		Estimated
Steepness, h		0.5
Proportion of recruitment to component c , p_c	Pre-RAP scenario:	0.79:0.21 (open: closed)
	RAP scenario:	0.59:0.41 (open: closed)
Extent of variation in recruitment, σ_R		0.7
Recruitment deviations, ε_y		Estimated
<i>Growth-related</i>		
Asymptotic size, ℓ_∞		54.05cm
Growth rate		0.339 yr ⁻¹
Size-at-age 0		10.43cm
$CV_{\min}$		0.14
$CV_{\max}$		0.09
Weight-at-age, w_a		Fig. A.1(b)
<i>Selectivity-related</i>		
Length-at-50%-selectivity, L_{50}^g		Estimated
Width of the selectivity ogive, δ^g		Estimated

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Figure A.1 (a) Maturity-at-age and (b) weight-at-age curves used in the assessment model