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Modelling the effects of density-dependent mortality in juvenile red snapper caught as bycatch in Gulf of Mexico shrimp fisheries: Implications for management

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ABSTRACT

Density-dependent mortality of juvenile fishes is a key population regulation mechanism that is usually assumed to occur before fish recruit to fisheries. When density-dependent mortality occurs simultaneously with bycatch of juvenile fish but is not accounted for in stock assessments, estimates of population size and fishery reference points may be biased as a result. This paper develops an instantaneous, age-structured model accounting for simultaneous density-dependent mortality and bycatch in age-0 red snapper (*Lutjanus campechanus*), using equations derived from the Beverton–Holt stock-recruit function. Model equations are first presented and deterministic equilibrium properties of the model are explored. Two simplified Bayesian models (with and without post-recruitment density-dependent mortality) are then fitted to data from the 2009 Gulf of Mexico red snapper stock assessment to illustrate the effects of post-recruitment density-dependent mortality on estimates of stock size, stock status and recovery potential. Finally, the Bayesian models are re-run using simulated indices of abundance and age composition data to explore the estimability of model parameters under different amounts of process and observation error; and also to illustrate policy implications of model mis-specification in terms of timing of density-dependent processes. All analyses show that failure to account for post-recruitment density-dependent mortality in stock assessments can lead to overestimation of true abundance and recovery potential. Equilibrium analyses show that fishery reference points MSY and B_{MSY} may be overestimated if true post-recruitment density-dependent mortality is not accounted for. These analyses also illustrate the problematic nature of defining and calculating reference points in the presence of numerous sources of mortality that affect different demographic components of the population. We note that when population dynamics were simulated without density-dependent age-0 mortality simultaneous with bycatch, estimates of stock size and productivity obtained from an assessment model that assumed density-dependent age-0 mortality had relatively little bias. This was because the density-dependence parameter was correctly estimated to be close to zero. This suggests that it may be advisable to use the density-dependence model if there is a possibility that post-recruitment density-dependent mortality is a factor governing population dynamics.

1. Introduction

Studies of variability and regulation in benthic marine fish populations have proposed that density-dependent processes generally occur in the early juvenile phase, following settlement to benthic habitats (Cowan et al., 2000; Iles and Beverton, 2000; Fromentin et al., 2001). Although large stochastic variability and difficulty observing juvenile fish have made identification of the exact processes and phase at which population regulation occurs difficult in many cases (Sissenwine, 1984; Shepherd and Cushing, 1990; Hixon, 1998), evidence suggests that population variability arises principally from stochastic density-independent environmental processes acting on larval fish, with this variability attenuated by density-dependent processes occurring in the juvenile phase (e.g., van der Veer, 1986; Beverton and Iles, 1992; Myers and Cadigan, 1993). The degree to which fish populations can compensate for reductions in population size through improvements in survival of juveniles and other negative feedback mechanisms is a key

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component of their resilience to fishing and forms the basis of the theory of sustainable fishing (Schaefer, 1954; Beverton and Holt, 1957; Myers and Mertz, 1998).

Mechanisms for density-dependent survival of juvenile fishes have been reviewed by Myers and Cadigan (1993), Rose et al. (2001) and Houde (2008), among others. A key underlying mechanism is intraspecific competition for food, habitat or other resources, although rates of predation, cannibalism and movement may also be impacted by density (Hixon, 1998). These mechanisms may be highly inter-related, especially rates of growth and mortality (Cowan et al., 2000; Hixon and Jones, 2005; Houde, 2008). Intraspecific competition for food can result in decreased growth rates and longer duration in smaller-sized stages that are more vulnerable to predators (Houde, 1987; Sogard, 1997), have higher overwintering mortality (Martino and Houde, 2012) or are forced to move to suboptimal habitats where prey is limiting (Hixon, 1998; Martino and Houde, 2012) or where risk of predation is greater (Walters and Juanes, 1993). Beverton (1995) proposed the "concentration hypothesis", which predicted higher compensation and lower annual deviations in recruitment for fish populations whose juveniles concentrate on nursery grounds, i.e., fish that transition from a three-dimensional pelagic habitat to a limiting two-dimensional benthic habitat. These types of juvenile populations may approach the carrying capacity of their habitat in high settlement years and experience greater intraspecific competition and predation risk than juveniles of species that are pelagic or do not otherwise concentrate during the juvenile phase. Iles and Beverton (2000) analysed stock-recruit data for 63 fish stocks and found general support for the concentration hypothesis, although some exceptions were noted. The overall effect of such mechanisms is dampening of the high variability in larval supply, resulting in more similar levels of stock size across a range of densities.

In fishery stock assessments, density-dependent effects in recruitment are usually represented with a stock-recruit function. The most commonly-used are the two-parameter Beverton and Holt (1957) and Ricker (1954) forms, although others have been derived (e.g., Shepherd, 1982; Barrowman and Myers, 2000). The Ricker model assumes that the juvenile mortality rate is a function of the number of spawners, whereas the Beverton–Holt model assumes that juvenile mortality is a linear function of juvenile density. Walters and Korman (1999) linked foraging behaviour with mortality of juvenile fish and showed that an asymptotic Beverton–Holt type stock-relationship is an emergent consequence of the trade-off between increased time spent feeding and risk of predation at higher densities, where increased juvenile density results in increased foraging in suboptimal habitats with greater risk of predation. Species that exhibit strong ontogenetic movement from habitat to habitat may be expected to exhibit density-dependent mortality at multiple stages in their early life history. In such cases, the two parameters of the Beverton–Holt stock-recruit function, representing survival from egg to the final recruitment stage, can be shown to be aggregate functions of the parameters of each of a set of stage-specific Beverton–Holt functions (see Beverton and Holt, 1957; Walters and Korman, 1999; Brooks and Powers, 2007 for details). This property of the Beverton–Holt function, where the dynamics of multiple juvenile phases are captured in a simple two-parameter function, has been suggested as an explanation for its versatility and applicability across a wide range of species with diverse patterns of early life history (Walters and Korman, 1999; Myers, 2002).

Most fishery stock assessment models define recruitment as the stage at which fish recruit to a fishery, even if they are not fully vulnerable to the fishing gear. A fundamental assumption of most age-structured stock assessments is that all density-dependent processes are complete by the time recruitment occurs. This assumption implies that a stock-recruit function can be used to represent average density-dependent survival through all juvenile stages from egg to recruit, and that survival of subsequent fished age classes can be modelled using a density-independent function of numbers and natural and fishing mortality. This greatly simplifies model dynamics with respect to predicting abundance and fishery catch at age. This assumption will be violated, however, in fisheries that catch juvenile fish (e.g., as bycatch) before natural density-dependent dynamics are complete. In such cases, there will be an interaction between density-independent fishing mortality (which reduces juvenile density), and density-dependent natural mortality, which may offset the effects of bycatch through improvements in the survival of remaining juveniles. Conversely, density-dependent natural mortality in juvenile fish may take many of the juveniles "saved" through bycatch reduction measures. Understanding the timing of density-dependent processes is therefore of key importance when considering the impacts of fishing mortality on juvenile fish (McAllister, 2005a; Brooks and Powers, 2007; Gazey et al., 2008).

1.1. *Gulf of Mexico red snapper*

The timing of density-dependent juvenile mortality has been raised by several authors as an important factor in management of red snapper (*Lutjanus campechanus*) in U.S. Gulf of Mexico fisheries (McAllister and Gazey, 2005; SEDAR, 2005; Brooks and Powers, 2007; Gazey et al., 2008). Red snapper is one of the most important commercial and recreational species in the Gulf of Mexico and is caught in directed commercial line fisheries as well as in a large recreational fishery, which is of similar magnitude to the commercial fishery (SEDAR, 2009). Juvenile (age-0 and age-1) red snapper are also highly vulnerable to shrimp trawling (Goodyear, 1995; Wells et al., 2008). Recent estimates suggest that annual bycatch of juvenile snapper has been a significant source of mortality for juvenile snapper over the past two decades (between 20 and 70 million fish per year since 1990; SEDAR, 2009), although economic factors including damage following the 2005 hurricane season, low shrimp prices and high fuel costs have led to a reduction in total shrimp effort since 2005 (GMFMC, 2007). The red snapper stock has been assessed as overfished and undergoing overfishing in all recent assessments (Goodyear, 1995; Schirripa and Legault, 1999; SEDAR, 2005, 2009). Mortality due to shrimp trawling has been identified as a major concern for management, with large reductions in bycatch seen as necessary for stock recovery (Goodyear, 1995). The rebuilding plan for red snapper (GMFMC, 2004) was updated in 2007 to include specific targets for reduction of mortality in shrimp and directed fisheries (GMFMC, 2007).

Red snapper undergo successive ontogenetic shifts in habitat as they transition from the egg and larval stages to more structured habitat and deeper water. The life history and habitat stages of juvenile red snapper have been reviewed by Gallaway and Cole (1999) and Gallaway et al. (2009) (see also Szedlmayer and Shipp, 1994; Wells et al., 2008; Cowan et al., 2010). Peak spawning of red snapper occurs during the months of June through August in the northern Gulf of Mexico. After the pelagic egg and larval stages, rapidly-growing pre-recruits settle to low-relief oyster shell or sand/mud habitat at 26–30 days of age, before moving to larger, more structured habitat as they outgrow the initial habitat (Gallaway et al., 2009). Juvenile snapper become vulnerable to the shrimp fishery at around 50 mm in length, after around 67 days, and are fully vulnerable to the shrimp fishery by they time they reach 100 mm in late fall (Gallaway and Cole, 1999). They recruit to the commercial and recreational fishery at around two years of age, by which stage a cohort may have already been exposed to significant mortality from the shrimp fishery. Although confounded with other factors (Cowan et al., 2010), it is likely that density-dependent processes are occurring simultaneously with fishing mortality during the first year of life. Gazey et al. (2008) used a length-based, age-structured model to analyse length-frequency data from the Gulf of Mexico shrimp fishery and concluded there was some evidence for density-dependent mortality between age-0 and age-1. Gallaway et al. (2009) reviewed the literature describing red snapper life history and ecology and drew similar, qualitative, conclusions.

Actions 6 and 7 of Amendment 27 (GMFMC, 2007) state that the management goal is to reduce bycatch mortality on juvenile snapper to 0.16 yr^{-1} in the western Gulf (representing a 74% reduction in bycatch from 2005 levels). This was thought to have already been partly achieved (59%) through significant effort reductions and implementation of bycatch reduction devices (BRD) in the shrimp fishery (although Gallaway and Cole, 1999 have found that reductions in bycatch due to BRDs may have been overestimated). If simultaneous bycatch and density-dependent juvenile mortality are occurring, but not accounted for in the stock assessment of red snapper, however, the impact of the shrimp fishery could be overestimated, and the impact of the directed fishery underestimated. Recent reductions in bycatch from the shrimp fishery could therefore be insufficient to facilitate rebuilding of the red snapper stock. Furthermore, fishery reference points, which are used as benchmarks in determination of stock status, will be biased if they do not correctly account for mortality occurring in bycatch fisheries (Powers, 2005), even more so if density-dependent mortality is present but not accounted for (McAllister, 2005a; McAllister and Gazey, 2005; Brooks and Powers, 2007).

Density-dependent mortality in juvenile fish that are vulnerable to shrimp fishery has not so far been incorporated into the red snapper stock assessment, although it was discussed extensively in the 2007 assessment workshop report (SEDAR, 2005), and listed as a priority research item in the 2009 update (SEDAR, 2009). Alternative model runs have been included in attempts to address the problem (including removing age-0 fish from the assessment so that their dynamics are captured in the stock-recruit function) and increasing the age-specific natural mortality used for age-0 and age-1 fish, but none have explicitly addressed simultaneous fishing mortality with density-dependent natural mortality (see Gazey et al., 2008). Brooks and Powers (2007) derived a general Beverton–Holt stock-recruit function that explicitly defines density-dependent and density-independent sources of mortality at different life stages and calculated equilibrium properties of scenarios with alternative timing of density-dependent and independent mortality (see also Powers and Brooks, 2005). McAllister and Gazey (2005) and McAllister (2005a) developed stock reduction analyses (SRA) that were used to illustrate the effect of alternative assumptions about density-dependent juvenile mortality on calculation of MSY-based reference points and the likelihood of achieving rebuilding targets through reduction in shrimp catch and directed TAC. Their models used discrete functions to model survival at age. They concluded there was evidence for density-dependent juvenile mortality and that this implied reduction of shrimp bycatch alone would be insufficient to meet rebuilding targets for the red snapper fishery.

1.2. Aims

The purpose of this paper is to develop an instantaneous, age-structured model accounting for simultaneous density-dependent mortality and bycatch in post-recruitment age-0 red snapper, using equations derived from the Beverton–Holt stock-recruit function, where we define a recruit as an age 0 fish vulnerable to the shrimp fishery. We consider a simple case where simultaneous bycatch and density-dependent mortality occur only in age-0 fish – in reality these processes are likely also occurring in age-1 and even possibly age-2 fish (Gallaway et al., 2009). The paper proceeds in four main steps: (1) model equations are presented; (2) deterministic equilibrium properties of the model are shown and compared with a model that does not incorporate post-recruitment density-dependent mortality; (3) two Bayesian models (with and without post-recruitment density-dependent mortality) are fitted to data from the 2009 Red Snapper Update (SEDAR, 2009); and (4) the models are run again using simulated indices of abundance and age composition data, generated with known underlying parameters. The simulation-estimation approach in (4) is first used to explore the estimability of model parameters under different magnitudes of process and observation error. The model is then used to illustrate policy implications of model mis-specification in terms of timing of density-dependent processes. These analyses extend previous analyses in a number of ways by incorporating all of the following: (i) natural and fishing mortality are represented by instantaneous equations; (ii) bycatch and density-dependent mortality are considered simultaneously; (iii) assessment models are fitted to fishery catch, catch-age and survey data; and (iv) the simulation-estimation analysis allows exploration of parameter-estimability and policy implications under conditions where “true” underlying parameters and variables are known. Because this model is greatly simplified compared to the red snapper stock assessment (SEDAR, 2005, 2009) and, critically, uses some of the outputs of the 2009 stock assessment (e.g., estimates of vulnerability-at-age and density-independent natural mortality), we emphasise that it cannot be viewed as an alternative assessment for Gulf of Mexico red snapper.

2. Methods and results

The following sections describe a model that explicitly incorporates density-dependent survival from the time that age-0 red snapper become vulnerable to the shrimp fishery at around two months of age to age 1. We define a recruit as an age 0 fish that is vulnerable to the shrimp fishery and the model has an annual time-step. A list of model parameters and variables is given in Table 1. The model is described in Table 2 (initial conditions) and Table 3 (time dynamics), which also show the equivalent equations for a conventional age-structured model that does not include post-recruitment density-dependent mortality. For convenience, we will refer to the model that includes density-dependent age-0 to age-1 survival as the density-dependence model and the model that includes density-independent age-0 to age-1 survival as the conventional model, although both models include density-dependent survival from egg to the age-0 age class via the stock-recruit function. Tables 2 and 3 are organised so that equations unique to the density-dependence model are in the left-hand column and equations that are unique to the conventional model are in the right-hand column. Equations that are common to both models are shown in the centre column.

The basis of the model is a standard statistical catch at age model (in numbers of fish) with 51 age classes (0–50), with the final age class treated as an accumulator group (plus group). Unless otherwise specified, all data in the model were taken from the input file of the 2009 red snapper assessment update (SEDAR, 2009). Only data from the western portion of the Gulf of Mexico (west of the Mississippi River) were used. The model is a stock-reduction analysis (Kimura et al., 1984; Walters et al., 2006) and is driven by the ‘ultra-historical’ catch series from 1880 to 2008 (SEDAR, 2009). The model is greatly simplified compared to the stock assessment (SEDAR, 2005, 2009), which includes several directed fishing sectors and two areas (eastern and western Gulf of Mexico) with linked recruitment. The present model only considers two fisheries (combined directed and shrimp). The combined directed fishery incorporates catch data from the commercial handline and longline fisheries, the recreational fishery (all recreational sectors) and out-of-season

Table 1
List of parameters. Estimated parameters are highlighted in bold type.

Parameter	Description
Indices	
a	Age (years)
A	Maximum age (years)
t	Time (years)
j	Index of abundance
k	Fishery (d = combined directed; s = shrimp)
Time-invariant parameters	
$\boldsymbol{R_0}$	**Unfished age 0 recruits**
CR	**Goodyear compensation ratio**
$\boldsymbol{M_{d0}}$	**Density-dependent natural mortality at age 0**
M_{i0}	Density independent natural mortality at age 0
α	Slope of the stock-recruit function at the origin (egg to age 0)
β	Scaling parameter of stock-recruit function (egg to age 0)
Equilbrium per recruit calculations	
φ_{E0}	Equilibrium unfished eggs per recruit
φ_{Ee}	Equilibrium fished eggs per recruit
φ_q	Equilibrium vulnerable biomass per recruit
Age schedules (fixed)	
M_a	Natural mortality at age
s_a	Unfished survival rate at age
$\hat{s}_a$	Fished survival rate at age
l_a	Unfished survivorship at age
$\hat{l}_a$	Fished survivorship at age
m_a	Maturity at age
f_a	Fecundity at age
w_a	Weight at age
Age schedules (time-varying)	
$vd_{a,t}$	Vulnerability-at-age to the combined directed fishery
$vs_{a,t}$	Vulnerability-at-age to the shrimp fishery
$vh_{a,t}$	Vulnerability-at-age to the directed handline fishery
$Z_{a,t}$	Total mortality at age
$N_{a,t}$	Numbers at age
$C_{a,t}$	Catch at age
Time-varying	
$\boldsymbol{\omega_t}$	**Log-recruitment deviations**
$\breve{\alpha}_t$	Time-varying slope at the origin of the age 0 to age 1 survival function
$\breve{\beta}_t$	Time-varying scaling parameter of the age 0 to age 1 survival function
Fd_t	Fishing mortality in the combined directed fishery
Fs_t	Bycatch fishing mortality in the shrimp fishery
SN_t	Spawning numbers
SB_t	Spawning biomass
E_t	Eggs
VNd_t	Numbers vulnerable to the combined directed fishery
VNs_t	Numbers vulnerable to the shrimp fishery
VNh_t	Numbers vulnerable to the directed handline fishery
$I_{k,t}$	Index of abundance
Likelihood components	
σ_R	Standard deviation in log recruitment deviations
$\boldsymbol{\sigma_{I,k}}$	**Standard deviation in observation residuals**[a]
$\sigma_{C,k}$	Standard deviation in observed catch
$\boldsymbol{\tau_k}$	**Variance in age composition residuals**[b]
$\boldsymbol{q_k}$	**Constant of proportionality in indices of abundance (catchability)**[b]
$\eta_{k,a,t}$	Residual difference between observed and predicted proportions at age
$d^2_{k,t}$	Residual difference between observed and predicted indices of abundance
Fishery reference points	
MSY	Maximum sustainable yield
F_{MSY}	Long-term fixed fishing mortality that produces MSY
B_{MSY}	Long-term fixed spawning biomass at MSY

[a] Fixed in Section 2.3; conditional MLE estimates in Section 2.4.
[b] Conditional MLE estimates.

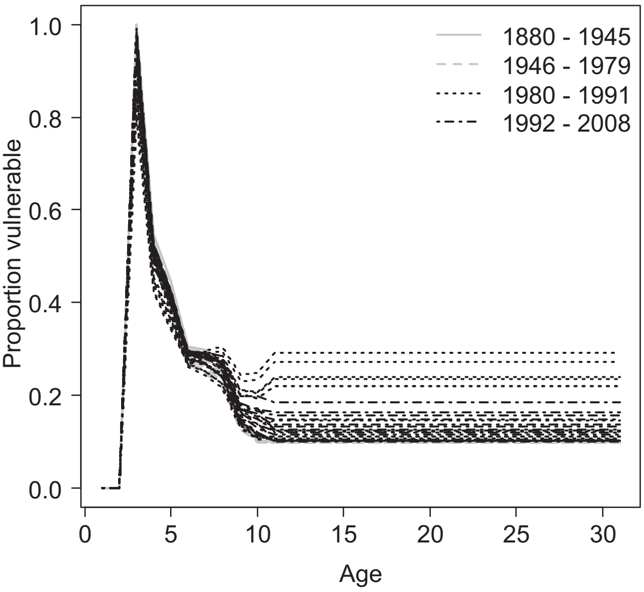

Fig. 1. Annual weighted vulnerability at age for the combined directed fishery. Line types represent four different time periods. Differences among time periods are driven by the relative sizes of the handline and long-line fishery (see text).
Data source: SEDAR (2009).

discards from the commercial fisheries. See SEDAR (2009) for detailed description of these fisheries.

For simplicity, the model utilises estimates of vulnerability-at-age output from the 2009 assessment update (continuity run). In all analyses, vulnerabilities-at-age from the four western Gulf directed fisheries (commercial handline, commercial longline, out of season commercial discards and combined recreational) were weighted according to relative annual catch and combined into a single vulnerability-at-age schedule. Because relative catch among the four directed sectors varied from year to year, the weighted vulnerability curve also varied from year to year but was strongly dome-shaped in all years due to the dominance of the handline fishery, reflecting the location of this fishery in shallower water (Fig. 1). For illustrative purposes, bycatch vulnerability in the deterministic analysis (Section 2.2) was set to 1 for age-0 fish and 0 for all other ages. In the Bayesian and simulation-estimation analyses (Sections 2.3 and 2.4), bycatch vulnerability was taken directly from the output of the 2009 update continuity run (western Gulf). Our decision to use the estimated fixed schedules of vulnerability-at-age from the 2009 assessment update is expected to influence our results. However, we opted for a simpler approach to enable more direct comparison of the models with and without explicit representation of post-recruitment density-dependent mortality. Attempting to estimate annual dome-shaped vulnerability parameters in addition to other parameters would have added complication to the model that could confound comparison of the models.

2.1. Model incorporating density-dependence in age-0 survival

2.1.1. Dynamic equations

A Beverton and Holt (1957) stock-recruit function is used to model recruitment from egg to the age-0 stanza (i.e., the age at which fish first become vulnerable to the shrimp fishery at around 2 months)

$$N_{0,t} = \frac{\alpha E_t}{1 + \beta E_t} \tag{1}$$

where $N_{0,t}$ is number of new age-0 recruits in year t, α and β are the parameters of the Beverton–Holt stock-recruit function (assumed

Table 2

Summary of equilibrium model initialisation. See text for definitions of parameters. Note that equations (T2.9) and (T2.10) refer to the directed fishery only.

Density-dependence model	Common to both models	Conventional model
(T2.1) Natural mortality at age	$M_a = \left\{ \begin{array}{ll} 1.0^a & a=0 \\ 0.6 & a=1 \\ 0.1 & a \geq 2 \end{array} \right\}$	
(T2.2) Beverton–Holt parameters	$\alpha = \dfrac{CR}{\varphi_{E_0}} \quad \beta = \dfrac{\alpha\varphi_{E_0} - 1}{R_0\varphi_{E_0}}$	
(T2.3) Unfished eggs per recruit	$\varphi_{E_0} = \sum_{a=0}^{A} l_a m_a w_a$	
(T2.4) Unfished survival rate at age $s_a = \left\{ \begin{array}{ll} \dfrac{e^{-M_{i0}}}{1+(M_{d0}/M_{i0})(1-e^{-M_{i0}})R_0} & a=0 \\ e^{-M_a} & a \geq 1 \end{array} \right\}$		$s_a = e^{-M_a}$
(T2.5) Unfished survivorship at age	$l_a = \left\{ \begin{array}{ll} 1 & a=0 \\ l_{a-1}s_{a-1} & 1 \leq a < A \\ l_{a-1}s_{a-1}/(1-s_a) & a=A \end{array} \right\}$	
(T2.6) Initial unfished numbers at age	$N_{a,1} = l_a R_0$	
(T2.7) Fished survival rate at age $\hat{s}_a = \left\{ \begin{array}{ll} \dfrac{e^{-M_{i0}+\upsilon s_0 Fs}}{1+(M_{d0}/(M_{i0}+\upsilon s_0 Fs))(1-e^{-M_{i0}+\upsilon s_0 Fs})R_e} & a=0 \\ e^{-(M_a+\upsilon d_0 Fd_a+\upsilon s_0 Fs_a)} & a \geq 1 \end{array} \right\}$		$s_a = e^{-(\upsilon d_0 Fd_a+\upsilon s_0 Fs_a+M_a)}$
(T2.8) Fished survivorship at age	$\hat{l}_a = \left\{ \begin{array}{ll} 1 & a=0 \\ \hat{l}_{a-1}\hat{s}_{a-1} & 1 \leq a < A \\ \hat{l}_{a-1}\hat{s}_{a-1}/(1-\hat{s}_a) & a=A \end{array} \right\}$	
(T2.9) Long-term equilibrium catch	$C_e = F_e R_e \varphi_q$	
(T2.10) Vulnerable biomass per recruit	$\varphi_q = \sum_{a=1}^{\infty} \dfrac{\hat{l}_a w_a \upsilon d_a}{M_a+\upsilon d_a Fd_a+\upsilon s_a Fs_a}[1-e^{-(M_a+\upsilon d_a Fd_a+\upsilon s_a Fs_a)}]$	
(T2.11) Equilibrium recruits	$R_e = R_0 \dfrac{CR-(\varphi_{E0}/\varphi_{Ee})}{CR-1}$	

[a] $M_0 = M_{i0}$ in the density-dependence model.

Table 3

Summary of time-dynamic equations. See text for description of parameters.

Density-dependence model	Common to both models	Conventional model
(T3.1) Total mortality	$Z_{a,t} = M_a + \upsilon d_{a,t} Fd_t + \upsilon s_{a,t} Fs_t$	
(T3.2) Parameters for $N_{1,t}$ (Eq. (3) and (T2.3)) $\breve{\alpha}_t = e^{-(M_{i0}+\upsilon s_0 Fs_t)}$ $\breve{\beta}_t = \dfrac{M_{d0}}{(M_{i0}+\upsilon s_0 Fs_t)}(1-e^{-(M_{i0}+\upsilon s_0 Fs_t)})$		NA
(T3.3)[a] Numbers at age ($t \geq 2$) $N_{a,t} = \left\{ \begin{array}{ll} \dfrac{\alpha E_{t-1}}{1+\beta E_{t-1}} & a=0 \\ \dfrac{\breve{\alpha}_{t-1}N_{0,t-1}}{1+\breve{\beta}_{t-1}N_{0,t-1}} & a=1 \\ N_{a-1,t-1}e^{-Z_{a-1,t-1}} & 2 \leq a < A \\ N_{a-1,t-1}e^{-Z_{a-1,t-1}} + N_{a,t}e^{-Z_a} & a=A \end{array} \right\}$		$N_{a,t} = \left\{ \begin{array}{ll} \dfrac{\alpha E_{t-1}}{1+\beta E_{t-1}} & a=0 \\ N_{a-1,t-1}e^{-Z_{a-1,t-1}} & 1 \leq a < A \\ N_{a-1,t-1}e^{-Z_{a-1,t-1}} + N_{a,t}e^{-Z_a} & a=A \end{array} \right\}$
(T3.4) Catch at age $C_{a,t} = \left\{ \begin{array}{ll} \dfrac{\upsilon s_{0,t}Fs_t}{M_{d0}} \ln\left(1+\dfrac{M_{d0}}{M_{i0}+\upsilon s_{0,t}Fs_t}(1-e^{-(M_{i0}+\upsilon s_{0,t}Fs_t)})N_{0,t}\right) & a=0 \\ \dfrac{\upsilon d_{a,t}Fd_t+\upsilon s_{a,t}Fs_t}{Z_t}(1-e^{-(Z_t)})N_{a,t} & a \geq 1 \end{array} \right\}$		$C_{a,t} = \dfrac{\upsilon d_{a,t}Fd_t+\upsilon s_{a,t}Fs_t}{Z_t}(1-e^{-(Z_t)})N_{a,t}$
(T3.5) Vulnerable numbers at age (combined directed)	$VNd_t = \sum_{a}^{\infty} \upsilon d_{a,t}N_{a,t}$	
(T3.6) Vulnerable numbers at age (shrimp bycatch)	$VNs_t = \sum_{a}^{\infty} \upsilon s_{a,t}N_{a,t}$	
(T3.7) Vulnerable numbers at age (directed handline)	$VNh_t = \sum_{a}^{\infty} \upsilon h_{a,t}N_{a,t}$	

[a] See Eq. (T2.2) for calculation of α and β. See Eq. (2) for E_t.

time-invariant) and E is the number of eggs from the current year's spawners, given by

$$E_t = \sum_{a}^{A} N_{a,t} w_a m_a \tag{2}$$

where $N_{a,t}$ is numbers at age $a > 0$ in year t, w_a is weight at age > 0 and m_a is the fraction mature at age > 0 (where $w_a m_a$ is assumed proportional to fecundity at age). Vectors of weight and maturity at age were taken from the 2009 stock assessment (SEDAR, 2009). The interpretation of parameters α and β will be discussed in the next section.

The key difference between this model and most statistical catch at age models is the representation of survival from age-0 to age-1. Here, the number of age-0 fish surviving to age 1 is assumed to be governed by density-dependent processes. Therefore a second Beverton–Holt equation is used, allowing the proportion of fish that survive to age 1 to be a saturating function of the number of age-0 fish alive at time t, i.e.,

$$N_{1,t} = \frac{\breve{\alpha}_{t-1} N_{0,t-1}}{1 + \breve{\beta}_{t-1} N_{0,t-1}} \tag{3}$$

where the parameters $\breve{\alpha}$ and $\breve{\beta}$ are assumed to vary annually with shrimp fishing mortality (see next section for details). Finally, since natural survival from age 1 to age 2 and older ages is assumed to be density-independent for the purposes of this study, numbers at age 2 and older $N_{a,t}$ can be modelled as a simple function of total mortality at age $Z_{a,t}$ (T3.1), i.e.,

$$N_{a,t} = N_{a-1,t-1} e^{-Z_{a-1,t-1}} \quad \text{for} \quad a \geq 2 \tag{5}$$

where Fs_t, Fd_t, $vs_{a,t}$ and $vd_{a,t}$, the fishing mortality component parameters of $Z_{a,t}$, are defined in Table 1 and M_a is density-independent natural mortality at age. Equations for the calculation of numbers at age for the cases with and without post-recruitment density-dependent mortality are summarised in Table 3 (T3.3).

On the basis of a review of published studies, natural mortality rate values used in the 2009 update (SEDAR, 2009) were 1.0 and 0.6 yr^{-1} for age-0 and age-1 fish respectively. These values have been used here, with the rate of natural mortality for all other age-classes set to 0.1 yr^{-1} (SEDAR, 2005, 2009). See next section for differences in the treatment of age-0 natural mortality between the density-dependence and conventional models.

2.1.2. *Decomposing α and β*

Here we discuss the derivation of Eqs. (1) and (3), as shown by Beverton and Holt (1957; see also Walters and Martell, 2004; Brooks and Powers, 2007). Dropping age and time subscripts, Beverton and Holt's derivation began with the assumption that the natural mortality rate of juvenile fish M is a linear function of density and is composed of a density-independent component (M_i) and a density-dependent component M_d, i.e.,

$$M = M_i + M_d N \tag{6}$$

where N is number (i.e., density) of fish in a given cohort. Eq. (6) has the form of a straight line, with M and N the dependent and independent variables, respectively. M_i therefore represents the intercept and M_d represents the slope. The instantaneous rate of decay of a population undergoing natural mortality is given by the differential equation

$$\frac{dN}{dt} = -MN_t \tag{7a}$$

with time-step t. Substituting Eq. (6) into Eq. (7a) gives

$$\frac{dN}{dt} = -(M_i + M_d N_t) N_t \tag{7b}$$

Integrating (7b) to get total numbers at the end of the time step, N_{t+1}, gives

$$N_{t+1} = \frac{e^{-M_i \Delta t} N_t}{1 + (M_d/M_i)(1 - e^{-M_i \Delta t}) N_t} \tag{8}$$

This is a saturating equation of the same form as the Beverton–Holt stock-recruit function (Eq. (1)). The parameters of the Beverton–Holt equation can therefore be more properly defined in terms of density-dependent and independent mortality terms, where

$$\alpha = e^{-M_i} \tag{9}$$

and

$$\beta = \frac{M_d}{M_i}(1 - e^{-M_i}) \tag{10}$$

(Beverton and Holt, 1957; Walters and Martell, 2004; Powers and Brooks, 2005). Note that we have used the same notation as Hilborn and Walters (1992; Chapter 7) for these parameters. Eqs. (6)–(10) demonstrate the key underlying assumption of the Beverton–Holt stock recruit relationship, i.e., the rate of natural mortality is a linear function of density.

Note that in the absence of density-dependence, integrating Eq. (7a) with $M = M_i$ would result in the equation $N_{t+1} = \alpha N_t$. This is a straight line through the origin with slope α. Therefore, the biological interpretation of α is the survival rate from egg to recruit at very low egg density, when density-dependent processes can be assumed negligible. In an asymptotic stock-recruitment relationship parameterised in terms of eggs and recruits, α is therefore the maximum juvenile survival rate (Beverton and Holt, 1957; Myers et al., 1999).

The α and β parameters of Eqs. (9) and (10) are routinely used to model recruitment dynamics when it is assumed that all density-dependent mortality has occurred prior to fishing mortality. Usually, α and β (or population parameters analytically related to them such as steepness and R_0) are estimated directly, with the pre-recruitment mortality terms implicit in them (see Walters and Korman, 1999).

In the presence of simultaneous natural and fishing mortality, the fishing mortality term can be assumed to be density-independent and added to the density-independent mortality term M_i. The resulting equations for the time-varying $\breve{\alpha}_t$ and $\breve{\beta}_t$ parameters of Eq. (3) are shown in Table 3 (T3.2), where a zero subscript on a parameter indicates that it applies to age-0 fish. In T3.2, it is assumed that the only fishing mortality on age-0 fish is from the shrimp fishery. Note that the density-dependence model reduces to the conventional model as M_{d0} tends towards zero (T3.2 and T3.3).

In summary, we have a simulated population where survival from egg to age-0 recruit is density-dependent and occurs prior to any fishing mortality. Numbers at age-0 are therefore modelled using a standard Beverton–Holt stock-recruit function (Eq. (1)). Survival from age-0 to age-1 is also density-dependent and occurs simultaneously with fishing mortality. Numbers at age-1 are therefore modelled using a second Beverton–Holt stock-recruit function, with fishing mortality and density-dependent and density-independent mortality explicitly represented (T3.2 and T3.3).

2.1.3. *Modelling catch*

The instantaneous catch rate for an age-class is calculated as a function of the fishing mortality rate and the number of fish alive in that age class at any given instant t

$$\frac{dC_a}{dt} = (\nu s_{a,t} Fs_t + \nu d_{a,t} Fd_t) N_{a,t} \tag{11}$$

If there is no density-dependent mortality, $N_{a,t}$ is given by Eq. (5). To obtain the total catch at age over a whole year t, Eq. (5) is therefore substituted into Eq. (11), which is integrated to give the Baranov catch equation (Hilborn and Walters, 1992), i.e.,

$$C_{a,t} = \frac{vd_{a,t}Fd_t + vs_{a,t}Fs_t}{Z_{a,t}}(1 - e^{-Z_{a,t}})N_{a,t} \tag{12}$$

which is used here to model catch of all age classes ≥1.

However, when numbers in the age-0 class are governed by density-dependent processes, the conventional Baranov catch equation cannot be used. Numbers at age for this age-class at are described by an equation of the Beverton–Holt form (Eq. (8)). Substituting this into Eq. (11) and integrating to get total catch at age over the whole year results in

$$C_{0,t} = \frac{vs_{0,t}Fs_t}{M_{d0}} \ln\left(1 + \frac{M_{d0}}{M_{i0} + vs_{0,t}Fs_t}(1 - e^{-(M_{i0}+vs_{0,t}Fs_t)})N_{0,t}\right) \tag{13}$$

(see also Powers and Brooks, 2005, their Eq. (6)). Eq. (13) is used here to model bycatch of age-0 fish. Eq. (13) has an unusual form in that part of it takes the natural logarithm of an equation similar in form to the Baranov catch equation plus 1. Catch of age-0 fish is therefore proportional to the natural logarithm of the number of surviving age-0 fish ($N_{0,t}$), where survival is the density-independent survival rate, modified by the relative fractions of density-dependent and independent mortality. The first fractional term of Eq. (13) has the effect of dampening the effect of bycatch mortality, Fs – i.e., the larger M_{d0} becomes, the smaller the effective Fs becomes. These two effects counteract each other, dampening the relative effects of fishing mortality as M_{d0} increases. Another way to interpret Eq. (13) is to say that, for any fixed values of $N_{0,t}$ and M_{d0}, increasing fishing mortality will increase the fraction caught but will also decrease the available numbers on a logarithmic scale, again counteracting the relative impacts of bycatch mortality. Eq. (13) is undefined when $M_{d0} = 0$. However, as M_{d0} approaches zero, the first term can become extremely large, while the second term approaches ln(1) and becomes extremely small. In this case, the solution will approach the solution to the Baranov equation (Eq. (12)). Catch equations for the cases with and without post-recruitment density-dependent mortality are summarised in Table 3 (T3.4). In our example, we note that bycatch of fish age >0 can be modelled using the conventional Baranov equation because we have assumed that density-dependent processes are complete by the end of the first year.

Numbers of vulnerable fish in the combined directed fishery (VNd_t), shrimp bycatch fishery (VNs_t) and handline only fishery (VNh_t; for calculating likelihood of CPUE data) are calculated as the sum-product of numbers at age and vulnerability at age (T3.5–T3.7), where $vh_{a,t}$ is vulnerability at age to the handline fishery in year t.

2.1.4. Initialising the model and leading parameters

Leading estimated parameters are ln(R_0), ln(CR) and M_{d0}, where R_0 is unfished equilibrium recruitment and CR is the Goodyear compensation ratio (Goodyear, 1977, 1989). A recruit is defined as a fish entering the age-0 age class (i.e., the age at which fish first become vulnerable to the shrimp fishery). The compensation ratio CR is the same as the $\hat{\alpha}$ parameter of Myers et al. (1999) and represents the maximum possible improvement in juvenile survival rate as spawning stock size is reduced from its unfished state. It is analytically related to steepness (Mace and Doonan, 1988) by the relationship CR = $4h/(1 - h)$ for the Beverton–Holt stock-recruit function (Myers et al., 1999). In this model, R_0 and CR are used to derive the parameters of Eq. (1) to initialise the number of age-0 recruits (T2.2; Walters and Martell, 2004). Equilibrium unfished eggs per recruit (φ_{E_0}; T2.3) is calculated as the sum product of unfished survivorship at age (l_a; T2.4), fraction mature at age and weight at age (Botsford, 1981). For ages 1 to A in both models, and ages 0 to A in the conventional model, the survival rate s_a is an exponential function of natural mortality at age (T2.4). For $a = 0$ in the density-dependence model, the unfished survival rate is dependent on R_0, via the Beverton–Holt relationship (T2.4), with $\breve{\alpha}$ and $\breve{\beta}$ calculated from Eqs. (9) and (10) with Fs set to zero. In the density-dependence model, the density-dependent mortality rate in age-0 fish M_{d0} is an estimated parameter and the density-independent mortality rate in age-0 fish M_{i0} is set to M_0 (T2.1), where M_0 is here assumed to be 1.0 yr^{-1} (SEDAR, 2009).

At age 0, survivorship at age, l_a, is 1, by definition. For subsequent ages, it is simply the product of l_{a-1} and s_{a-1}. A plus group correction is added to the calculation of survivorship for the terminal age class A (T2.5). Numbers at age in the first year ($N_{a,1880}$) are assumed to be at unfished equilibrium and are obtained by multiplying l_a by R_0 (T2.6).

2.1.5. Fishery reference points

The equations for unfished survival rate and survivorship at age (T2.4 and T2.5) can be modified to incorporate fixed values of directed and bycatch fishing mortality to give equilibrium fished survival rate at age $\hat{s}_a$ and equilibrium fished survivorship at age $\hat{l}_a$ (T2.7 and T2.8, respectively). These can then be used in calculation of biological reference points Maximum Sustainable Yield (MSY), the constant long-term directed fishing mortality that results in MSY (F_{MSY}), and the associated spawning biomass at MSY (B_{MSY}). Given leading estimates of CR and R_0, there is no analytical solution for MSY and F_{MSY}. They can, however, be obtained numerically by iteratively searching for the value of long-term fixed directed fishing mortality F_e that maximises long-term equilibrium directed catch (T2.9), where φ_q represents equilibrium vulnerable biomass per recruit (T2.10) with natural and fishing mortality occurring simultaneously (Martell et al., 2008). Here, R_e (T2.11) represents equilibrium long-term recruitment, where φ_{Ee} represents equilibrium eggs per recruit under long term fixed directed F_e, calculated by substituting the fished survivorship term T2.8 into T2.3. See Martell et al. (2008) for full derivation of T2.11. For the conventional model, a Newton–Raphson algorithm was used to search over the derivative of T2.9 to find the value of F_e that maximised long term yield.

Note that the calculation of R_e (T2.11) is straightforward in the conventional model. In the calculation of φ_{Ee}, the equilibrium unfished survival rate s_a is simply replaced with the equilibrium fished survival rate $\hat{s}_a$ (T2.7, right-hand column) to obtain fished survivorship $\hat{l}_a$ (T2.8). However, it should be apparent that a circularity occurs in the density-dependence model because the calculation of R_e (T2.11) includes calculation of a survival rate in age-0 fish (T2.7, left-hand column) that is dependent on the equilibrium density of recruits R_e. This is not a problem in the unfished state used to initialise the model (T2.4) because R_0 is estimated or pre-specified rather than calculated. To overcome this circularity for the fished state in the density-dependence model, R_e was obtained by running out the model for 200 years under constant directed F_e for each of a sequence of values of F_e (0–1 in increments of 0.001) and calculating the final equilibrium recruitment R_e from the stock-recruit function (Eq. (1)). Long-term yield was then calculated using this value of R_e. A set of visual and numerical tests were done to confirm that model had reached equilibrium and to ensure the final value of F_{MSY} indeed maximised the long-term equilibrium yield to give MSY.

It should also be apparent from examination of T2.7 that it is not possible to calculate biological reference points without specifying a value for bycatch mortality Fs. This problem is ubiquitous (although seldom acknowledged) in fisheries where multiple fleets target a single stock or in the presence of a predator that exerts significant mortality (Powers, 2005). For all of the analyses presented below, we therefore calculate biological reference points under four alternative levels of constant bycatch: $Fs = 0.0, 0.16, 0.5$ and $1.0\,\mathrm{yr}^{-1}$, where $0.16\,\mathrm{yr}^{-1}$ is the target for bycatch mortality stated in the red snapper rebuilding plan (GMFMC, 2007).

2.2. *Deterministic model properties*

Before attempting any model-fitting, we explored the key properties of the density-dependence model, particularly exploring the effect of the magnitude of the M_{d0} parameter. Essentially, this is the only parameter unique to the density-dependence model because the density-independent mortality term for age-0 fish (M_{i0}) was set to the same value of age-0 natural mortality (M_0; T2.1) used in the conventional model (T2.4).

In this section, the models were used deterministically (i.e., no error terms) with fixed input parameters and constant fishing mortality rates. For clarity, we set vulnerability in the shrimp fishery so that bycatch consisted only of age-0 fish that were fully vulnerable to the shrimp fishery. This simplifying assumption was made to clearly illustrate the differences between the models. We do not make this assumption in the later sections. Models were run under a constant combined directed fishing mortality ($Fd = 0.1\,\mathrm{yr}^{-1}$) and a range of shrimp bycatch mortalities ($Fs = 0$, 0.1, 0.2, 0.5 and $1.0\,\mathrm{yr}^{-1}$) for 129 years (the same time series length for catch as in the stock assessment; SEDAR, 2009). Other constant values of *Fd* were also tested but results looked very similar across values so we only present results for $Fd = 0.1\,\mathrm{yr}^{-1}$.

2.2.1. *Numbers at age*

The density-dependent mortality parameter (M_{d0}, T2.4) had a two-fold effect on model outputs. First, it affected the overall scale of the population because, depending on its magnitude, it had the effect of reducing the survivorship from age-0 to age-1 (Fig. 2, top panel). Therefore, the same number of age-0 recruits resulted in an overall smaller population in the density-dependence model than in the conventional model (Fig. 2, bottom panel). However, M_{d0} also had the effect of increasing the productivity of the population because it stabilised the number of surviving age-1 fish over a broader range of age-0 s. This is illustrated in Fig. 2, which shows a decrease in the range of number of age-1 and age-2 fish across bycatch mortality rates as M_{d0} increased. In other words, the relative impact of bycatch of age-0 fish decreased as M_{d0} increased.

2.2.2. *Fishery reference points*

The magnitude of post-recruitment density-dependent mortality had a significant effect on the calculation of fishery reference points. For a fixed value of R_0, increasing the magnitude of M_{d0} had the effect of reducing MSY, but slightly increasing F_{MSY} for any long-term fixed level of directed fishing mortality (Fig. 3, top panel). The reduction in MSY with increasing M_{d0} is due to the scaling effect of M_{d0} (Fig. 2). Increasing bycatch mortality reduced MSY and F_{MSY} within any given M_{d0} scenario (Fig. 3, top panel, dashed lines). However, the relative impact of bycatch decreased as M_{d0} increased (lines closer together in higher M_{d0} scenarios).

These results can be more clearly illustrated by re-running the analysis using calibrated values of R_0 that produce the same numbers of equilibrium unfished age-1 fish for each M_{d0} scenario (Fig. 3, bottom panel). This allows the relative impacts of long-term directed and bycatch fishing mortality and M_{d0} to be shown without the confounding effects of M_{d0} on population scale. In this example, the value of R_0 used for each of the three M_{d0} scenarios resulted in an equilibrium value of approximately 11 million age-1 fish in the absence of directed and bycatch fishing mortality. The analysis shows a reduction in the impact of bycatch as M_{d0} increased (lines are closer together in higher M_{d0} scenarios), as well as greater productivity as M_{d0} increased.

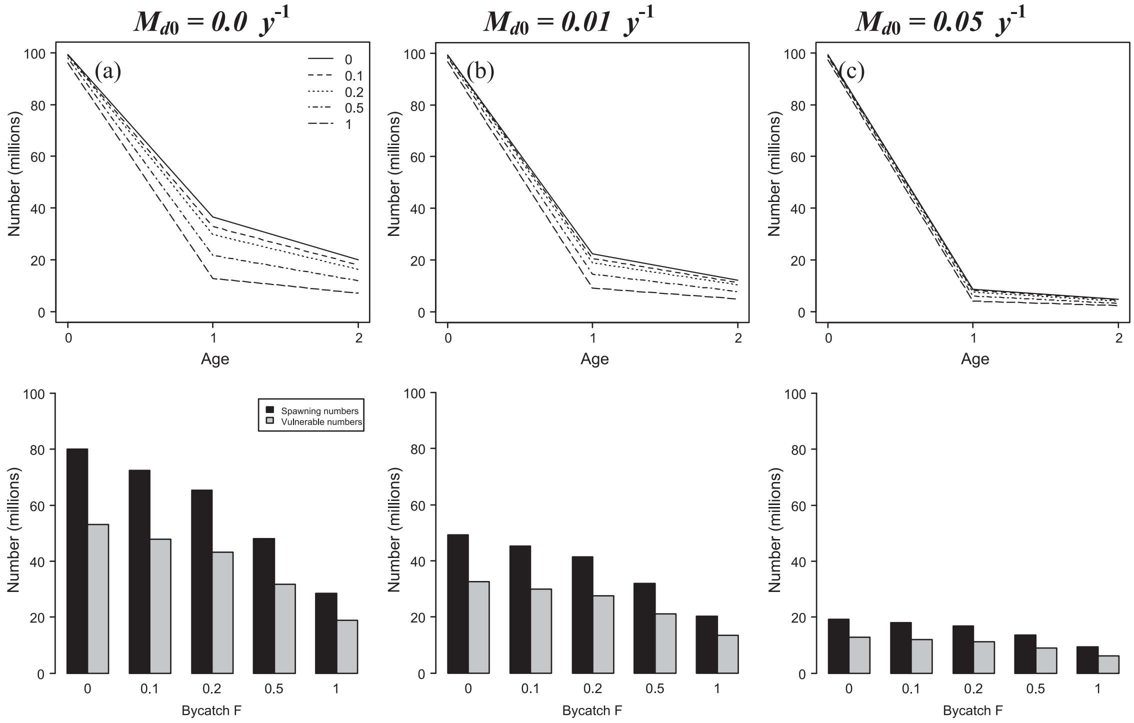

Fig. 2. Deterministic model properties after 129 years of fishing at a constant fishing mortality rate, under increasing magnitudes of post-recruitment density-dependent mortality: (a) $M_{d0} = 0.0\,\mathrm{yr}^{-1}$; (b) $M_{d0} = 0.01\,\mathrm{yr}^{-1}$; (c) $M_{d0} = 0.05\,\mathrm{yr}^{-1}$. Top panel: equilibrium numbers of age 0–2 fish. Bottom panel: equilibrium spawning numbers (black bars) and numbers vulnerable to the combined directed fishery (grey bars). Each graph shows numbers resulting from five alternative levels of constant shrimp bycatch mortality: $Fs = 0.0\,\mathrm{yr}^{-1}$, $Fs = 0.1\,\mathrm{yr}^{-1}$, $Fs = 0.2\,\mathrm{yr}^{-1}$, $Fs = 0.5\,\mathrm{yr}^{-1}$ and $Fs = 1.0\,\mathrm{yr}^{-1}$. Directed fishing mortality was held constant at $Fd = 0.1\,\mathrm{yr}^{-1}$ in all model runs.

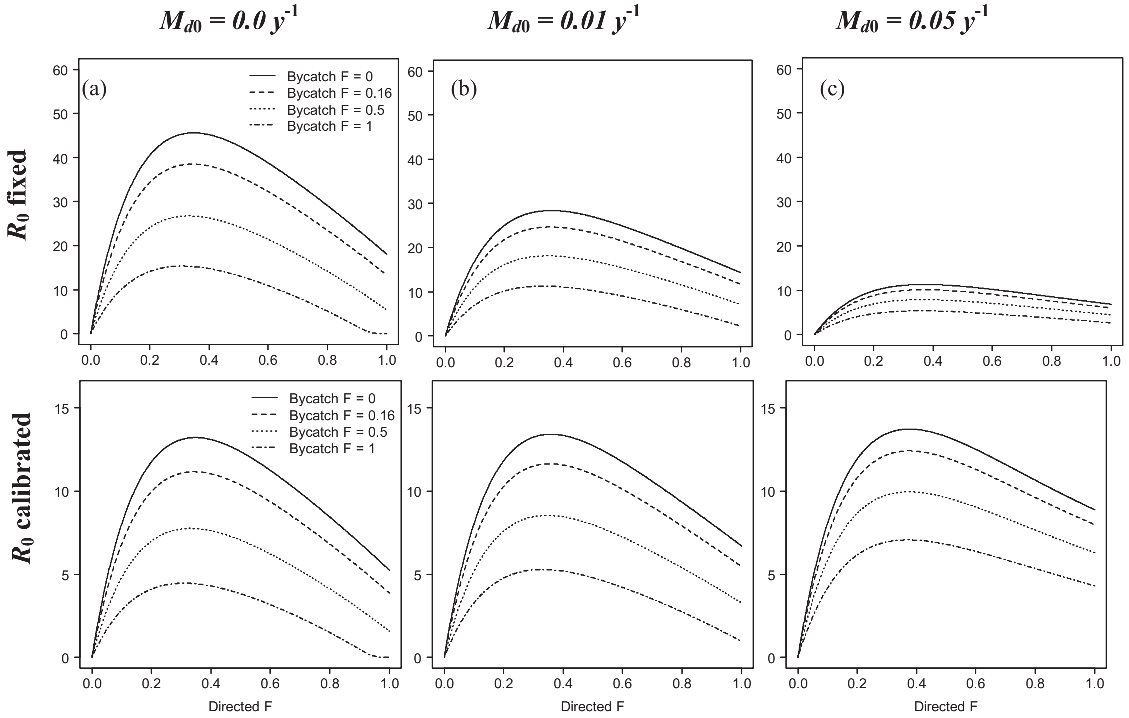

Fig. 3. Equilibrium long-term yield curves under increasing combined-directed fishing mortality and magnitudes of post-recruitment density-dependent mortality, with: (a) M_{d0} = 0.0 yr^{-1}; (b) M_{d0} = 0.01 yr^{-1}; and (c) M_{d0} = 0.05 yr^{-1}, under four alternative levels of constant shrimp bycatch mortality: Fs = 0.0 yr^{-1}, Fs = 0.16 yr^{-1}, Fs = 0.5 yr^{-1} and Fs = 1.0 yr^{-1}. Top panel: results with R_0 fixed at 100 million recruits in all cases. Bottom panel: results with R_0 calibrated to give the same number of unfished age 1 fish for each value of M_{d0} (see text).

2.2.3. *Effect of stopping bycatch*

The previous section showed that one of the main effects of post-recruitment density-dependent natural mortality in age-0 fish is a decrease in the relative impact of bycatch mortality on that age class. This is because compensatory natural mortality processes are expected to stabilise the number of fish surviving to age-1 across a range of population sizes. To test the effects of reducing bycatch on a simulated population, the model was re-run for 90 years with constant directed fishing and bycatch mortality, followed by 39 years with no bycatch, under six different values of M_{d0} (Fig. 4).

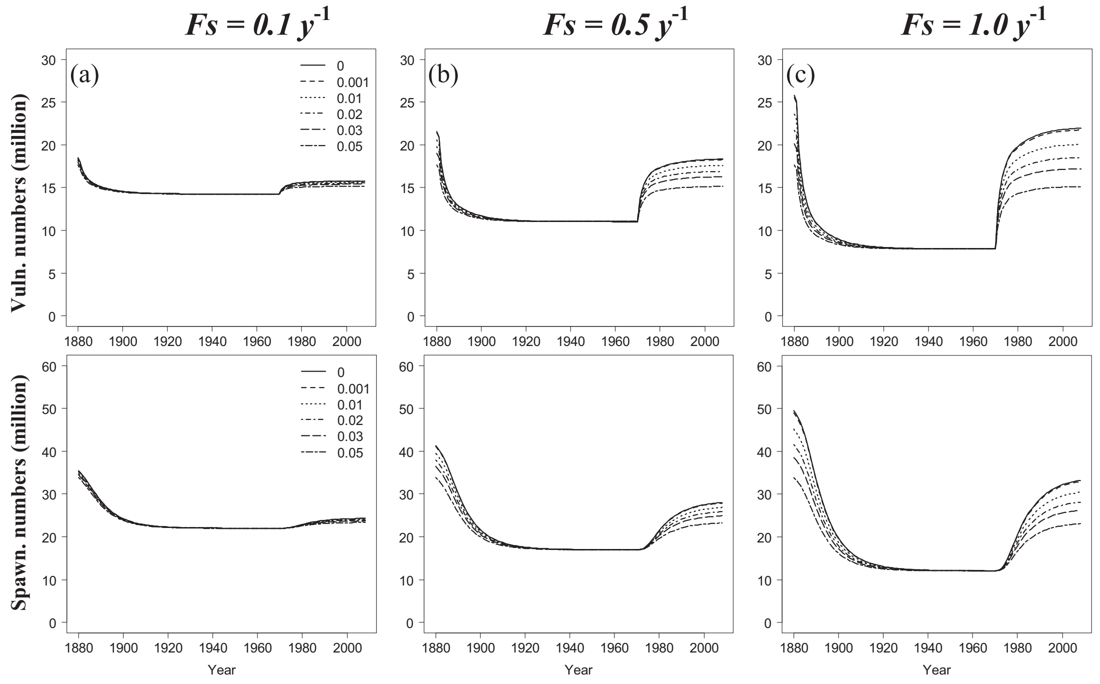

Fig. 4. Vulnerable (top panel) and spawning (bottom panel) numbers of fish for six values of M_{d0}, with bycatch mortality stopped after 90 years. Graphs show results for three scenarios of constant shrimp bycatch during the first 90 years: (a) Fs = 0.1 yr^{-1}; (b) Fs = 0.5 yr^{-1}; and (c) Fs = 1.0 yr^{-1}. Directed fishing mortality Fd was fixed at 0.1 yr^{-1} for all years in all graphs. R_0 was adjusted so equilibrium age-1 numbers were the same across all scenarios of M_{d0} within each bycatch scenario (see text).

For each different M_{d0} scenario, this resulted in a time series of 129 years, which matches the length of the catch time series in the stock assessment (SEDAR, 2009). Three different constant bycatch scenarios ($Fs = 0.0$, 0.5 and 1.0 yr^{-1}), were applied for the first 90 years. As in the previous section, R_0 was calibrated so that the equilibrium number of surviving age-1 fish was the same for all values of M_{d0}. This meant that, as M_{d0} was increased within any bycatch scenario, R_0 needed to be set higher to offset the increased mortality to produce the same number of age-1 fish. Within each bycatch scenario, the absolute and relative magnitude of recovery after stopping bycatch was reduced with increasing M_{d0} (Fig. 4). The initial spawning and vulnerable numbers were actually lower under high density-dependence scenarios (Fig. 4), despite having higher R_0, but equilibrated over time to the same level as lower density-dependence scenarios due to the increased productivity effect of M_{d0}.

2.3. Bayesian model

To illustrate the effect of timing of density-dependent mortality on estimates of stock status, reference points and projected future biomass, a Bayesian version of the model presented in Tables 2 and 3 was fitted to data from the 2009 assessment update (SEDAR, 2009). The model is a stock reduction analysis (Kimura et al., 1984; Walters et al., 2006) conditioned on western Gulf of Mexico catches from 1880 to 2008. Two versions of the model were run, with and without post-recruitment density-dependent mortality. As in previous sections, these models are referred to as the density-dependence model and conventional model, respectively, although both models include density-dependent recruitment from egg to the age-0 age class. In both models, leading estimated parameters were the natural logarithms of R_0 and CR. In the density-dependence model an additional leading parameter M_{d0} was estimated. Other estimated parameters included annual log recruitment deviations; annual log fishing mortalities; two variance parameters for the handline and bycatch age composition data; and catchability coefficients for the four indices of abundance.

We note that, since the 2009 assessment update does not include post-recruitment density-dependent mortality, yet both our models incorporate the vulnerability-at-age schedules output from the assessment model, it was not appropriate to apply formal model selection criteria to the two models.

2.3.1. Relative abundance indices

The models were fitted to four of the indices of abundance and two sets of age-composition data that were used in the 2009 assessment update (SEDAR, 2009). The model incorporated two types of error: (i) bias-corrected process error, assumed lognormal and applied to annual estimates of recruitment, i.e., $N_{0,t} = (\alpha E/(1+\beta E))e^{\omega_t - \sigma_R^2/2}$ with $\omega_t \sim N(0,\sigma_R)$ and standard deviation σ_R fixed at 0.3. We recognise that this is a low value for the standard deviation of log-recruitment anomalies. Preliminary tests indicated that higher values of σ_R created variability in results that reduced our ability to illustrate key differences between the two models.

The four indices of abundance were: (1) Commercial handline CPUE; (2) SEAMAP age-0 bottom trawl survey; (3) SEAMAP age-1 bottom trawl survey; and (4) SEAMAP larval survey, respectively assuming that these data were proportional to: (1) predicted vulnerable numbers in the handline fishery; (2) predicted number of age-0 fish; (3) predicted number of age-1 fish; and (4) predicted number of spawners. We assumed lognormal observation error, i.e., for each index j

$$I_{j,t} = q_j \hat{N}_{j,t} e^{\nu_t} \tag{18}$$

where $I_{j,t}$ is the observed index of abundance for index j in year t, q_j is the constant of proportionality (catchability coefficient) for index j, $\hat{N}_{j,t}$ is the model-predicted abundance being indexed by $I_{j,t}$, and ν_t is a random variable, where $\nu_t \sim N(0,\sigma_I)$. For $j = 1$–4, $\hat{N}_{j,t}$ represents: (1) VNh_t (T3.7); (2) $N_{0,t}$ (T3.3); (3) $N_{1,t}$ (T3.3); and (4) E_t (Eq. (2)), where predicted VNh_t was calculated using vulnerability-at-age for the handline fishery (not the combined schedules shown in Fig. 1).

The parameters q_j were treated as uncertain. The conditional maximum likelihood estimates (MLE) of q_j were used in the marginal negative log-likelihood L for each index j, i.e.,

$$L_j = \sum_{t=1}^{n_j} \left(0.5 \ln\left(\sigma_{Ij}^2\right) + \frac{d_{j,t}^2}{2\sigma_{Ij}^2} \right) \tag{19}$$

where $d_{j,t} = z_{j,t} - \bar{z}_j$, where $z_{j,t} = \ln(I_{j,t}) - \ln(\hat{N}_{j,t})$ and

$$\bar{z}_j = \frac{\sum_t^{n_j} z_{j,t}}{n_j} \tag{20}$$

where n_j is number of observations in index j. In this notation, $\bar{z}_j$ represents the maximum likelihood estimate of $\ln(q_j)$, conditional on other model parameters (Walters and Ludwig, 1994).

For simplicity the same σ_I was used for all four indices and was fixed at 0.3, therefore giving all these indices equal weight (see Section 2.4 for alternative treatment of σ_I). In the 2009 assessment update (SEDAR, 2009), annually-varying CV weights, based on the outcome of GLM models, were used to weight the different indices. Our assumption of fixed observation and process error in this section is a major simplifying assumption in our analysis that will have a large effect on model results (see Francis, 2011). However, since identical values were used in both our density-dependence and conventional models, the simplified model results should be sufficient to illustrate differences between the two models. As for σ_R, $\sigma_I = 0.3$ for all indices is likely unrealistically low, but helps to improve the comparative nature of this analysis.

2.3.2. Age composition

Age-composition data for both the shrimp and handline fisheries were assumed to conform to a multivariate logistic distribution (see Richards et al., 1997; Richards and Schnute, 1998), where the predicted proportion-at-age $P_{a,t}$ is a function of the predicted population age structure $N_{a,t}$ and vulnerability-at-age, where $\eta_{k,t,a}$, the residual difference between the observed $p_{t,a}$ and predicted $\hat{p}_{t,a}$ proportion in fishery k, at age a in time t is given by

$$\eta_{k,t,a} = \ln(p_{k,t,a}) - \ln(\hat{p}_{k,t,a}) - \frac{1}{A}\sum_{a=0}^{A}[\ln(p_{k,t,a}) - \ln(\hat{p}_{k,t,a})] \tag{21}$$

In this approach, similar to the approach used for q_k in the previous section, the marginal likelihood for the age-composition data for each fishery k was evaluated at the conditional maximum likelihood estimate of the residual variance τ_k, which was calculated as

$$\tau_k = \frac{1}{(A-1)T}\sum_{t=1}^{T}\sum_{a=0}^{A}\eta_{k,t,a}^2 \tag{22}$$

with the negative log-likelihood LA_k given by the log residual variance, weighted by the total number of observations, i.e.,

$$\mathrm{LA}_k = (A-1)T\ln(\tau_k). \tag{23}$$

Note that the residual variance τ_k was assumed to be the same for each year and age, i.e., a single variance term was marginalised for each fishery.

2.3.3. Catch

The model was conditioned on total catches, where annual log fishing mortality rates for each fishery (combined directed and shrimp) were estimated directly and used to predict catch using the equations in T3.4. Predicted catches were then fit to the observed catches, assuming residuals given by

$$\eta_{Ck,t} = \ln(C_{k,t} + o) - \ln(\hat{C}_{k,t} + o) \tag{24}$$

with o a small constant (1.e−10) to prevent undefined residuals in years without observed catch. The residuals were assumed to be normally distributed with standard deviation σ_C fixed at 0.02 to ensure almost perfect fit to observed catches. The negative log-likelihood LC_k is given by

$$\mathrm{LC}_k = \sum_{t=1}^{n_k} \left(0.5 \ln(\sigma_C^2) + \frac{\eta_{C,k,t}^2}{2\sigma_C^2} \right) \tag{25}$$

2.3.4. Prior probability distributions

Lognormal prior probability distributions were placed on the estimated parameters R_0 and CR, with mean 150 million (unfished recruits) and 150 (no units), respectively, both with standard deviation (SD) of 0.5 in log space. A CR value of 150 is equivalent to steepness, $h = 0.97$, which is the estimated value of steepness reported in the 2009 assessment update (continuity run). The mean of the R_0 prior was based on preliminary runs and was selected to keep the model away from states where catch exceeded biomass, while preventing extremely large, implausible values. No prior was placed on M_{d0}.

2.3.5. Objective function

The objective function consisted of six main components: (1) the four negative log-likelihoods of the relative abundance indices (Eq. (19)); (2) the negative log-likelihood of the catch-age proportions in the commercial handline fishery (Eq. (23)); (3) the negative log-likelihood of the catch-age proportions in the shrimp bycatch fishery (Eq. (23)); (4) the negative log-likelihood of the catch (Eq. (25)); (5) the prior probability distributions for model parameters; and (6) a penalty function that constrained the log recruitment anomalies ω_t to conform to a normal distribution, $\omega_t \sim N(0,\sigma_R)$.

2.3.6. Posteriors

Maximum posterior density (MPD) parameter values were estimated using AD Model Builder (Fournier et al., 2012). Posteriors were approximated using a Metropolis Hastings MCMC algorithm (Gelman et al., 1995), implemented in AD Model Builder, initialised at the MPD parameter values. The models were run for 5 million iterations, retaining every 2500th sample, resulting in 2000 posterior samples. The first 400 samples were removed to allow for burn in. The models were informally checked for convergence by examination of posterior trace plots and smoothness of posterior distributions.

2.3.7. Scenarios

The model was run in two configurations: (1) the density-dependence model (leading estimated parameters: $\ln(R_0)$, ln(CR), M_{d0}, $\ln(\omega_t)$ and log fishing mortality rates); and (2) the conventional model (leading estimated parameters: $\ln(R_0)$, ln(CR), $\ln(\omega_t)$ and log fishing mortality rates). In all other respects, the initial conditions, prior probability distributions and objective function were identical. The models were compared in terms of posterior estimates of numbers of spawning, vulnerable, age-0 and age-1 fish. In addition, posterior spawning biomass estimates relative to B_{MSY} under four constant bycatch scenarios were compared.

Both models were projected forward for 50 years under a management scenario with combined directed catches held constant at the 2008 level, and future shrimp bycatch mortality set to zero. Annual log-recruitment deviations were drawn from the posterior distribution. This simple scenario allowed comparison of the two models' predictions of the effect of stopping bycatch in future years. We chose to set the bycatch to zero (rather than the target 0.16 yr^{-1} or some other fixed level) because this represented an extreme policy and also ensured that bycatch was reduced from the current state in all scenarios, given the possibility that the models could predict current bycatch mortality less than 0.16 yr^{-1}.

2.3.8. Results

Both versions of the model produced similar fits to the data. The conventional model estimated median spawning numbers and vulnerable numbers to be almost four times those estimated in the density-dependence model, despite median estimated age-0 numbers in the density-dependence model around five times greater than in the conventional model (Fig. 5). Median estimates of R_0 (millions of fish) were 952.2 (SD = 392.1) and 202.7 (SD = 50.0) from the density-dependence and conventional model, respectively. The density-dependence model estimated the density-dependent mortality parameter M_{d0} to be non-zero, with a median posterior estimate of $M_{d0} = 0.023\ \mathrm{yr}^{-1}$ (SD = 0.004), although it should be noted that there was a very strong positive correlation between posterior estimates of M_{d0} and $\ln(R_0)$ (Fig. 7). This implies that the data are consistent with either a larger unfished recruitment with stronger density-dependent age-0 mortality or a smaller unfished recruitment with weaker density-dependent age-0 mortality. This is reflected in the smaller range in estimates of numbers of age-1 fish in the density-dependence model, despite very large variability in estimated age-0 fish (Fig. 5) and the narrower probability intervals in general for the density-dependence model. Recall that a population with high density-dependent mortality can be thought of as more productive than a population with low or no density-dependent mortality. This is, in part, why the density-dependence model can explain the observed historical catches with a smaller number of spawners than the conventional model (Fig. 5).

The two models produced markedly different results in terms of estimated vulnerable numbers (Fig. 5), with lower numbers in the density dependence case, implying higher estimates of directed fishing mortality. There was also a large difference in estimated spawning biomass relative to the reference point B_{MSY} (Fig. 6), with the conventional model predicting a larger and more rapid stock recovery under a future no-bycatch scenario than the density-dependence model. Note that the horizontal lines in Fig. 6, which represent median posterior estimates of reference points under the four constant bycatch mortality scenarios, are closer together for the density-dependence model than for the conventional model, indicating a smaller relative impact of bycatch in the density-dependence model, as was illustrated in the deterministic simulations above.

The density-dependence model estimated median posterior B_{MSY} to be between 57.9 and 303.6 million lb, depending on the assumed fixed bycatch mortality, whereas the conventional model estimated the range in median posterior B_{MSY} estimates to be 178.7–1140.1 million lb. In both models, the lowest median posterior estimate of B_{MSY} was obtained under the highest bycatch mortality ($Fs = 1.0\ \mathrm{yr}^{-1}$). The density-dependence model estimated median posterior 2008 spawning biomass to be below B_{MSY} for the $Fs = 0.0$ and 0.16 yr^{-1} scenarios; and at or above B_{MSY} for the $Fs = 0.5$ and 1.0 yr^{-1} scenarios (Fig. 6), although the 95% probability interval of the posterior envelope extended below B_{MSY} in 2008 for all scenarios except $Fs = 1.0\ \mathrm{yr}^{-1}$. The conventional model estimated median 2008 spawning biomass to be above B_{MSY} for all scenarios, with the 95% probability interval of the posterior envelope extending below B_{MSY} for the $Fs = 0.0$ and 0.16 yr^{-1} scenarios. While the difference between the predictions of the two models in terms of

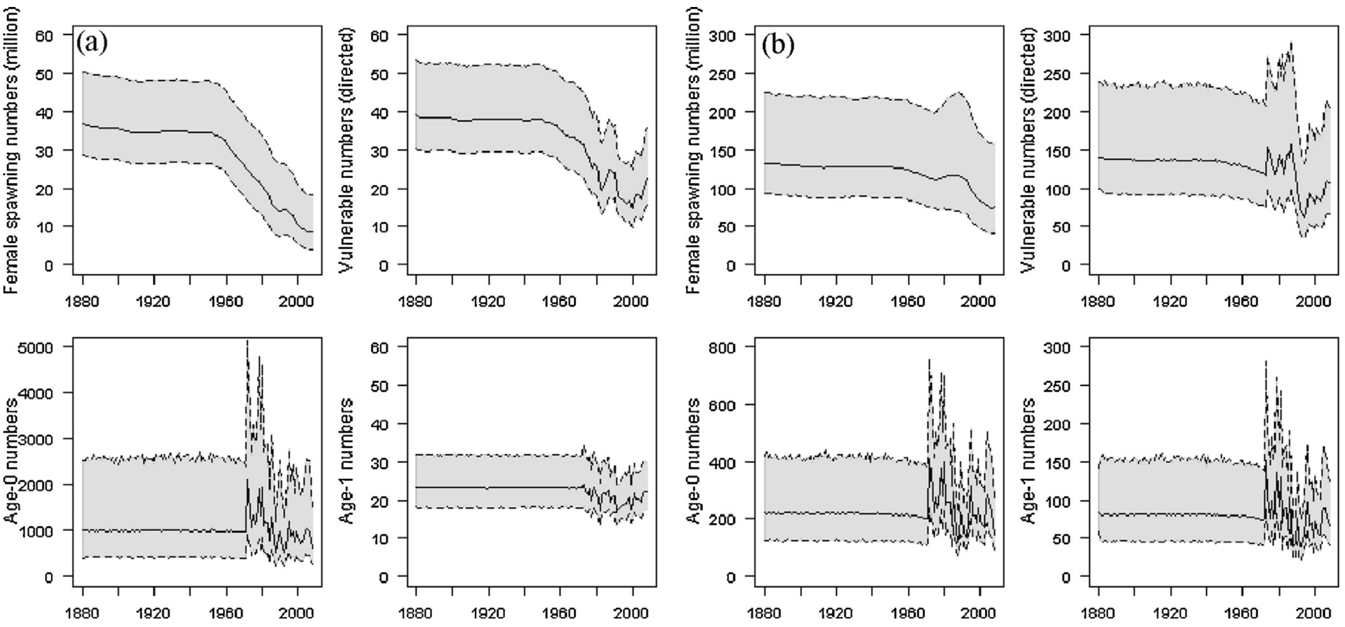

Fig. 5. Posterior estimates (with 95% probability interval) of female spawning numbers; vulnerable numbers (combined directed fishery); age-0 numbers and age-1 numbers (millions of fish) from: (a) the density-dependence model; and (b) the conventional model. In each graph, the median posterior estimate is shown as a solid black line. Note different scales.

stock status is striking, we note that interpretation of the reference points here is not straightforward because each value of B_{MSY} was calculated using a long-term fixed value of shrimp bycatch mortality. This highlights the problem of defining reference points in the presence of fisheries that catch different demographic components of the population.

These results illustrate that interpretation of stock size, the relative impacts of directed and bycatch fishing mortality and stock recovery potential is strongly influenced by structural assumptions about timing of density-dependent mortality.

2.4. Simulation-estimation study

2.4.1. Methods

In the previous section, while the density-dependence model estimated M_{d0} to be non-zero, this parameter was confounded with the estimate of R_0 (Fig. 7), and results were influenced by fixed variance parameters and other simplifying assumptions in the model. Simulation-estimation studies can be useful because underlying parameter values, reference points and stock status are known perfectly. The effects of making incorrect assumptions about model structure can also be investigated, especially with respect to projected performance of alternative management actions.

A simulation-estimation study was done to: (i) investigate the estimability of leading model parameters under increasing variability in recruitment and noise in abundance indices and age-composition data; and (ii) to evaluate the effect of making an incorrect assumption about timing of density-dependent mortality on evaluation of stock status and projected stock recovery.

The study included an operating model and an assessment model. The operating and assessment models were the same as those described in Tables 2 and 3, with the addition of estimated process and observation errors. Here we used the approach of Walters and Ludwig (1994) and evaluated the marginal likelihood

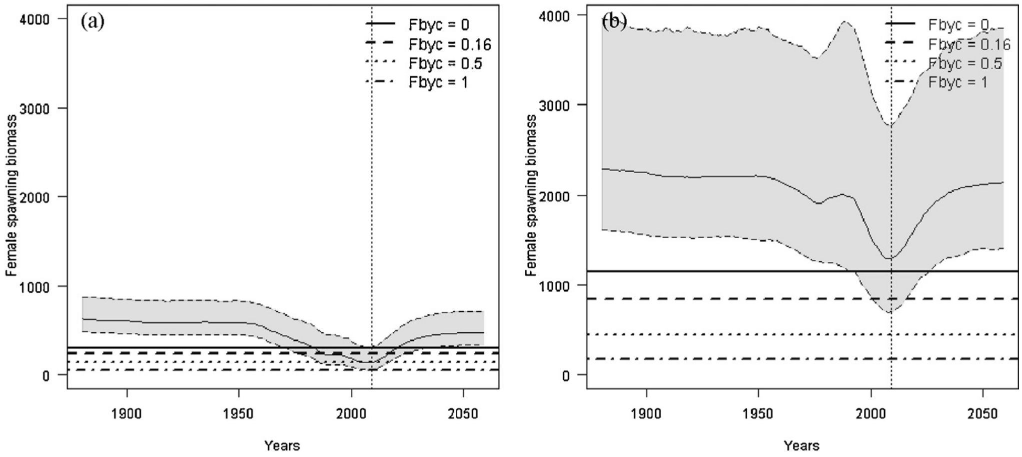

Fig. 6. Posterior estimates (with 95% probability interval) of historical and projected female spawning biomass (million lb) relative to biological reference points B_{MSY}, calculated under four fixed scenarios for constant bycatch *Fs* (see text and figure legends) for: (a) the density-dependence model; and (b) the conventional model (right). In each graph, the median posterior estimate is shown as a solid black line (historical estimate) and broken black line (50 projected years with directed catch in numbers held constant at the 2008 level and bycatch set to zero in all future years). The vertical line represents first year of projections.

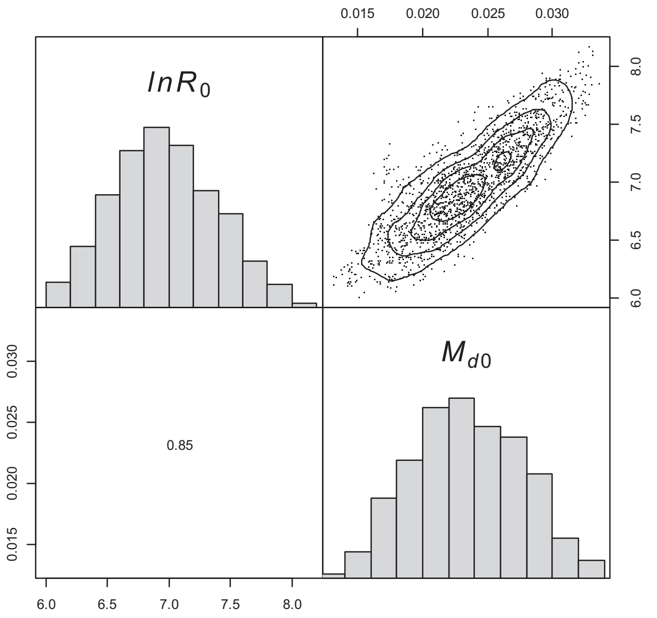

Fig. 7. Histograms and contour plot for the joint posterior probability density of M_{d0} and $\log(R_0)$ from the density-dependence model. The correlation coefficient is shown in the lower left panel.

of the observations at the conditional maximum likelihood estimate of σ_{Ij}, i.e.,

$$L_j = \frac{ss^2}{2(n_j - 1)} \tag{26}$$

where ss^2 is the sum of squared differences between log observed and predicted indices of abundance and n_j is number of observations in each index j (Walters and Ludwig, 1994). This approach essentially allows the data to "self-weight" (see Walters and Ludwig (1994) for derivation). We did not use this approach in the previous section because we could not achieve satisfactory model convergence, possibly because of conflicting signals in the spawner and CPUE indices of abundance (SEDAR, 2009).

As described in the previous section, both operating and assessment models were stock reduction analyses conditioned on the observed historical catches used in the 2009 red snapper assessment update. The operating model was used to simulate indices of abundance and age composition data with known ('true') underlying parameter values and associated observation and process error. Lengths of the time series for indices and age composition data were set to be the same as in the previous section. The operating model was conditioned on the observed catches used in the previous section, where the annual fishing mortality rate for each fishery (combined directed and shrimp bycatch) was determined by solving the equations in T3.4, using the observed catches and vulnerabilities, and the estimated vulnerable numbers in each fishery (T3.6 and T3.7). The catch equations were solved for Fs_t and Fd_t using a Newton–Raphson algorithm. The algorithm was checked for accuracy using simulated data for which underlying fishing mortality rates were known. Age composition data were generated by sampling from the simulated proportions at age in the bycatch and directed fisheries, assuming a multivariate logistic distribution of errors with fixed variance τ_k (see below and Table 4 for values). The assessment model was fitted to the simulated data using the likelihood functions described in the previous sections to produce posterior distributions of estimated parameters that could be compared with the true underlying parameter values and stock status. As in the previous section, models were projected forward for 50 years with combined directed catches held constant at the 2008 level, and future shrimp bycatch mortality set to zero.

We note that there are alternative options for evaluating uncertainty in simulation-estimation studies. One approach is to use the operating model with sampled error terms to generate a large number of datasets for each scenario, then run the assessment model once with each dataset to get an estimate of uncertainty across the datasets. A simpler approach is to generate a single dataset for each scenario and run a Bayesian assessment to generate posterior distributions of results to gain estimates of uncertainty. We have chosen the latter approach for simplicity. Unless otherwise stated, the assessment models were run for two million iterations, retaining every 1000th sample, resulting in 2000 posterior samples. The first 500 samples were removed to allow for burn-in. There were two parts to the study, described below.

2.4.1.1. Estimability of leading model parameters CR, R_0 and M_{d0}. In all, there were six scenarios that varied in the true parameter values used to generate the simulated data in the operating model (Table 4). The density-dependence model was used as both operating and assessment model in all scenarios. The fixed values chosen for the six scenarios were arbitrarily chosen to bracket a range of circumstances for parameter-estimation. Scenarios were compared to a base case scenario (S1) which had underlying true parameter values of $\mathrm{M}_{d0} = 0.01\ \mathrm{yr}^{-1}$, $\sigma_R = 0.2$, $\sigma_I = 0.2$ (for all indices) and $\tau_k = 0.1$ (for both shrimp *s* and combined directed *d* fisheries). These variances are unrealistically low, especially σ_R, but were selected to produce unbiased estimates of M_{d0} in the assessment model for use as a base case.

For scenarios S2–S6, these parameters were varied systematically (Table 4). Alternative true values for these parameters were $\sigma_R = 0.6$ or 0.9, $\sigma_I = 0.6$, $\tau_s = 0.5$ or 1.0 and $\tau_d = 0.5$. These values had the effect of increasing variability in the underlying recruitment, indices of abundance, and bycatch and combined directed age compositions, respectively. A sixth, high variability scenario (S6) used higher values for all four variance parameters (Table 4). Underlying true values for leading parameters, R_0 and CR were 150 million recruits and 150, respectively, for all scenarios. Estimated parameters were $\ln(R_0)$, $\ln(\mathrm{CR})$, M_{d0}, log recruitment deviations and log fishing mortality rates, with marginal likelihoods estimated at the conditional maximum likelihood estimate for σ_{Ij}, q_j and τ_k as described above. In all assessment models, σ_R was fixed at 0.3. A lognormal prior was placed on CR, with mean 150 and standard deviation (SD) of 0.5 in log space. Preliminary tests indicated that the assessment models could produce plausible estimates of R_0

Table 4
Scenarios used in the operating model for the simulation–estimation study (Section 2.4i). All simulations were done with true CR = 150 and true R_0 = 150 million. The same value of true σ_I was used for all four indices of abundance.

Scenario	True M_{d0} (yr^{-1})	True σ_I	True σ_R	True τ_s	True τ_d
S1: Base	0.01	0.2	0.2	0.1	0.1
S2: Higher variability (recruitment)	0.01	0.2	0.6	0.1	0.1
S3: Higher variability (recruitment)	0.01	0.2	0.9	0.1	0.1
S4: Higher variability (indices of abundance)	0.01	0.6	0.2	0.1	0.1
S5: Higher variability (bycatch age comp. data)	0.01	0.2	0.2	1.0	0.1
S6: Higher variability (ages, indices, recruitment)	0.01	0.6	0.6	0.5	0.5

without a prior being placed on this parameter (i.e., estimates did not tend towards extreme high values as in the previous section). This was likely because the simulated indices of abundance and age composition data were more consistent with each other and contained more information about model parameters than the real data. No prior was placed on M_{d0}.

2.4.1.2. Effect of incorrect assumptions about post-recruitment density-dependent mortality. Section 2.3 showed that structural assumptions about the timing of density dependence could have a large effect on conclusions drawn from a stock assessment. To illustrate this further, four scenarios were run, with the density-dependence model and the conventional model used as operating model and assessment model in alternative configurations: (C1) operating model = density-dependence model; assessment model = density-dependence model (*correct assessment model*); (C2) operating model = density-dependence model; assessment model = conventional model (*incorrect assessment model*); (C3) operating model = conventional model; assessment model = density-dependence model (*incorrect assessment model*); and (C4) operating model = conventional model; assessment model = conventional model (*correct assessment model*). This approach is similar to a four-way contingency analysis, where the scenarios of most interest are: C2, representing a "Type II" error (false negative in terms of the presence of post-recruitment density-dependent mortality); and C3, representing a "Type I" error (false positive). In all four scenarios, reference points were generated using the true operating model.

Underlying true values for leading parameters, R_0 and CR were 150 million recruits and 150, respectively, for all scenarios. As in the previous section, a lognormal prior was placed on CR, with mean 150 and standard deviation (SD) of 0.5 in log space. No prior was placed on R_0 (or on M_{d0} in the density-dependence model). In all assessment and operating models σ_R was fixed at 0.3. While this value is likely to be unrealistically low, it was selected so that the effects incorrect structural assumptions could be separated from effects of bias due to high process errors (see results of previous section). True σ_I and both true τ_k parameters were fixed at 0.2. Estimated parameters were $\ln(R_0)$, $\ln(\mathrm{CR})$ (and M_{d0} where applicable), log recruitment deviations and log fishing mortality rates, with marginal likelihoods estimated at the conditional maximum likelihood estimates of σ_{Ij}, q_k and τ_k. MCMC chains in the C1 and C3 configurations (density-dependence model as assessment model) were run for five million iterations to improve convergence properties. Every 2,500th sample was retained, resulting in 2000 posterior samples, with the first 400 samples removed to allow for burn-in.

2.4.2. Results

2.4.2.1. Estimability of model parameters and stock status. The median posterior estimate of M_{d0} in the base case scenario (S1) was unbiased (Fig. 8). There was slight bias in the estimates of

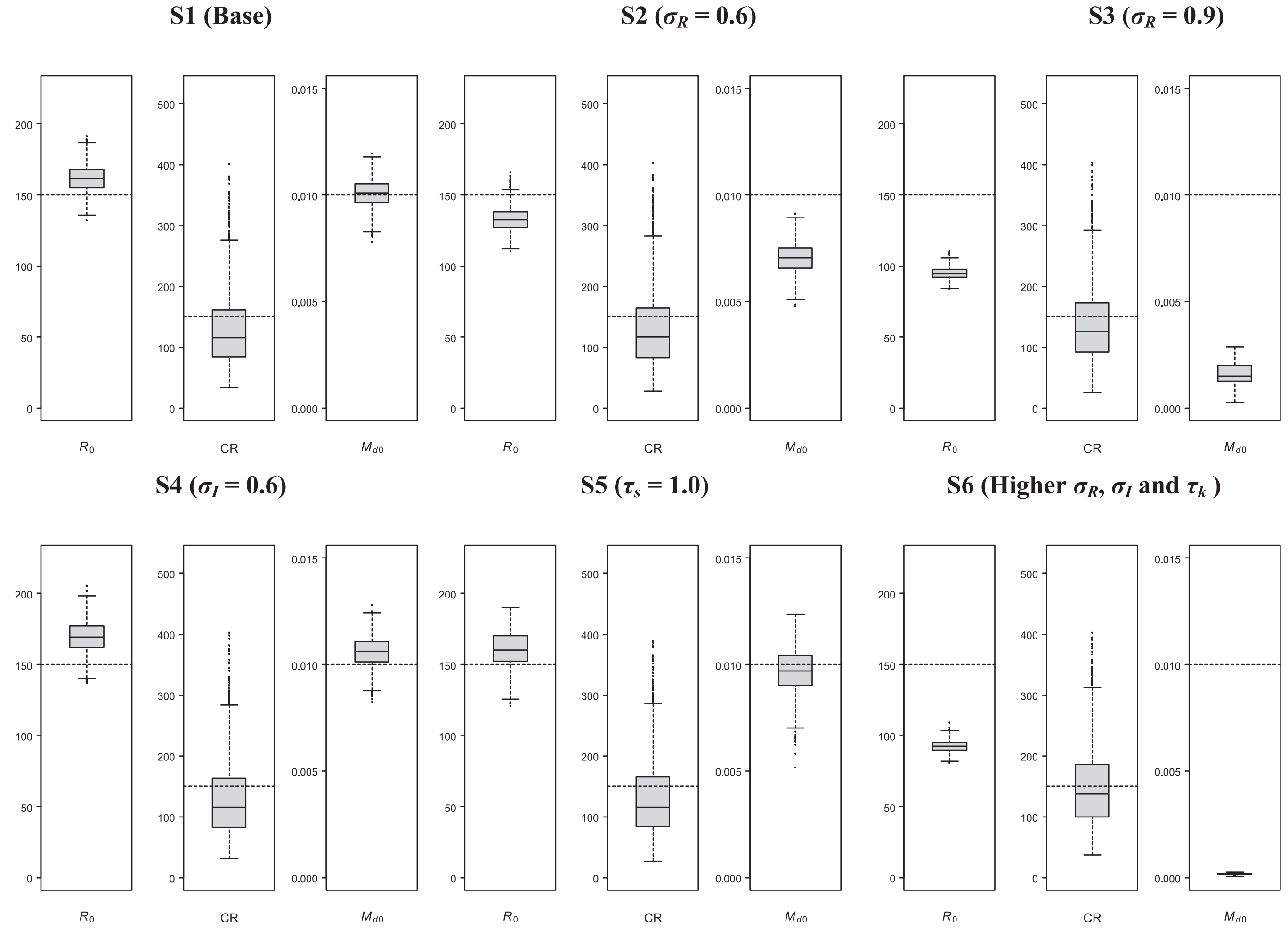

Fig. 8. Posterior estimates of leading parameters from six scenarios in the simulation studies (see Table 4). Horizontal dashed lines show true parameter values. Median estimates are shown as a black bar. Boxes represent the interquartile range (IQR). Whiskers represent 1.5 IQR, with outliers shown as dots. Note that the density-dependence model was used as both operating and assessment model in all scenarios.

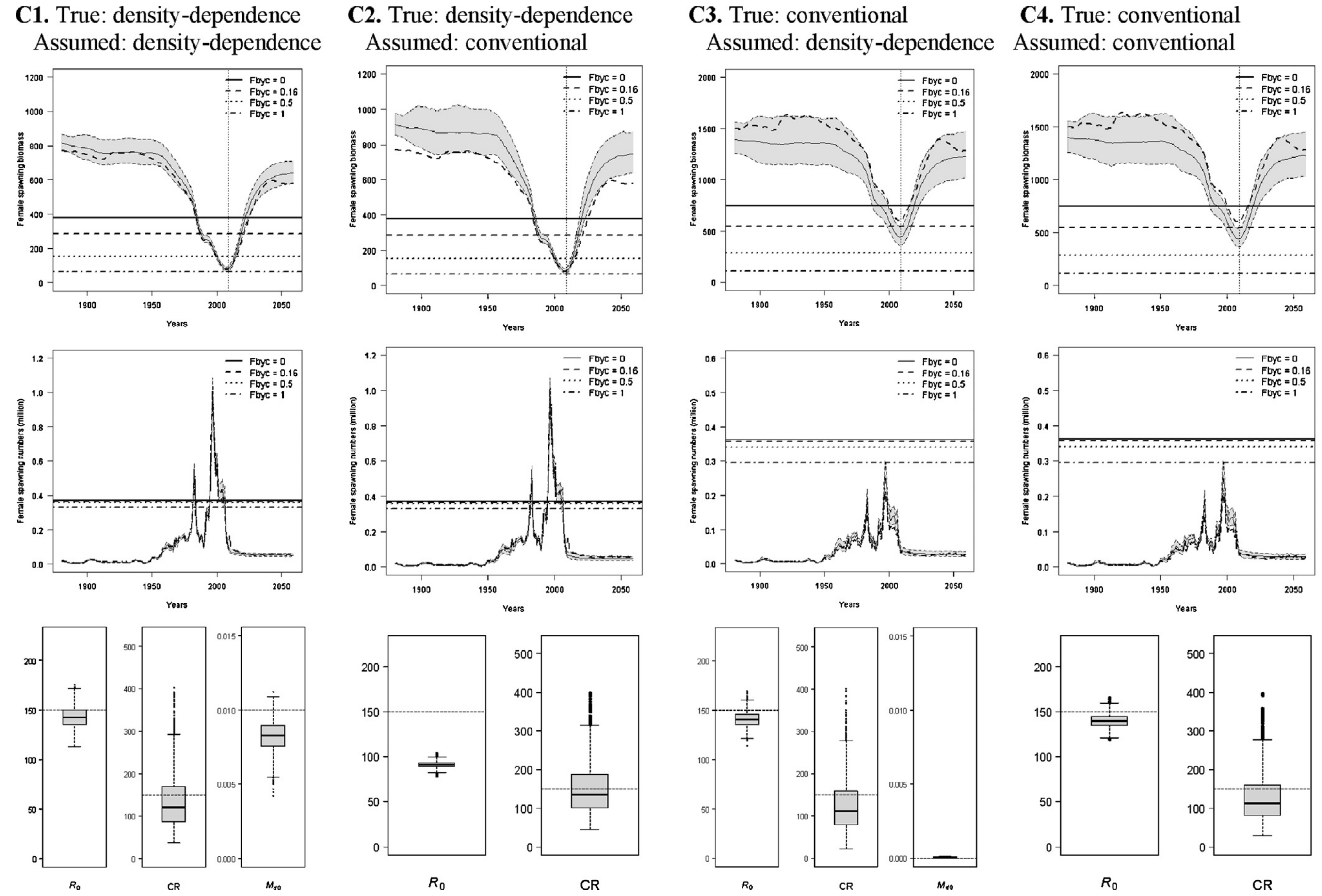

Fig. 9. Posterior estimates (with 95% probability interval) of spawning biomass (million lb; top panel), directed fishing mortality (middle panel) and parameter estimates (bottom panel) for the four configurations of true vs assumed model (C1–C4). Thin solid lines represent the median posterior estimates, thin dotted lines represent median projected values, thick dotted lines represent the true values. Horizontal lines represent true B_{MSY} or F_{MSY} under four bycatch scenarios. The vertical line represents first year of projections. Boxes represent the interquartile range (IQR). Whiskers represent 1.5 IQR, with outliers shown as dots. Note different scales.

R_0 and CR, although the true values were within the probability interval for both parameters. The posterior estimate of CR was very imprecise. Increasing σ_R to 0.6 (S2) resulted in negative bias in the estimates of R_0 and M_{d0}. This effect was greatly increased when σ_R was increased to 0.9 (S3), with the entire posterior ranges for R_0 and M_{d0} well below the true values. Increasing the variance in the simulated observations (S4) slightly increased positive bias in the estimates of R_0 and M_{d0} and also reduced precision. Increasing the variance in the simulated bycatch age composition data (S5) did not cause bias in estimates of R_0 and M_{d0} but did decrease the precision in these estimates. Finally, increasing the variance in the simulated observations (indices), recruitment and age composition data simultaneously (S6) resulted in M_{d0} to be estimated near zero with large negative bias in the estimate of R_0 (Fig. 8). Convergence properties tended to deteriorate as process errors increased, although trial runs with different chain lengths implied that the median estimates were stable. In all cases, the direction of bias in the estimates of R_0 and M_{d0} was the same, due to strong confounding between these two parameters (see Fig. 7). We note that posterior estimates of CR tended to be much more uncertain than estimates of ln(R_0) or M_{d0} in all scenarios. We suggest this is due to the relatively reduced role of this parameter in population regulation when density-dependent processes are also operating on recruited age classes, resulting in less information in the data about this parameter.

2.4.2.2. Effect of incorrect structural assumptions about post-recruitment density-dependent mortality. Two of the four configurations paired the correct assessment model with the correct operating model (C1 and C4). Not surprisingly, these models performed reasonably well in terms of their ability to estimate current spawning biomass and very well in estimating fishing mortality (the true trajectory was inside the posterior envelope in both cases) (Fig. 9). In configuration C1, very good estimates of spawning biomass and directed fishing mortality were obtained, despite slight negative bias in estimates of both log(R_0) and M_{d0}. In this case, the assessment model essentially compensated for underestimating M_{d0} by also underestimating R_0. The results of the previous section suggest that the negative bias in estimates of these parameters was in part due to the choice of value of σ_R used in the operating model.

The model that incorrectly assumed no post-recruitment density-dependent mortality (C2) overestimated spawning biomass, with median posterior estimates of both historical and projected spawning biomass above the true biomass (Fig. 9, top panel). Posterior estimates of directed fishing mortality were well-estimated, however. The close agreement in estimates of fishing mortality was because the model was able to closely match the true vulnerable biomass for the recent period of high catches (post-1970) by greatly underestimating the parameter that determines the overall scale of the population, R_0 (Fig. 9, bottom panel) despite the incorrect assumption of no density-dependent age-0 mortality.

The model that incorrectly assumed the existence of post-recruitment density-dependent mortality (C3) slightly underestimated historical and projected spawning biomass, although the

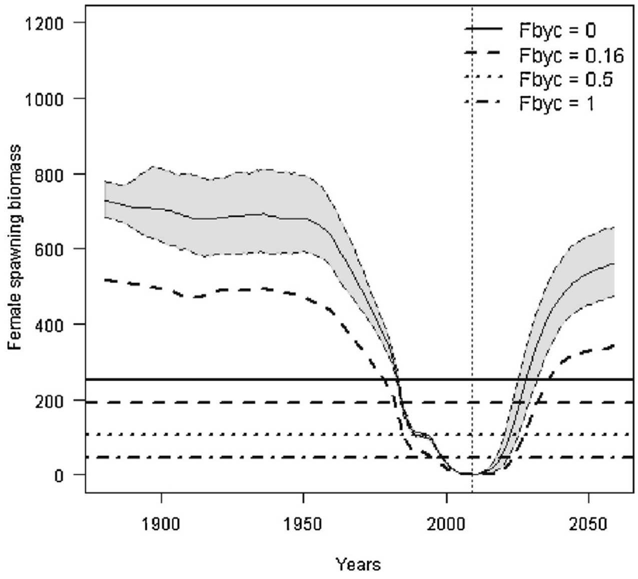

Fig. 10. Posterior estimates (with 95% probability interval) of spawning biomass (million lb) for the C2 configuration of true vs assumed model (see Fig. 9 for definition), with true M_{d0} set to 0.02. Thin solid lines represent the median posterior estimates, thin dotted lines represent median projected values, thick dotted lines represent the true values. Horizontal lines represent true B_{MSY} or F_{MSY} under four bycatch scenarios. The vertical line represents first year of projections.

degree of bias was less than in C2 (Fig. 9) and the true values were inside the posterior envelope in all years. In this case, M_{d0} was estimated to be near zero and R_0 was estimated with very little bias, allowing the model to more closely match the true biomass values (Fig. 9). Note that the true vs estimated rates of decline and recovery in C2 are different (i.e., if the estimated spawning biomass series were rescaled to begin at the same value as the true series, the two trajectories would not overlay each other). The true series declines and recovers at a different rate than the estimated series, illustrating the effect of M_{d0} on productivity. In C3, the true and posterior estimated series are almost parallel, suggesting only a scale effect. This was because the conventional model is a specific case of the density-dependence model and is therefore able to mimic the behaviour of the conventional model by estimating M_{d0} to be close to zero, resulting in estimates of stock status and rate of recovery closer to true values. While the conventional model in C2 also achieved good estimates of current stock status by underestimating R_0, estimates of recovery potential were overestimated because it could not capture the dampening effects of M_{d0} when age-0 fish were released from bycatch mortality in the projections. This result is emphasised by repetition of the C2 configuration with the true value of $M_{\mathrm{d}0}$ in the operating model increased to $0.02\,\mathrm{yr}^{-1}$ (all other parameters the same as in the previous run). Increasing the true underlying value of $M_{\mathrm{d}0}$ resulted in even greater overestimation of historical and future biomass in the C2 configuration (Fig. 10).

We emphasise that these results were highly dependent on assumed fixed parameter values, especially density-independent M_a, the variance parameters σ_R, σ_I, σ_C and τ_k, and our assumptions about prior probability distributions and vulnerability. The previous section illustrated the effect of the variance parameters on model performance, with estimability of parameters worsening as variance in indices of abundance, recruitment and age composition data increased.

3. Discussion

This paper explored the implications of timing of density-dependent juvenile mortality and simultaneous bycatch in an age-structured stock assessment model. Disaggregating the parameters of the Beverton–Holt stock recruit function into density-dependent and independent natural mortality and density-independent fishing mortality components was straightforward (Beverton and Holt, 1957; Walters and Martell, 2004; Brooks and Powers, 2007). A major effect of introducing a density-dependent survival component to the age-0 to age-1 model dynamics was to reduce the proportion of fish surviving their first year, while also stabilising age-1 numbers across a range of bycatch fishing mortality rates. Therefore, for the same number of age-0 recruits, while the overall scale of the population was reduced, the productivity of the population was effectively increased as density-dependent survival buffered the stock from the impacts of bycatch. This was also reflected in the rate and magnitude of population recovery following cessation of bycatch – recovery rates were less variable across a range of bycatch rates in scenarios with higher density-dependence but the absolute magnitude of recovery was reduced. These results are consistent with the findings of Brooks and Powers (2007), who showed that relative impacts of exogenous sources of mortality (i.e., bycatch) were reduced if they occurred before or during a compensatory stage. These authors also showed that a greater proportion of unfished recruits would remain if bycatch occurred during a compensatory stage, compared with the case when bycatch occurred after density-dependent mortality had ceased. This is consistent with our finding that the same spawning and vulnerable numbers could be produced from successively smaller pools of initial spawning and vulnerable numbers as the magnitude of density-dependent mortality increased.

These scale and productivity effects were also reflected in the equilibrium reference points, MSY, B_{MSY} and F_{MSY}. In the absence of post-recruitment density-dependent mortality, fishery reference points, especially MSY and B_{MSY}, were strongly impacted by the amount of bycatch mortality used in the calculation. In our deterministic example, in the absence of post-recruitment density-dependent mortality, there was an approximate four-fold decrease in MSY as constant bycatch mortality was increased from 0.0 to $1.0\,\mathrm{yr}^{-1}$. Our results illustrate the problematic nature of defining and calculating reference points in the presence of numerous sources of mortality that affect different demographic components of the population. In our example, it was impossible to define reference points for the combined directed fishery without specifying a bycatch mortality rate. Similarly, future projections of stock status could only be made once a fixed bycatch rate was specified – both for calculation of reference points and for projecting forward. Powers (2005) discussed this problem with reference to U.S. fisheries and concluded that fishery managers must determine their desired mix of fishing (i.e., directed catch vs bycatch) before MSY and other fishery reference points can be defined. This problem is not confined to fisheries with bycatch. It is fairly common in fishery stock assessments to combine target fisheries with different vulnerabilities into an aggregate fishery with an overall vulnerability function and calculate the reference points for the aggregate fishery. This approach implicitly assumes that the relative proportions of the component fisheries remains constant on average throughout the fishing season. This was discussed by Goodyear (1996), who concluded that MSY is an insufficient management objective for multi-gear fisheries with different vulnerabilities, unless long-term objectives for factors such as age composition of the catch are specified. The problem also applies to fisheries that compete with predators (e.g., marine mammals), where reference points cannot be defined without some assumption about predation mortality (Spencer and Collie, 1996; Collie and Gislason, 2001; Walters et al., 2005).

This problem is compounded with the addition of density-dependent juvenile mortality. In our example, increasing density-dependent age-0 mortality reduced the magnitude of MSY and

B_{MSY} (for the fixed R_0 scenario) and also reduced the range of values for these reference points among bycatch scenarios. Therefore, failure to account for density-dependent mortality in juveniles caught as bycatch could result in overestimation of MSY in the directed fishery, as well as overestimation of the impacts of bycatch. Our findings are in qualitative agreement with those of McAllister and Gazey (2005), who used a discrete stock reduction analysis to compare results from models that assumed "benthic-limitation" (density-dependent mortality occurring before bycatch) to those that assumed "reef-limitation" (density-dependent mortality occurring after bycatch at either age 1 or age 2). For the reef-limitation scenario (the case closest to the one presented here) they reported that estimated MSY decreased by a factor of up to four, and estimated current abundance shifted from five times B_{MSY} to about half B_{MSY}, compared to the benthic-limitation scenario.

Gallaway et al. (2009) concluded that red snapper early life settlement behaviour was consistent with density-dependent juvenile mortality. Gazey et al. (2008) analysed length-frequency data for red snapper caught as bycatch in Gulf of Mexico shrimp fisheries and found some evidence for density-dependent juvenile mortality in cohorts up to one year old. The present study also estimated the density-dependent mortality parameter to be non-zero, although it should be remembered that apparent density-dependence in juvenile survival can arise as a result of an "errors-in-variables" effect (Hilborn and Walters, 1992) where the data show similar levels of recruitment across a broad range of spawners due to measurement errors in number of spawners. Beverton (1995) proposed the "concentration hypothesis", which predicted higher compensation and lower annual deviations in recruitment for fish populations (like red snapper) whose juveniles concentrate on nursery grounds. Iles and Beverton (2000) analysed stock-recruitment data for 63 fish stocks and found general support for the concentration hypothesis, although they found some exceptions. A large number of studies have demonstrated mechanisms of density-dependent mortality in reef-associated (e.g., Hixon, 1998; Rose et al., 2001; Hixon and Jones, 2005) and temperate (e.g., Beverton and Iles, 1992; Myers and Cadigan, 1993; Martino and Houde, 2012) fish populations. However, most of these authors note the difficulty relating specific density-dependent processes with population regulation (see also Cowan et al., 2010). While the present study was able to characterise the linkage between density-dependence and population productivity and scale, our results suggest that the magnitude of density-dependent juvenile mortality may be difficult to characterise due to strong confounding with other parameters, especially in the presence of strong observation or process error. The 1999 (Schirripa and Legault, 1999), 2005 (SEDAR, 2005) and 2009 (SEDAR, 2009) red snapper assessments all recognised the possible existence of density-dependent juvenile mortality but were unable to reach consensus on the timing and magnitude of density-dependent mortality or on the best approach for its inclusion into a stock assessment (Gazey et al., 2008).

Our simulation-estimation study showed that failure to account for post-recruitment density-dependent mortality could lead to overestimation of true abundance, stock status and recovery potential. The two model configurations that had the correct assessment model paired with the correct operating model performed reasonably well in terms of their ability to estimate spawning biomass and fishing mortality, although these results were generated with low levels of recruitment and observation errors. Performance would be expected to deteriorate in situations with greater underlying variances (e.g., Methot and Taylor, 2011; this study). When the true state of nature included post-recruitment density-dependent mortality, the conventional model overestimated spawning biomass, with posterior estimates of both historical and projected spawning numbers above the true biomass. This suggests that, depending on the magnitude of density-dependent mortality, the rate of population recovery could be overestimated if true underlying post-recruitment density-dependent mortality is ignored. When the true state of nature did not include post-recruitment density-dependent mortality, the density-dependence model underestimated spawning biomass, although the bias was small. In this case, M_{d0} was estimated to be near zero and R_0 was estimated with little bias, allowing the model estimates to more closely match the true biomass. Because the conventional model is a specific case of the density-dependence model, the density-dependence model was able to mimic the behaviour of the conventional model to some extent by estimating M_{d0} to be close to zero. This suggests that it may be advisable to use the density-dependence model if there is a possibility that post-recruitment density-dependent mortality is a factor governing population dynamics, although more extensive testing over a much broader range of scenarios would be needed, including those with alternative settings for leading parameters such as the compensation ratio, vulnerability-at-age, and observation and process error variances.

We found positive confounding between R_0 and M_{d0} in all of our attempts to estimate these parameters, both with real and simulated data, and the confounding became worse as underlying variability in the data increased. Without a strong signal in the data, particularly the age-0 to age-1 age-composition data, it may not be possible to reliably estimate these parameters simultaneously. Because these parameters are so strongly linked (i.e., observations may be equally well explained by a large population with strong density-dependent mortality, or a smaller population with little to no density-dependent mortality), placing a strong prior on either parameter will force the model to a particular state if the data are uninformative about these parameters. Given our finding that R_0 and M_{d0} are not independent *a posteri*, it may make more sense to place a prior on the equilibrium unfished number of age-1 fish. We have not explored this possibility but suggest it is worth further investigation.

3.1. Caveats and limitations

We considered a very simple case where simultaneous bycatch and density-dependent mortality only occur in age-0 fish. In the red snapper population, these processes are likely occurring in age-1 and even possibly age-2 fish (Gallaway et al., 2009). Our assessment model was highly simplified compared to the actual red snapper stock assessment (SEDAR, 2009), used fixed variances in the assessment models and, in particular, used vulnerability-at-age and natural mortality estimates output from the stock assessment. Therefore, while we have provided a tractable framework for representing density-dependent juvenile mortality, based on established theoretical concepts, our results should be viewed only as illustrative and cannot be compared to the results of the real assessment.

An extension of this work could be to apply a version of the model that has simultaneous density-dependent mortality and fishing mortality up to age 25 months. Presumably, the effects reported here would be more substantial with the addition of more age-classes undergoing simultaneous fishing and density-dependent mortality. A further extension would be to include estimation of vulnerabilities-at-age in the directed and bycatch fisheries, as it is probable that our results were biased by our choice to use fixed outputs from a stock assessment model that had a number of structural differences to our own models. Mortality and vulnerability to fishing gear are known to be confounded, especially when the vulnerability schedule is dome-shaped (Thompson, 1994). Given the spatial distribution of the bycatch and directed fisheries relative to the distribution of the red snapper population in the Gulf of Mexico, several of the vulnerability-at-age schedules, including for the bycatch and directed handline fishery, are known to be strongly dome-shaped (SEDAR, 2009; Cowan, 2011). In light of the present findings, confounding among vulnerability and density-dependent and independent mortality parameters would therefore be expected. Investigation of sources of bias and confounding due to estimation of dome-shaped vulnerability-at-age as well as density-dependent mortality parameters could be incorporated into a simulation-estimation framework similar to that presented here. Other assumptions about natural mortality could also be considered. For example, we assumed, for comparative purposes, that density-independent age-0 mortality was the same for both the density-dependence and conventional models. In reality, it is possible that the value of density-independent age-0 mortality is lower in the presence of density-dependent mortality than in its absence. Other treatments of natural mortality at age should also be considered (e.g., a Lorenzen function), or alternative values for M in fully-recruited age classes. McAllister (2005b) suggested methods for developing priors for M in age-0 and age-1 snapper and this has also been an area of active research for red snapper in the Gulf of Mexico (e.g., Szedlmayer et al., 2005; Brooks and Porch, 2005).

3.2. Dealing with structural uncertainty

Bycatch of juveniles of commercially and recreationally important fish is of serious concern for fishery management (Powers, 2005). The red snapper commercial and recreational fisheries are among the most important fisheries in the Gulf of Mexico. Mitigation of juvenile bycatch mortality has been and remains a key strategy in the rebuilding plan for red snapper (Schirripa and Legault, 1999; SEDAR, 2005; GMFMC, 2007). McAllister and Gazey (2005) suggested that if if bycatch mortality occurred simultaneously with density-dependent mortality, stock rebuilding policies could not rely solely upon reductions in shrimp trawling, and must include reductions in directed catch. Our results showed that it is possible to greatly overestimate the impacts of bycatch when age-0 density-dependent mortality is not accounted for. Furthermore, fishery reference points may be very biased. Importantly, the size of the stock may also be overestimated, leading to underestimation of impacts of directed fishing.

Given the complexity of the red snapper stock assessment (the 2009 update considered 14 alternative states in addition to the continuity run), and confounding of model parameters and early life history processes (Cowan et al., 2010), it seems likely that the question of the timing and magnitude of density-dependent juvenile mortality will remain an unresolved concern in the near future. In such cases, where structural issues cannot be resolved, decision tables can be used to probabilistically represent outcomes of alternative management actions under alternative structural assumptions (e.g., Stewart et al., 2012). A more thorough approach may be to perform a full decision analysis that models the effects of alternative assumptions about the presence of post-recruitment density-dependent mortality across alternative true states of nature and characterises loss according to some pre-defined utility function and performance measures (e.g., Morgan and Henrion, 1990; Seijo et al., 1998). This could also be done in a Management Procedure Evaluation (MPE) framework that would enable all aspects of the assessment cycle (including data-collection, assessment model structure, and harvest control rule) to be simulated and evaluated in terms of meeting pre-defined fishery objectives (Butterworth and Punt, 1999; Smith et al., 1999; Cox and Kronlund, 2008). It has been suggested by one of us that the best way to determine the net impact of bycatch reduction on the red snapper fishery would be to conduct a large-scale adaptive management experiment, involving closure of some areas to trawling and careful comparative monitoring of red snapper juvenile abundances in closed vs open areas (C.J. Walters in SEDAR7 Assessment Workshop Proceedings; SEDAR, 2005). Development of an MPE framework would enable evaluation of the utility of such an experiment as well as provide insight into the most appropriate management options, given large uncertainties in the dynamics of this important and valuable fish stock.

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