



## Contribution to Special Issue: 'Towards a Broader Perspective on Ocean Acidification Research' Original Article

# Effects of long-term exposure to ocean acidification conditions on future southern Tanner crab (*Chionoecetes bairdi*) fisheries management

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Demographic models of pre- and post-recruitment population dynamics were developed to account for the effects of ocean acidification on biological parameters that affect southern Tanner crab (*Chionoecetes bairdi*) larval hatching success and larval and juvenile survival. Projections of stock biomass based on these linked models were used to calculate biological and economic reference points on which fisheries management advice is based and thus provide fisheries managers with strategic advice on the likely long-term consequences of ocean acidification. The models utilized information for southern Tanner crab in the eastern Bering Sea. This information included the monitoring data on which conventional size-structured stock assessments are based, as well as the functional relationships that determine survival based on experiments that evaluated the consequences of ocean acidification over the next 100–200 years on crab larval hatching success, larval survival, and the survival of juvenile crab. The results highlighted that juvenile survival had the largest effect (~20% decrease over 75 years) on biological and economic reference points, while hatching success, particularly if density dependence occurs after hatching, and larval survival have smaller effects (<10% decrease). Catch and profits would be expected to decrease by >50% in 20 years if natural mortality is affected by ocean acidification. Additional laboratory data on oocyte and embryo development leads to large changes in biological reference points depending on the timing of ocean acidification effects relative to natural mortality. The results highlight the need for experiments to evaluate the longer term physiological effects of ocean acidification on multiple life history stages and to measure indices that directly inform population dynamics models to evaluate future management scenarios.

**Keywords:** *Chionoecetes bairdi*, North Pacific, ocean acidification, southern Tanner crab, stock assessment.

## Introduction

Ocean acidification is the change in seawater chemistry due to increases in dissolved anthropogenic CO<sub>2</sub> that has already reduced the mean global ocean surface water pH by 26% (0.1 pH units) below preindustrial levels (Caldeira and Wickett, 2003; Orr *et al.*, 2005). The reduction in pH leads to a decrease in the depth below which calcium carbonate will dissolve. The increased difficulty in precipitating calcium carbonate may negatively affect the formation of shells and support structures by some calcifying organisms such as crustaceans (Caldeira and Wickett, 2003; Feely *et al.*, 2004; Orr *et al.*, 2005), in addition to affecting their physiology

and acid–base balance (e.g. Spicer *et al.*, 2007; Small *et al.*, 2010). Southern Tanner crab, *Chionoecetes bairdi*, are ecologically and commercially important crustaceans that inhabit the North Pacific shelf where the saturation depth of calcium carbonate is already relatively shallow without the added effects of ocean acidification (Doney *et al.*, 2009). Laboratory studies found that the condition, shell calcification, and in particular, survival of southern Tanner crab were negatively affected by average global levels of ocean acidification conditions expected by the year 2200 (Long *et al.*, 2013, This volume; Swiney *et al.*, This volume). In particular, these studies found that incorporating long-term exposure to

increased  $p\text{CO}_2$  (and subsequent decreased pH) during oocyte development compounded the effects of ocean acidification in later stages. The population level effects of decreased individual survival on the biological reference points used to manage crab stocks in Alaska, and the sensitivity of those reference points to short- vs. long-term experimental results are, however, unknown.

Ocean acidification may have significant effects on the development of marine invertebrate embryos (Kurihara *et al.*, 2004a, b; Findlay *et al.*, 2009; Parker *et al.*, 2009) and larvae (Kurihara *et al.*, 2007; Dupont *et al.*, 2008; Talmage and Gobler, 2009). Southern Tanner crab larvae (known as zoea) hatch at depth after an ~12-month brooding period and live pelagically in surface waters before settling to the benthos during the megalopa stage and molting to the juvenile stage. In the Gulf of Alaska, juvenile female southern Tanner crab are found in shallow water (<13 m) before their molt to maturity (Stevens *et al.*, 1993), and adult females aggregate in deeper water (~150 m) (Stevens *et al.*, 1993). Adult southern Tanner crab in the eastern Bering Sea are found at depths from 18 to 440 m. As such, the different life stages of southern Tanner crab are exposed to variable ocean acidification conditions, ranging from surface waters exposed to anthropogenic-driven changes in ocean pH to waters undersaturated in  $\text{CaCO}_3$  at depth.

The effects of decreased ocean pH on southern Tanner crab were assessed during short- and long-term laboratory experiments conducted from 2011 to 2013 where developing oocytes, embryos, and larvae were reared in one of three pH treatments to simulate current and expected average global conditions in approximately 2100 and 2200 (Swiney *et al.*, this volume; Long *et al.*, this volume). Three experiments were conducted where (i) oocyte and embryo development occurred *in situ* while larvae were in treatments, (ii) oocytes developed *in situ* but embryos and larvae developed in laboratory treatment conditions, and (iii) oocytes, embryos, and larvae were developed in laboratory treatment conditions. Larvae were exposed to the same three pH treatments in a fully crossed experimental design to examine starvation survival, morphology, condition, and calcium/magnesium content. Embryo development in ambient and pH 7.8 treatments differed from the pH 7.5 treatment in both years. Hatching success was much lower for embryos that were exposed during both oogenesis and embryogenesis. At the larval stage, effects were also substantially greater for larvae exposed to more acidified conditions during oogenesis and embryogenesis. Larval crab differed morphometrically, were smaller, and had lower calcium and magnesium contents (Swiney *et al.*, This volume; Long *et al.*, This volume).

Crab, including southern Tanner crab, contributes substantially to the revenue generated by the fisheries off Alaska, USA. Alaska crab stocks are jointly managed by the North Pacific Fishery Management Council (NPFMC) and the Alaska Department of Fish and Game (ADFG). The NPFMC makes recommendations for the overfishing level (OFL) and the acceptable biological catch (ABC) for each crab stock, while the State of Alaska makes decisions on total allowable catches (TACs), which have to be less than the ABCs. The OFLs are set using a tier system that includes five tiers depending on data availability, and the ability to estimate key stock assessment parameters (NPFMC, 2008). The scientific basis for setting of OFLs, ABCs, and TACs derive from quantitative stocks assessments. For the more data-rich crab stocks, including southern Tanner crab in the eastern Bering Sea, these assessments are based on fitting sex- and size-structured population dynamics models to monitoring data from the fishery and surveys (e.g. NPFMC, 2014). These assessments provide estimates of key biological

reference points such as the fishing mortality rate at which mature male-per-recruit is reduced to 35% of its unfished level,  $F_{35\%}$ , and the proxy for the biomass at which MSY is achieved,  $B_{\text{MSY}}$  (NPFMC, 2008). These biological reference points are then used in the control rules for calculating the OFL.

Increasingly, management bodies are using economic information to make decisions regarding management practices and reference points (e.g. Kompas *et al.*, 2010; Punt *et al.*, 2012, 2014a). While reference points and OFLs for Alaska crab stocks are still currently based on biological considerations only, the selection of the buffer between the OFL and ABC for these stocks takes economic as well as biological information into account (Punt *et al.*, 2012). The changes in population dynamics due to ocean acidification conditions will likely have biological and economic consequences.

The overall goal of this study was to incorporate laboratory results on crab mortality associated with decreased ocean pH into existing stock assessment models to evaluate how ocean acidification conditions can affect the survival of juvenile crab and hence the yield and revenue from the fishery (c.f. Punt *et al.*, 2014b). In contrast, to the earlier modelling work, this study examined the effects of ocean acidification conditions on several life stages and developed models that can represent these effects. In addition, the models were used to examine the sensitivity of quantities of management interest to the increased information on crab mortality gained by conducting long- vs. short-term laboratory experiments (Long *et al.*, This volume; Swiney *et al.*, This volume). Specific objectives included (i) developing a pre-recruitment model for southern Tanner crab, (ii) developing a post-recruitment model for southern Tanner crab, and (iii) informing the pre- and post-recruitment models using laboratory data on crab survival in acidified conditions to predict biological and economic reference points.

## Methods

### Crab collection and experimental design

Data from short- and long-term experimental results from early life stages (pre-juvenile) exposed to ocean acidification conditions were used to inform the pre-recruitment model. Detailed laboratory experimental design and results can be found in Swiney *et al.* (this volume) and Long *et al.* (this volume). Two collections of mature female Tanner crab were made in May and June 2011 from Chiniak Bay, Kodiak Island, in the Gulf of Alaska and held at the Alaska Fisheries Science Center's (AFSC) Kodiak Laboratory. In the first collection, ovigerous females were collected and larvae hatched immediately. Larvae were randomly assigned to a control or treatment that simulated current (ambient) and predicted future (about 2100 and 2200) ocean pH levels: (i) ambient pH (~8.1), (ii) pH 7.8, and (iii) pH 7.5 (Caldeira and Wickett, 2003). In the second collection, 48 mature female Tanner crab were collected and randomly assigned to the same control and treatments as above. These females were held for 2 years where they were mated with mature males, extruded a new clutch in spring of 2011 and 2012, and each clutch was brooded for ~1 year. Larvae hatched and were collected in spring of 2012 and 2013. Therefore, reproductive development did not occur in treatments for larvae hatched immediately in 2011, only embryo development occurred in treatments for 2012 larvae, and both oocytes and embryo development occurred in acidified treatments for larvae hatched in 2013. Embryological assessment included embryo development, hatching success, and hatch duration. Larval experiments were conducted by isolating five replicates of 20 larvae in containers from a

pool of larvae from multiple adult females within each pH treatment for a fully crossed design between embryo and larval treatments. Larvae were not fed during this starvation experiment and larval response variables included morphology, condition, calcification, and starvation survival.

Data from experimental results from juvenile crab exposed to decreased ocean pH (Long *et al.*, 2013) were used to inform the pre- and post-recruitment models for southern Tanner crab. This experiment was separate from that used to obtain the embryo and larval data. Ninety newly settled juvenile southern Tanner crab (carapace width 2.8–5.2 mm) were collected from Chiniak Bay, Alaska in May 2010 and held at the AFSC’s Kodiak Laboratory. Each juvenile crab was randomly assigned to the same pH treatments as described for the pre-juvenile experiments above. During the 199 day experiment, calcification, growth, and survival decreased, while the condition did not change with exposure to lower pH (Long *et al.*, 2013).

**Informing pre- and post-recruitment models with experimental results**

The pre-recruitment (recruitment is to the range 25–64 mm carapace width (CW), the smallest size included in the post-recruitment model.) model considered 11 pre-recruitment stages: two pelagic larval (zoal) stages (Z1–Z2), one megalopa settling stage (ME), and eight juvenile benthic instars (C1–C8) (Table 1). Based on laboratory experimental results, ocean acidification conditions were assumed to change the mortality rates for all pre-recruitment stages, except the megalopa stage for which no experimental data were available. The following experimental results were used to inform the pre-recruitment model: hatching success, larval survival during each stage, and juvenile survival during each stage. In contrast, Punt *et al.* (2014b) only considered ocean acidification effects on juvenile survival.

Hatching success was defined as the proportion of embryos that hatch with viable larvae standardized by the total number of larvae hatched under experimental conditions for the treatment groups relative to this proportion for the control group (pH = 8.1). The hatching success for the control group is confounded with average recruitment and density-independent mortality in the model. The model consequently sets hatching success for the control group and density-independent survival to 1, and selects the average recruitment to match the monitoring data. The hatching success for the two treatment levels of pH (7.8 and 7.5) were 0.917 and 0.688 (Swiney *et al.*, This volume). Interpolation of hatching success to other levels of

pH was achieved using the simplest equation that has a shape that allows interpolation between pHs of 7.5 and 8.1:

$$H = \left( 1 - \alpha_1 \left[ \frac{8.1 - \text{pH}}{8.1} \right]^{\alpha_2} \right), \tag{1}$$

where  $\alpha_1$  and  $\alpha_2$  were selected so that the predictions from Equation (1) match the observed hatching successes at pHs of 7.8 and 7.5.

Survival over  $t$  days during larval stages (Z1–Z2) was modelled using the equation:

$$S_t = 1 - (1 + \exp(-\beta(t - t_{50})))^{-1}, \tag{2a}$$

where  $t_{50}$  is the number of days until half of the larvae die, which is itself a function of pH, i.e.:

$$t_{50} = \gamma_1 \left( 1 - \gamma_2 \left[ \frac{8.1 - \text{pH}}{8.1} \right]^{\gamma_3} \right), \tag{2b}$$

where  $\gamma_1$ ,  $\gamma_2$ , and  $\gamma_3$  are parameters determining the relationship between  $t_{50}$  and pH, and  $\beta$  determines the slope in the logistic curve in Equation (2a). The values for the parameters of Equations (2a) and (2b) were estimated by fitting this model to data from the larval experiments (Figure 5 in Long *et al.*, this volume). This involves maximizing the following likelihood, i.e.:

$$\prod_p \prod_i \left( (S_{p,t_{\max}})^{N_{p,i,t_{\max}}} \prod_{t < t_{\max}} (M_{p,t})^{N_{p,i,t}} \right), \tag{3}$$

where  $M_{p,t}$  is the probability of a larva dying during day  $t$ :

$$M_{p,t} = \begin{cases} 1 - S_{p,1} & \text{if } t = 1 \\ S_{p,t-1} - S_{p,t} & \text{otherwise} \end{cases}, \tag{4}$$

where  $S_{p,t}$  is the survival rate over  $t$  days during the larval stages when pH is  $p$ , and  $N_{p,i,t}$  is the observed number of mortalities in container  $i$  on day  $t$  ( $N_{p,t,t_{\max}}$  is the number of animals that were still alive on the last day of the experiment) when pH is  $p$ . To test the effects of crab development in acidified treatments and on short- vs. long-term experimentation, four variants of the analysis for the larval data were conducted: (i) 2013 data, basing the analysis on crab that developed entirely in ambient conditions; (ii) 2013 data, basing the analysis on crab that developed in pH 7.8 or 7.5 treatments through oocyte, embryo, and larval development; (iii) same as for (i) except using 2012 data where oocyte development occurred *in situ* (i.e. not in treatment); and (iv) same as for (ii) except using 2012 data.

The data on juvenile survival were analysed using an equation of the form:

$$S_t = \tilde{S}^t, \tag{5a}$$

where  $\tilde{S}$  is the daily survival rate, related to pH according to the equation:

$$\tilde{S} = \delta_1 \left( 1 - \delta_2 \left[ \frac{8.1 - \text{pH}}{8.1} \right]^{\delta_3} \right), \tag{5b}$$

where  $\delta_1$ ,  $\delta_2$ , and  $\delta_3$  are parameters determining the relationship between  $\tilde{S}$  and pH. The values for the parameters of Equations

**Table 1.** Stage durations for southern Tanner crab.

Stage	Duration (Average) (days)	Source
Z1	30	Haynes (1973, 1981), Incze <i>et al.</i> (1982)
Z2	30	Haynes (1981), Incze <i>et al.</i> (1982)
ME	30–180 <sup>a</sup>	Jewett and Haight (1977), Incze <i>et al.</i> (1982)
C1	21	Donaldson <i>et al.</i> (1981)
C2	30	Donaldson <i>et al.</i> (1981)
C3	42	Donaldson <i>et al.</i> (1981)
C4	51	Donaldson <i>et al.</i> (1981)
C5	69	Donaldson <i>et al.</i> (1981)
C6	90	Donaldson <i>et al.</i> (1981)
C7	120	Donaldson <i>et al.</i> (1981)
C8	156	Donaldson <i>et al.</i> (1981)

<sup>a</sup>Taken to 105 days for the purposes of this paper.

(5a) and (5b) were estimated by fitting this model to data from juvenile experiments (Figure 3 in Long et al., 2013). The likelihood function maximized to estimate the parameters of Equation (5b) followed Equation (3), except that there was only one container.

**Southern Tanner crab pre-recruitment model**

As in Punt et al. (2014b), a stage-structured population model was used to forecast the changes over time in recruitment to the first size class in the post-recruitment model (25–64 mm CW):

$$N_{T+t+1} = G_T \Omega_T N_{T+t}, \tag{6}$$

where  $N_{T+t}$  is the vector of numbers-at-stage at time  $T + t$  (all embryos enter the first stage when they are spawned),  $G_T$  is the growth transition matrix (i.e. the matrix of probabilities of growing from one stage to each other stage for embryos spawned at time  $T$ ; consistent with assessments for most crustaceans, the matrix  $G_T$  was assumed to be lower triangular, reflecting the assumption that very few animals shrink following moulting), and  $\Omega_T$  is the survival matrix for embryos spawned at time  $T$ . The survival and growth rates for animals spawned at time  $T$  until they reach 25–64 mm CW were set to those calculated for time  $T$ . This was an adequate approximation given the slow change over time in pH relative to the time between spawning and reaching 25 mm CW (Punt et al., 2014b). The last stage in this model was the first size class in the post-recruitment model. Several crab assessment models allow recruits to enter the model over a range of size classes. However, the size classes selected for the post-recruitment model were chosen to be sufficiently large that all the recruitment occurs to one size class.

The stage with the shortest duration, C1, lasts on average 21 days (Table 1). The time-step for the model (6 days) was set so that the time-step is able to match the lengths of each stage relatively closely (the mortality by stage was allocated equally across the time-steps that constitute a stage, so that the fact that some stages durations were not exact multiples of 6 days is inconsequential). Following Punt et al. (2014b), it was assumed that all individuals within a stage were subject to the same survival probability and stage duration, and that individuals must stay in a stage for a defined minimum amount of time before progressing to the next stage. This was achieved by dividing each of the 11 stages into sub-stages where the number of sub-stages was one plus the number of time-steps that an animal needs to remain in a stage.

The matrix  $G_T \Omega_T$  determines the combined effects of growth and mortality. This matrix can be written as:

$$G_T \Omega_T = \begin{pmatrix} \begin{matrix} (-\text{From-}) \\ (-Z1-) \end{matrix} & \begin{matrix} (-\text{From-}) \\ (-Z2-) \end{matrix} & \begin{matrix} (\text{From}) \\ (\text{Stages 3 +}) \end{matrix} & & & \\ \begin{matrix} 0 & 0 & 0 & 0 & 0 & \dots \\ S_{1,T} & S_{1,T}(1 - P_{1,T}) & 0 & 0 & 0 & \dots \\ 0 & S_{1,T}P_{1,T} & 0 & 0 & 0 & \dots \\ 0 & 0 & S_{2,T} & 0 & 0 & \dots \\ 0 & 0 & 0 & S_{2,T} & S_{2,T}(1 - P_{2,T}) & \dots \\ 0 & 0 & 0 & 0 & S_{2,T}P_{2,T} & \dots \\ 0 & 0 & 0 & 0 & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{matrix} \end{pmatrix} \tag{7}$$

for the case in which animals must stay at least one time-step in Z1 and two time-steps in Z2. The variable  $S_{i,T}$  is the probability of survival for stage  $i$  for animals spawned at time  $T$ , and  $P_{i,T}$  is the probability of growing out of stage  $i$  for animals spawned at time  $T$ .

The values for  $S_{i,T}$  and  $P_{i,T}$  were solved to match values for expected survival predicted from the functions fitted to the experimental data ( $\tilde{S}_{i,T}$ ) for stage  $i$  for embryos spawned at time  $T$  and the expected stage duration ( $\tilde{d}_i$ ), which was not affected by ocean acidification. The predicted values for  $\tilde{S}_{i,T}$  and  $\tilde{d}_i$  for a stage with  $n$  sub-stages were (see Appendix A of Punt et al., 2014b):

$$\tilde{S}_{i,T} = \frac{S_{i,T}^n P_{i,T}}{1 - S_{i,T}(1 - P_{i,T})}; \quad \tilde{d}_i = \frac{\sum_{y=T}^{T+tt} (y + 1)x_{i,y}S_{i,T}P_{i,T}}{\sum_{y=T}^{T+tt} x_{i,y}S_{i,T}P_{i,T}}, \tag{8}$$

where  $x_{i,y}$  is the number of animals leaving stage  $i$  at time-step  $y$  [for stage 1, this would be the numbers entering class 2 in Equation (7)], and  $tt$  is the total number of time-steps ( $tt \sim 1100$ ). The values for  $\tilde{S}_{i,T}$  were determined from Equations (2a) and (5b) [larvae and juveniles, respectively (The survival rate for megalopa was assumed to be constant, independent of ocean pH, in the absence of data to parameterize a model such as Equation (4.)).]. Table 1 lists the values for the stage durations.

**Southern Tanner crab post-recruitment model**

The dynamics of animals of 25 mm CW and larger (and hence the impacts of the fishery) were modelled using a population dynamics model with an annual time-step, which was a simplification of the current stock assessment model for southern Tanner crab in the eastern Bering Sea (Stockhausen, 2014) in which only males were modelled, fewer size classes were used, and no consideration was taken of shell condition and maturity stage. These simplifications facilitated quicker computations, but do not affect the results markedly as the fishery is only allowed to retain males. Mature male biomass (MMB) at the time of mating (taken to be 15 February) was used as a proxy for fertilized egg production in this model, consistent with how management advice is provided for Bering Sea and Aleutian Islands crab fisheries (NPFMC, 2008). The basic dynamics of the population in the model were:

$$N_{y+1} = X S_y N_y + R_{y+1}, \tag{9}$$

where  $N_y$  is the vector of numbers-at-stage (males only) at the start of year  $y$ ,  $X$  is the growth transition matrix (assumed as before to be lower triangular),  $S_y$  is the survival matrix for year  $y$ , and  $R_y$  is the vector of recruits for year  $y$ . The matrix  $S_y$  was diagonal with elements:

$$S_{y,i,i} = e^{-M_y} \prod_{k=1}^3 (1 - J_{i,k}^B F_{y,k}^B)(1 - J_i^D F_y^D), \tag{10}$$

where  $M_y$  is the instantaneous rate of natural mortality for year  $y$ ,  $J_{i,k}^B$  is selectivity due to the  $k$ th fleet which takes southern Tanner crab as bycatch on animals in size class  $i$  (the fleets are the pot fisheries that target snow crab, *Chionoectes opilio*, and red king crab, *Paralithodes camtschaticus*, and the pot and trawl fisheries that target groundfish),  $F_{y,k}^B$  is the proportionate exploitation rate due to  $k$ th fleet that takes southern Tanner crab as bycatch during year  $y$ ,  $J_i^D$  is selectivity for the directed fishery on animals in size class  $i$ , and  $F_y^D$  is the exploitation rate due to the directed fishery during year  $y$ . In model projections,  $F_{y,k}^B$  in Equation (10) was set to the average exploitation rate over 2008–2012. Future values for  $F_y^D$  were determined by the scenario under consideration (see below). The products in Equation (10) were constrained to be 1 or less in the projections.

Owing to a minimum size limit, some crabs caught during the directed fishery are discarded. The retained and discarded catch (in mass) by the directed fishery during year  $y$ ,  $\tilde{C}_y^D$ , and  $\bar{C}_y^D$ , were:

$$\tilde{C}_y^D = \sum_i Q_i w_i J_i^D F_y^D N_{y,i} e^{-0.5M_y} = \sum_i w_i \tilde{C}_{y,i}^D \quad (11a)$$

$$\bar{C}_y^D = \sum_i (1 - Q_i) w_i J_i^D F_y^D N_{y,i} e^{-0.5M_y} = \sum_i w_i \bar{C}_{y,i}^D \quad (11b)$$

where  $Q_i$  is the proportion of crab in size class  $i$  that is retained,  $w_i$  is the average mass of a male crab in size class  $i$ ,  $N_{y,i}$  is the number of animals in size class  $i$  at the start of year  $y$ , and the fishery is assumed to take place half way through the model year, which starts on 1 July.

The discard by the fleets that take southern Tanner crab as bycatch was computed under the assumption that the directed and the other fisheries are sequential (the directed fishery has historically occurred over a very short interval whereas the trawl fishery, one of those that takes Tanner crab as bycatch in the Bering sea, occurs essentially throughout the year):

$$\begin{aligned} \bar{C}_{y,k}^B &= \sum_i w_i J_{i,k}^B F_{y,k}^B N_{y,i} e^{-0.5M_y} (1 - J_i^D F_y^D) \prod_{l=1}^{k-1} (1 - J_{i,l}^B F_{y,l}^B) \\ &= \sum_i w_i \bar{C}_{y,i}^B \end{aligned} \quad (12)$$

In principle, the trawl fishery could be modelled as occurring over the entire year rather than as a pulse in the middle of the year. However, the catch by the trawl fishery is negligible compared with that by the directed fishery so this complication was ignored here.

Under the assumption that only the directed fishery occurs before mating, and that mating occurs on 15 February of year  $y + 1$ , the mature male biomass for year  $y$ ,  $MMB_y$ , is computed using the equation:

$$MMB_y = \sum_i N_{y,i} f_i e^{-0.75M_y} (1 - J_i^D F_y^D), \quad (13)$$

where  $f_i$  is the fecundity of a crab in size class  $i$ . Density-dependence was assumed to affect the survival rate of embryos [see Equation (16)] and was modelled based on the mature male biomass at the time of mating for consistency with how management advice is provided and projections conducted for crab stocks in Bering Sea (NPFMC, 2008). Consequently, high values for mature male biomass led to lower survival rates for embryos all other things being equal.

Recruitment only occurred to the first size class in the model (25–64 mm CW). Recruitment during future year  $y$  was calculated as the sum of the numbers recruiting during year  $y$  based on spawning during years  $y'$ , where the spawning year ranges from 1 to 10 years before year  $y$ .

$$R_y = \phi \sum_{y'=y-10}^{y-1} \kappa_{y'} f(\omega_{y'} MMB_{y'}) G(y', y), \quad (14)$$

where  $G(y', y)$  is the fraction of animals that were spawned during year  $y'$  that recruit during year  $y$ ,  $\kappa_{y'}$  is the effect of ocean acidification on the hatching rate that occurs after density-dependent embryo mortality and  $\omega_{y'}$  is the effect of ocean acidification on the hatching

rate that occurs before density-dependence. The matrix  $G$  is the link between the pre- and post-recruitment models. The entries in this matrix were computed by projecting the pre-recruitment model forward for embryos produced during year  $y'$ , and recording the fraction of these embryos that survived to the stage corresponding to the first size class in the post-recruitment model in each future year. The entries of the matrix  $G$  depended on ocean acidification because of ocean acidification-affected survival in the pre-recruitment model. The symbol  $\phi$  in Equation (14) was a constant, computed so that the population remained at its equilibrium unfished level in the absence of ocean acidification and exploitation ( $F_y^D = F_{y,k}^B = 0$ ). To find the value of  $\phi$ ,  $R_y$  was set to 1, the resulting MMB was found, and  $G(y', y)$  was set based on the pre-recruitment model with no ocean acidification effect, i.e.:

$$\phi = \frac{1}{\sum_{y'=y-10}^{y-1} f(MMB_{y'}) G(y', y)}. \quad (15)$$

The number of animals entering the first stage of the pre-recruitment model was governed by a Beverton–Holt relationship, i.e.:

$$f(MMB_{y'}) = \frac{4hR_0 MMB_{y'} / MMB_0}{(1-h) + (5h-1) MMB_{y'} / MMB_0}, \quad (16)$$

where  $MMB_y$  can be a historical or projected value. The variables  $R_0$  and  $MMB_0$  were the recruitment and mature male biomass, respectively, in an unfished state and  $h$  is the “steepness” of Equation (16) (the expected numbers entering the first stage of the pre-recruitment model when  $MMB = 0.2MMB_0$ , expressed as a proportion of  $R_0$ ; Francis, 1992).

### Computing fishery profits and maximum economic yield

The profit to the boats (excluding fixed costs that do not affect maximum economic yield, MEY) in the directed crab fishery during year  $y$  was given by

$$\pi_y = (p \tilde{C}_y^D - V_y), \quad (17)$$

where  $p$  is price of crab per kilogram (assumed to be time-invariant), and  $V_y$  is the summation of variable costs associated with fuel, food, and bait during year  $y$ :

$$V_y = E_y c_F + E_y c_G + P_y^D c_b, \quad (18)$$

where  $E_y$  is the sum of days fishing ( $E_y^F$ ) and days traveling ( $E_y^T$ ), and  $c_F$ ,  $c_G$ , and  $c_b$  are, respectively, the average daily costs of fuel, food, and bait, and  $P_y^D$  is the number of potlifts during year  $y$  (Table 2). The number of potlifts in the directed fishery during year  $y$ ,  $P_y^D$ , was a linear function of days fishing,  $P_y^D = 64.25 E_y^F$ , while days fishing was a linear function of  $F_y^D$ ,  $E_y^F = 29\,759.5 F_y^D$ , and days

**Table 2.** The values for economic parameters (USD; M. Dalton, unpublished data).

Price per kilogram	\$4.82
Fuel cost per day	\$1248.19
Food cost per day	\$176.18
Bait cost per pot lift	\$5.95

traveling was a linear function of days fishing,  $E_y^T = 0.4049E_y^F$  (see Punt et al., 2014b for how these relationships were derived).

**Projection model parameterization**

*Ocean acidification trends*

A simple approximation to a standard ocean acidification scenario with changes over time in ocean pH was calculated using the straight line that joins the predictions of average global pH levels in the oceans between 2000 and 2200;  $pH_{2000} = 8.1$ ,  $pH_{2200} = 7.4$  (Caldeira and Wickett, 2003). The expected stage survivals ( $\bar{S}_i$ ) in the absence of ocean acidification effects were calculated so the population remains stable in the absence of exploitation (i.e. no other climate change variables affect juvenile crab survival).

*Post-recruitment model*

The parameters of the post-recruitment model that were estimated by fitting it to the data collected from the fishery and assessment surveys during 1968–2013 were: (i) natural mortality ( $M$ ), (ii) the fully selected fishing mortality for each year for the directed fishery and the fisheries that took southern Tanner crab as bycatch when the catch was non-zero (e.g. when the directed fishery was not closed) ( $F_y^D$  and  $F_{y,k}^B$ ), (iii) the parameters that defined the growth transition matrix ( $X_{i,i+1}$ ), (iv) selectivity-at-length for each fishery ( $J_i^D$  and  $J_{i,k}^B$ ), (v) catchability and selectivity-at-length for male crab in the surveys conducted by the NMFs (separately before and after 1982), (vi) the probability of being landed and retained given being caught in the directed pot fishery ( $Q_i$ ), (vii) the initial size-structure of the population ( $N_{1965,i}$ ), (viii) the mean recruitment ( $\bar{R}$ ), and (ix) the deviations in recruitment about mean recruitment ( $\epsilon_y$ , i.e.  $R_y = \bar{R}e^{\epsilon_y}$ ). Appendix B of Punt et al. (2014b) outlines the likelihood function that was maximized to obtain the values for the parameters of the post-recruitment model. The values for fecundity- and weight-at-length were set based on the outcomes of auxiliary studies (Table 3).

The values for  $h$  and  $R_0$  were chosen so that  $F_{MSY} = F_{35\%}$  and  $B_{MSY} = B_{35\%}$ , where the recruitment at  $B_{35\%}$  was set to an average recruitment (from 1995 to present) selected by the Scientific and Statistical Committee of the NPMFC (NPFMC, 2008; Punt et al., 2012). The assumption that  $F_{MSY} = F_{35\%}$  and  $B_{MSY} = B_{35\%}$  are commonly made when conducting projections for North Pacific crab and groundfish stocks (e.g. Punt et al., 2012). Punt et al. (2014c) showed that the assumption  $F_{MSY} = F_{35\%}$  was supported for several North Pacific crab stocks.

*Economic model*

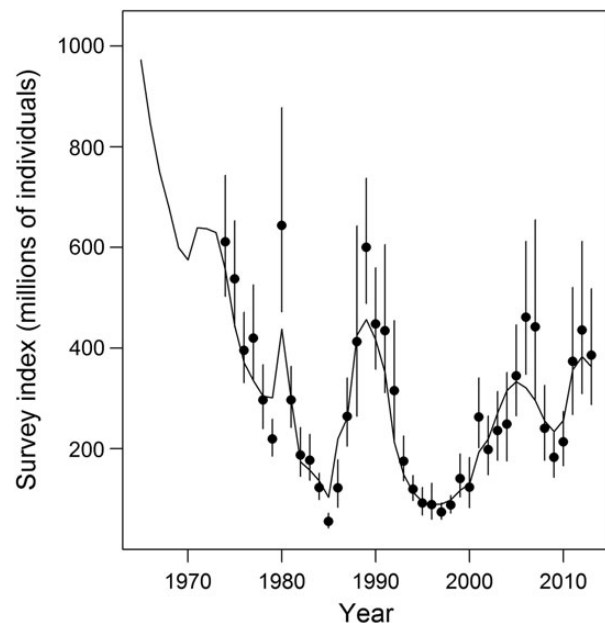
The average price per kilogram for Tanner crab from 2006 to 2013 was calculated from State of Alaska fish ticket data as the ratio of total ex-vessel revenues (current dollars corrected for inflation summed over 2006–2013) to total landings (crab weight in pounds summed over 2006–2020 and converted to kilograms). The average costs for fuel, food, and bait were calculated from

values in the Bering Sea and Aleutian Islands Crab Rationalization Program Economic Data Reports (EDRs) for the years 2006–2013 (Garber-Yonts and Lee, 2013). Fuel and food cost per day were calculated as the ratio of total fuel and food costs for 2006–2013 to the sum of days fishing and days traveling, which were reported in the EDRs in 2006–2011, but then were discontinued. For 2012–2013, days fishing and days traveling were derived from the confidential interview form of the State of Alaska shellfish observer programme. Bait cost per pot lift was calculated as the ratio of total bait costs for 2006–2013 to the total number of potlifts, where the number of potlifts was taken from fish ticket data.

**Projection model scenarios**

Model projections were made for a range of values for effort, with effort and hence fishing mortality assumed to be constant into the future. The parameters determining growth, costs, and prices were set to the estimates for the last year of the assessment period (2012).

The model scenarios explored the implications of various assumptions regarding which biological processes were affected by ocean acidification. The base model included all the effects on which data were available: (i) hatching success, (ii) mortality for the Z1 and Z2 larval stages, and (iii) mortality on juvenile stages C1–C8. It based the level of larval mortality on the 2013 hatched larvae (long-term experiments with treatments during oocyte and embryo development) in which pH was that expected in future years (linear decrease from 8.1 to 7.4 in 2200), assuming that ocean acidification effects on hatching success occurred before density-dependent effects on embryo survival and assuming that the level of natural mortality for animals of stage C8+ equalled that for the last juvenile stage. Results were shown for the alternative models:



**Figure 1.** Time-trajectory of area-swept survey indices of male biomass (1974–2013; dots) and the post-recruitment model fit (line). The vertical bars indicate 95% confidence intervals for the data.

**Table 3.** Weight- and fecundity-at-age (kg) for southern Tanner crab.

	25–	65–	85–	110–	135–	
Size class	64 mm	84 mm	109 mm	134 mm	159 mm	160 mm +
Weight	0.033	0.125	0.281	0.566	0.980	1.498
Fecundity	0.001	0.028	0.177	0.494	0.952	1.476

- (i) Ocean acidification only affects hatching success based on the 2013 hatched larvae data.
- (ii) Ocean acidification only affects larval mortality based on the 2013 hatched larvae data.
- (iii) Ocean acidification only affects the mortality of juvenile stages C1–C8.
- (iv) The level of larval mortality is based on analyses in which oocytes developed *in situ* and treatments occurred during embryo and larval development (larvae hatched in 2012; short-term experimental results).
- (v) The level of larval mortality is based on analyses in which oocytes and embryos developed *in situ* and treatments occurred during larval development (larvae hatched in 2011; short-term experimental results).
- (vi) The ocean acidification effects on hatching success occurred after, rather than before, density-dependent effects on embryo survival based on the 2013 hatched larvae data.

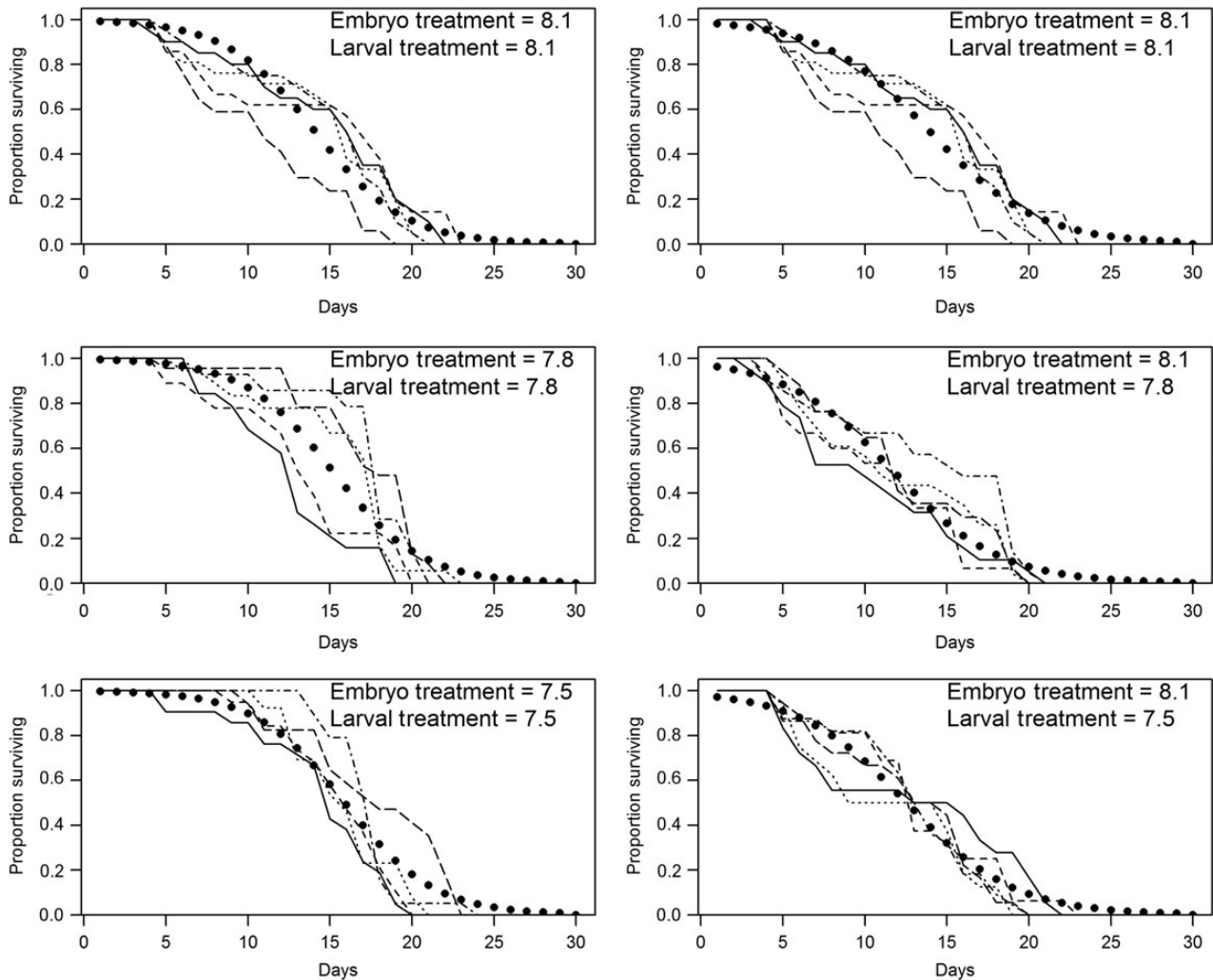
Cases (A)—(C) explored the consequences of only having experimental information on the effects of ocean acidification on one

biological process. The analyses conducted by Punt *et al.* (2014b) were effectively Case C because that study based its projections on ocean acidification affecting the mortality rate of juvenile stage animals. Case D explored ignoring the effect of oocyte development occurring in acidified treatments, but considered the effects of ocean acidification on hatching success, larval mortality, and juvenile mortality. Case E explored the implications of conducting experiments in which the oocytes and embryos are not developed in water with the same acidification as the waters in which the larvae develop. Case F explored the consequences of when the effects on hatching success occur. Results are shown for Cases A–F for the assumption that natural mortality for stages C8+ is equal to that under non-ocean acidification-affected conditions ( $0.25 \text{ yr}^{-1}$ ) and that natural mortality for such animals is equal to that for stage C8 crab. This should bound the range for this unknown process.

## Results

### Parameterization of the models

The post-recruitment population dynamics model was fitted to a variety of data sources. However, the ability to mimic the trends



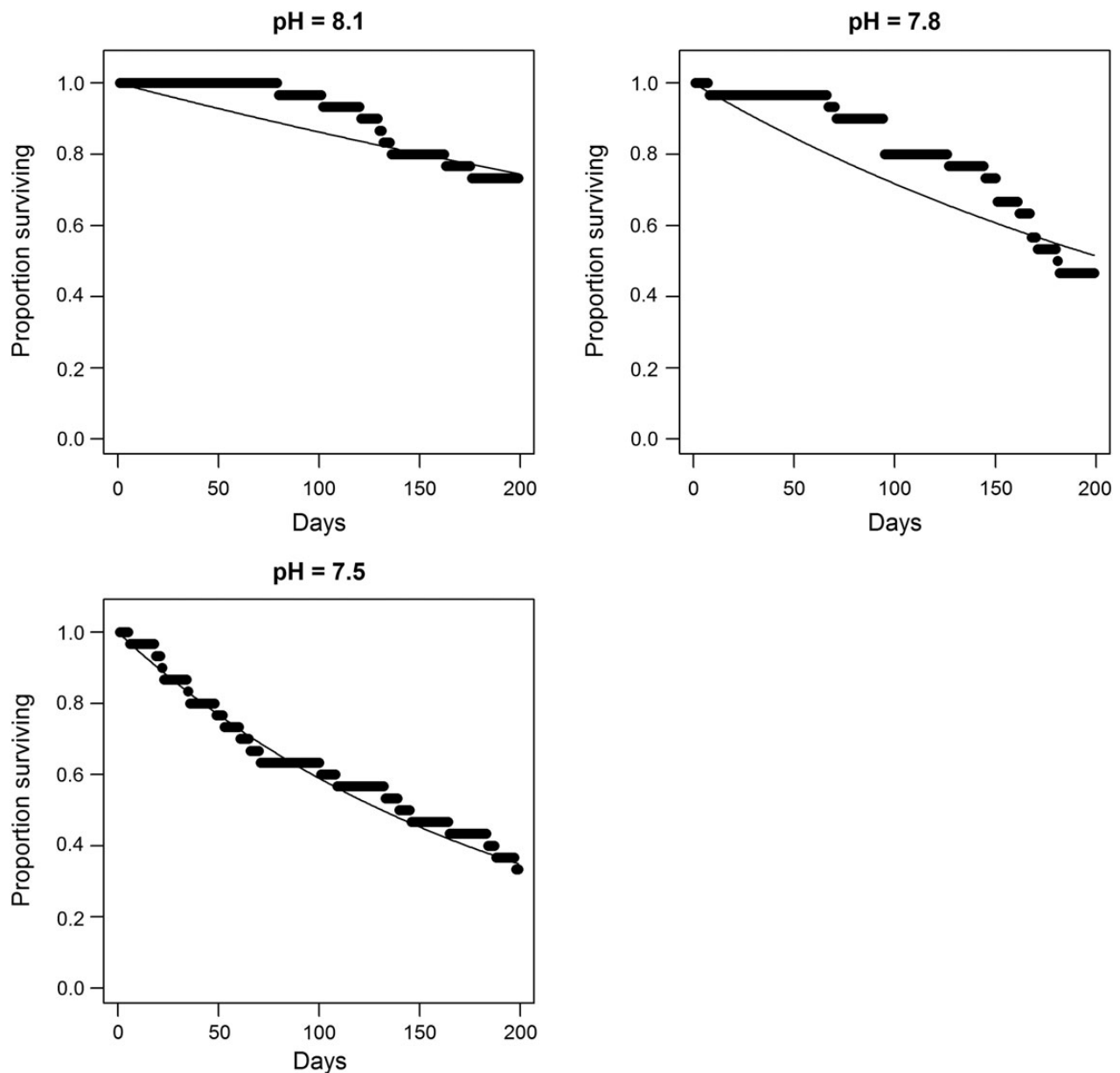
**Figure 2.** Observed (light lines) and model-predicted (dots) 2013 larval survival from long-term experiments. Each light line indicates a different container. Results are shown for experiments in which all animals were hatched at the same pH as they were developed (left panels) and under control conditions (right panels).

in abundance inferred from surveys is the most important in terms of the consequences for being able to adequately conduct long-term projections such as those on which this paper is based. Figure 1 therefore plots observed and model-predicted survey indices of male abundance. The observed indices were computed using area-swept analysis methods based on surveys conducted by the National Marine Fisheries Service. The post-recruitment model was able to mimic the marked fluctuations in abundance adequately, although it was unable to capture some of the outlying survey estimates, including the high 2006 and 2007 abundance estimates.

Figure 2 shows the base model fits to the data from 2013 larval survival experiment. There was a fairly large amount of between-container variation (light lines in Figure 2). However, given the small sample sizes, a random effects structure is not supported for these data. In addition, a model in which the parameter  $\beta$

[Equation (2a)] depends on pH was not supported by AICc. The model predictions for the two upper panels of Figure 2 are not identical because the predictions are based on fitting to the entire dataset and not each experiment individually. The model captures the data adequately. However, it tends to predict that more larvae should have survived beyond the end of the experiment than was observed. The model predicts little difference in survival rate over 30 days among treatments.

Figure 3 shows the fits of the constant survival rate model to the data from the experiment to determine the survival of juvenile stage southern Tanner crab. The model fits the data for pH = 7.5 very well, but the fits to the data for pH = 8.1 and 7.8 are poorer, with some evidence of increasing mortality rates with age or for increased mortality during periods of moulting. The poor fit for pH = 7.8 is similar to the fit obtained by Punt *et al.* (2014b) to similar data



**Figure 3.** Observed (solid dots) and model-predicted (lines) survival for juvenile stage southern Tanner crab.



for red king crab. An alternative model in which survival is a logistic function of age was not supported over the constant survival model. In principle, a model in which the relationship between survival and age or moulting event changes with pH would fit the data in Figure 3 best, but it would not be straightforward to infer the relationship between survival and age (or moulting) for different levels of pH.

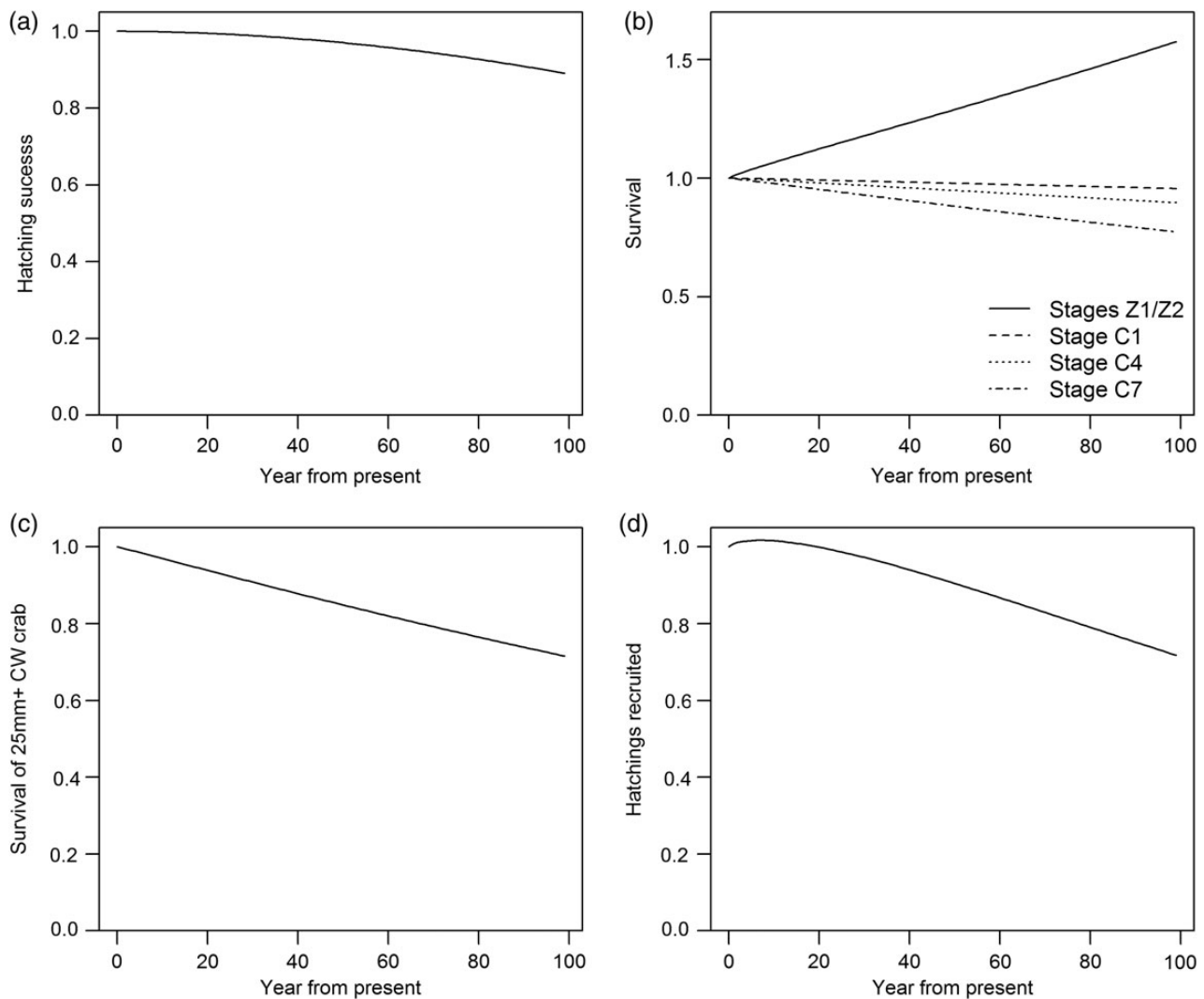
**Application of the pre-recruitment model**

Figure 4 shows various parameters of the pre-recruitment model for the base-case set of specifications (which include that the survival rate of larvae is best represented by experiments in which animals are spawned at the same pH at which they develop). The effects of ocean acidification on hatching success were fairly small even over a 100-year period. In contrast, the survival rate of juvenile stage animals could decline substantially over the next 100 years while the survival rate of larvae could increase. The effect of ocean acidification was greater for the later stages (Figure 4b) because the duration of these stages is longer (Table 1). Survival for 25 mm+ CW crab could be substantially reduced under the somewhat pessimistic

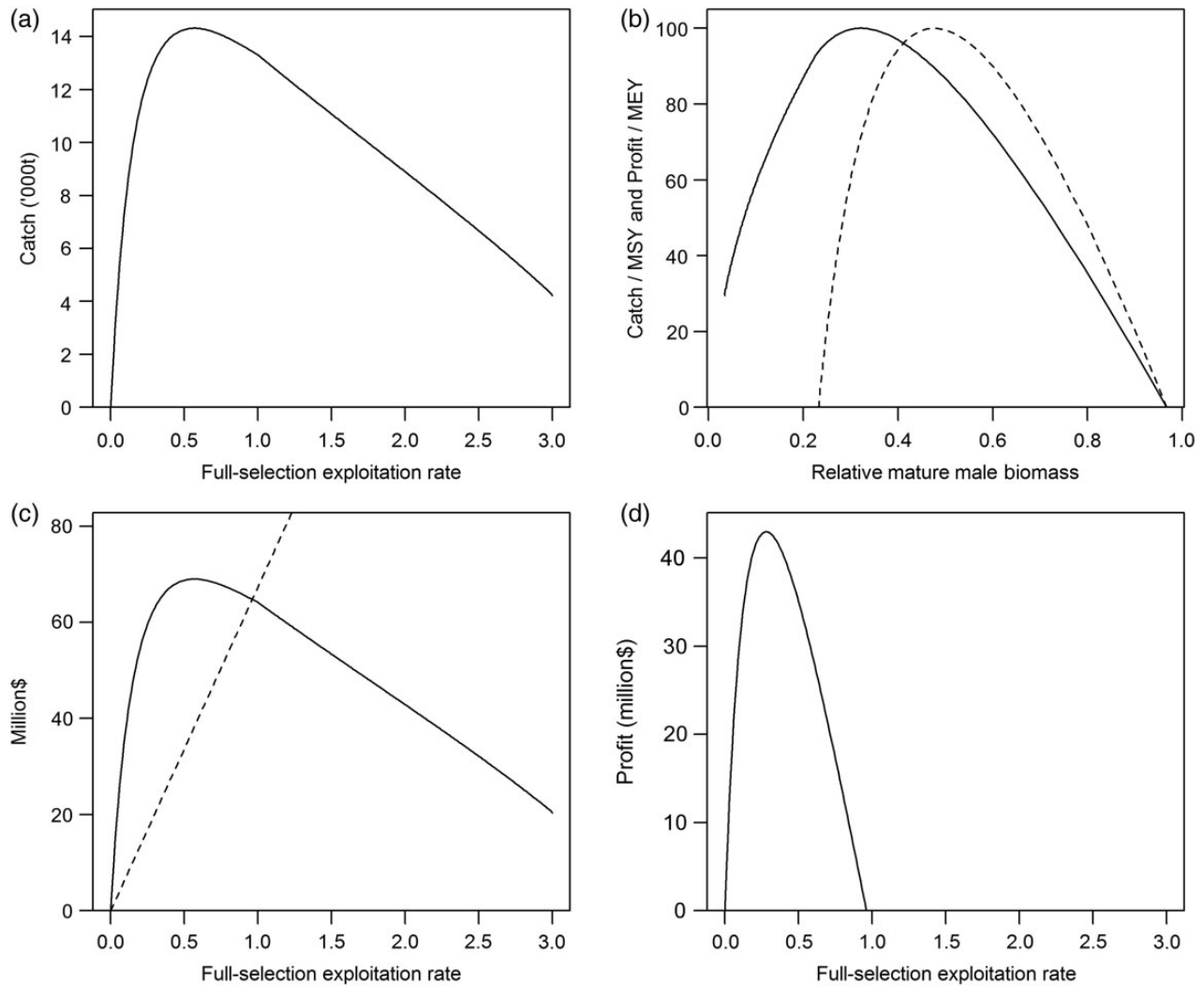
assumption that the daily survival rate for >25 mm CW crab equals that for stage C8 crab (Figure 4c). Combining the effect of ocean acidification on the survival rates of larvae and juvenile stages (glaucothoe stage animals being assumed not to be affected by ocean acidification) suggests that the proportion of hatchlings that survive to stage C8 (the first stage of the post-recruitment model) could decline by up to 25% over next 100 years.

**Yield and profit curves**

Figure 5 shows yield curves in the absence of ocean acidification as a reference against which the ocean acidification-affected scenarios can be compared. The equilibrium catch is maximized at a full-selection exploitation rate of 0.567 (Figure 5a) which is, by construction, equal to  $F_{35\%}$  given that stock–recruitment steepness was set (to 0.860) with the intent that  $F_{MSY} = F_{35\%}$ . MSY is estimated to be 14.3 kt, which is substantially larger than recent catches. The yield curve in Figure 5a does not hit the abscissa because some of the animals in the first post-recruitment stage are mature and because steepness is fairly high.



**Figure 4.** Temporal effects of ocean acidification for the base-case set of specifications: (a) proportion of embryos that hatch, (b) survival of a subset of the larval and juvenile stages, and (c) survival of stage C8+ crab. (d) The proportion of hatchlings that survive to recruit to 25 mm CW as a function of the year of spawning.



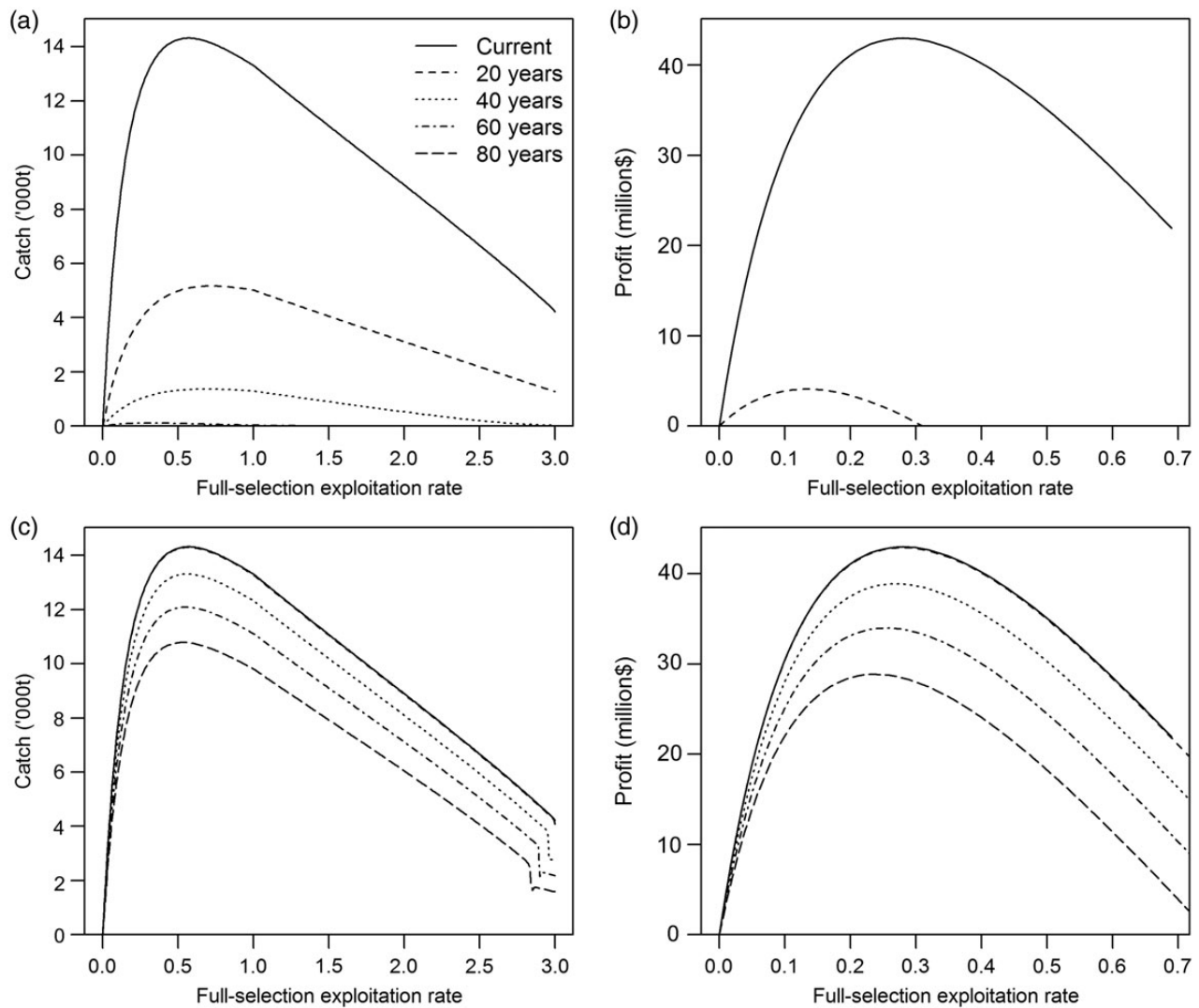
**Figure 5.** Equilibrium model behaviour in the absence of ocean acidification effects. (a) Equilibrium yield vs. full-selection exploitation rate, (b) catch relative to MSY (solid curve) and profit relative to MEY (dashed curve) vs. equilibrium mature male biomass expressed relative to the unfished mature male biomass, revenue (solid curve) and cost (dashed line) as a function of full-selection exploitation rate, and (d) profit as a function of full-selection exploitation rate.

In contrast to yield, profit, which is the difference between revenue and cost (Figure 5c), is maximized at a much lower full-selection exploitation rate (0.280) than the full-selection exploitation rate at which catch (and revenue) are maximized (Figure 5a and d). One consequence of this is that selecting a full-selection exploitation rate to maximize profit will stabilize the mature male biomass at a much higher level than selecting a full-selection exploitation rate to maximize catch (Figure 5b).

Figure 6 shows the sensitivity of the relationship between equilibrium catch and full-selection exploitation rate and that between equilibrium profit and full-selection exploitation rate at present and in 20, 40, 60, and 80 years into the future. Results are shown for the case in which natural mortality for 25 mm+ CW crab was affected by ocean acidification and the case in which this is not the case because this factor has the largest effect on the yield curve (and hence biological and economic reference points). In addition, there is no direct evidence that ocean acidification will reduce the survival rate for adult southern Tanner crab, let alone to the extent to which this is predicted for stage C8 crab.

As expected, ocean acidification reduced both MSY and  $F_{MSY}$  (Figure 6a and c), with the extent of change in these quantities depending markedly on whether ocean acidification affects natural mortality for animals of 25 mm+ CW crab. Ocean acidification also affected the relationship between profit and full-selection exploitation rate, except that the effect is much larger than for yield (Figure 6b and d). For example, MSY and  $F_{MSY}$  are zero after 60 years while MEY and the corresponding fishing mortality rate,  $F_{MEY}$ , are zero even after 40 years if ocean acidification affects natural mortality of 25 mm+ CW crab. In contrast, MSY and MEY are both non-zero if this natural mortality rate is not affected by ocean acidification (Figure 6b and d).

Figure 7 extends Figure 6 by providing the relationships between  $F_{35\%}$ ,  $F_{MSY}$ , MSY,  $B_{MSY}$ ,  $F_{MEY}$ , MEY,  $B_{MEY}$ , and years from the present. As expected from Figure 6, the values for all the reference points decline over time in the presence of ocean acidification, and do so faster when ocean acidification affects natural mortality for 25 mm+ CW crab (solid line). There is a perhaps somewhat surprising initial increase in  $F_{MSY}$  with time when ocean acidification



**Figure 6.** Equilibrium yield (a) and (c) and equilibrium profit (b) and (d) vs. full-selection exploitation rate by year. Results are shown when natural mortality for 25 mm+ CW crab is affected by ocean acidification and when this is not the case (upper and lower panels, respectively). [Note the difference in x-axis range between the left and right sets of panels].

impacts 25 mm+ CW crab (Figure 7a). This arises because  $F_{MSY}$  tends to be higher when natural mortality is higher. However, this tendency becomes swamped over time as the effect of ocean acidification increases because recruitment is reduced so fishing mortality must be reduced to prevent a collapse of recruitment.

The variable  $F_{35\%}$  equals  $F_{MSY}$  in the absence of ocean acidification effects (Figure 5a). However, the rate at which  $F_{35\%}$  (which does not depend on the form of the stock–recruitment relationship) changes over time differs from that of  $F_{MSY}$  (Figure 7a and g). This is because the biomass at which MSY is achieved drops over time (Figure 7e and f), but there is no requirement that it needs to stay above the level corresponding to  $F_{35\%}$ .

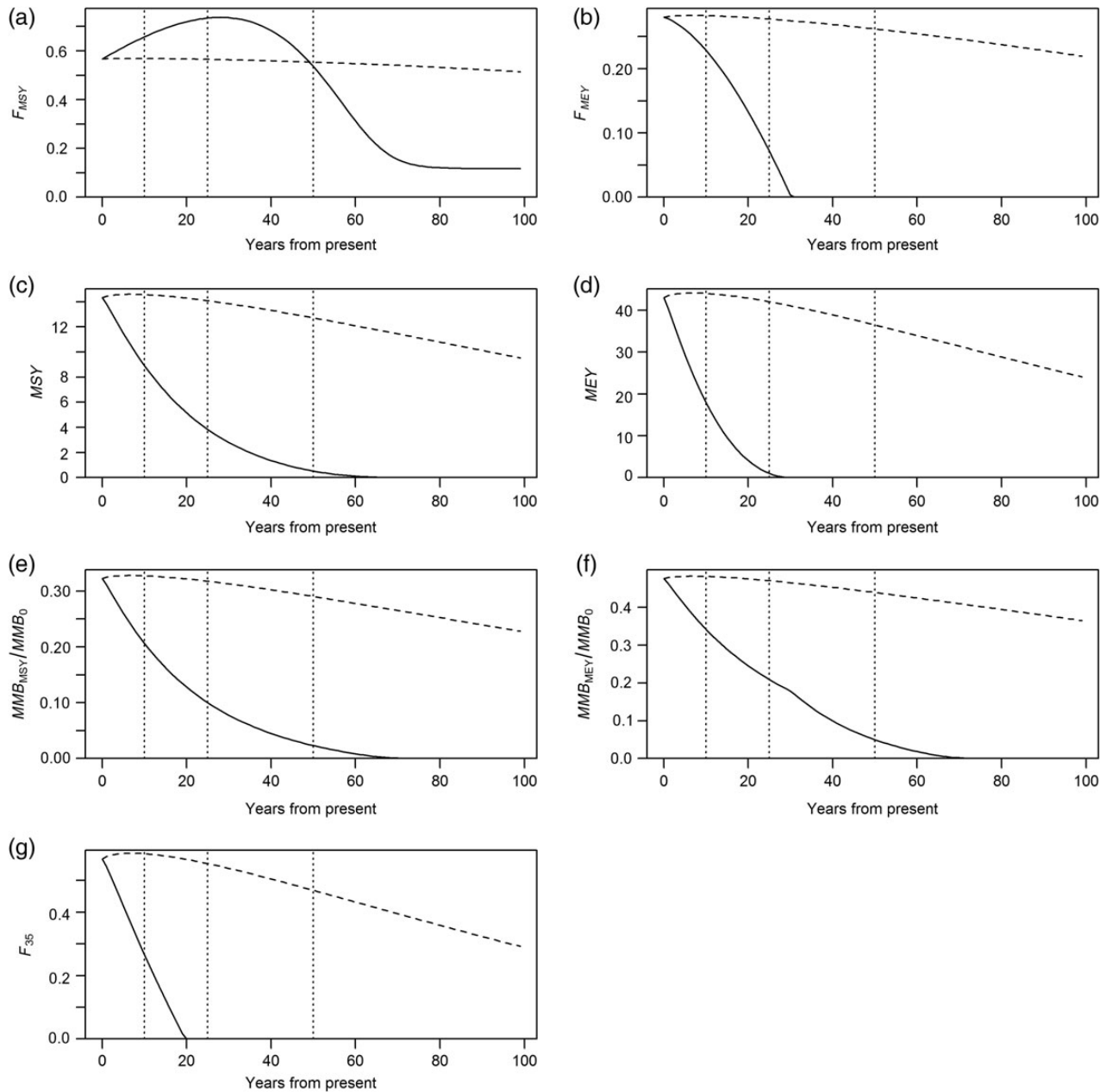
**Effects on biological reference points**

Figures 8 and 9 summarize the effect of ocean acidification on the biological reference points  $F_{35\%}$ ,  $F_{MSY}$ , and  $F_{MEY}$ , 10, 25, and 50 years into the future for each of the cases. Results are shown when ocean acidification affects natural mortality for 25 mm+ crab

(Figure 8) and when this is not the case (Figure 9). The values of the reference points are expressed relative to their value in the absence of ocean acidification. The results for the cases in which juvenile stage crab are not affected by ocean acidification, but animals 25 mm and larger are affected are presented but that case seems unrealistic.

As expected from Figures 6 and 7, the results are very sensitive to whether natural mortality for 25 cm+ CW crab is affected by ocean acidification. Also, and expected from Figure 7,  $F_{35\%}$  changes more over time than  $F_{MSY}$  and  $F_{MEY}$ . The upper right panel of Figure 8 is blank because  $F_{35\%}$  is zero within 50 years for all the cases when natural mortality for 25 cm+ CW crab is affected by ocean acidification.

Basing the analyses on ocean acidification only affecting larval survival (case B) would lead to the conclusion that the effects of ocean acidification are less negative than the base-case analysis (in fact they may be positive rather than negative if ocean acidification does not affect natural mortality of 25 mm+ crab), but only if the

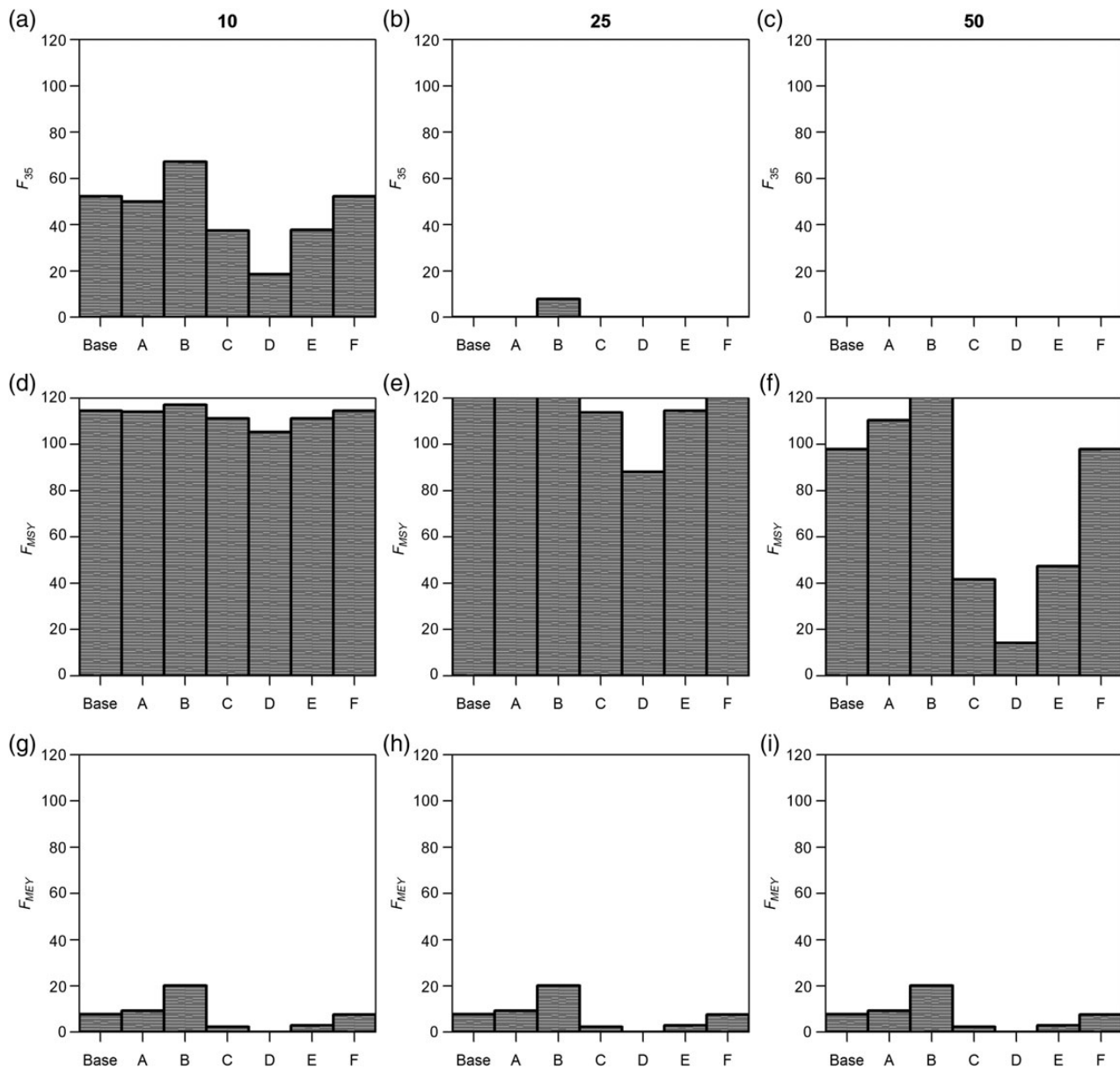


**Figure 7.** Effect of ocean acidification on biological reference points related to catch (a, c and e) and profit (b, d and f). The lower left panel (g) shows the relationship between  $F_{35\%}$  and time. The results are shown when ocean acidification affects post-recruitment natural mortality (solid curves) and when this is not the case (dashed curves). The vertical lines indicate the years for which results are shown in Figures 8 and 9.

larval survival was based on the experiments with treatments during oocyte, embryo, and juvenile development. In contrast, the results of projections for cases using the outcomes of the 2012 experiments and when ocean acidification is assumed to affect only during larval development (cases C and D) are markedly more pessimistic than the base-case analysis. Ignoring the effect of ocean acidification on hatching success leads to overestimates of  $F_{MSY}$  after 50 years compared with the base-case results (Figures 8f and 9f), but the effect is small. Assuming that the effect of ocean acidification on hatching success occurs after rather than before density-dependent effects on survival leads to larger effects than those for the base-case analysis (results not shown), but the effects remain small even over a 50-year projection period.

## Discussion

A framework within which the effects of ocean acidification can be integrated into how fisheries management advice is developed under the types of fisheries laws implemented within the USA. The current application to southern Tanner crab in the eastern Bering Sea accounts for ocean acidification effects on hatching success, survival rate of larvae, and survival of juveniles. It could be extended to allow other parameters to change with pH such as growth rates (both pre- and post-recruitment), fecundity (but that would likely require explicit modelling of females), and the extent of density-dependence. Growth rates of southern Tanner crab juveniles, for instance, were reduced in acidified treatments (Long et al., 2013). Inclusion of additional effects would require



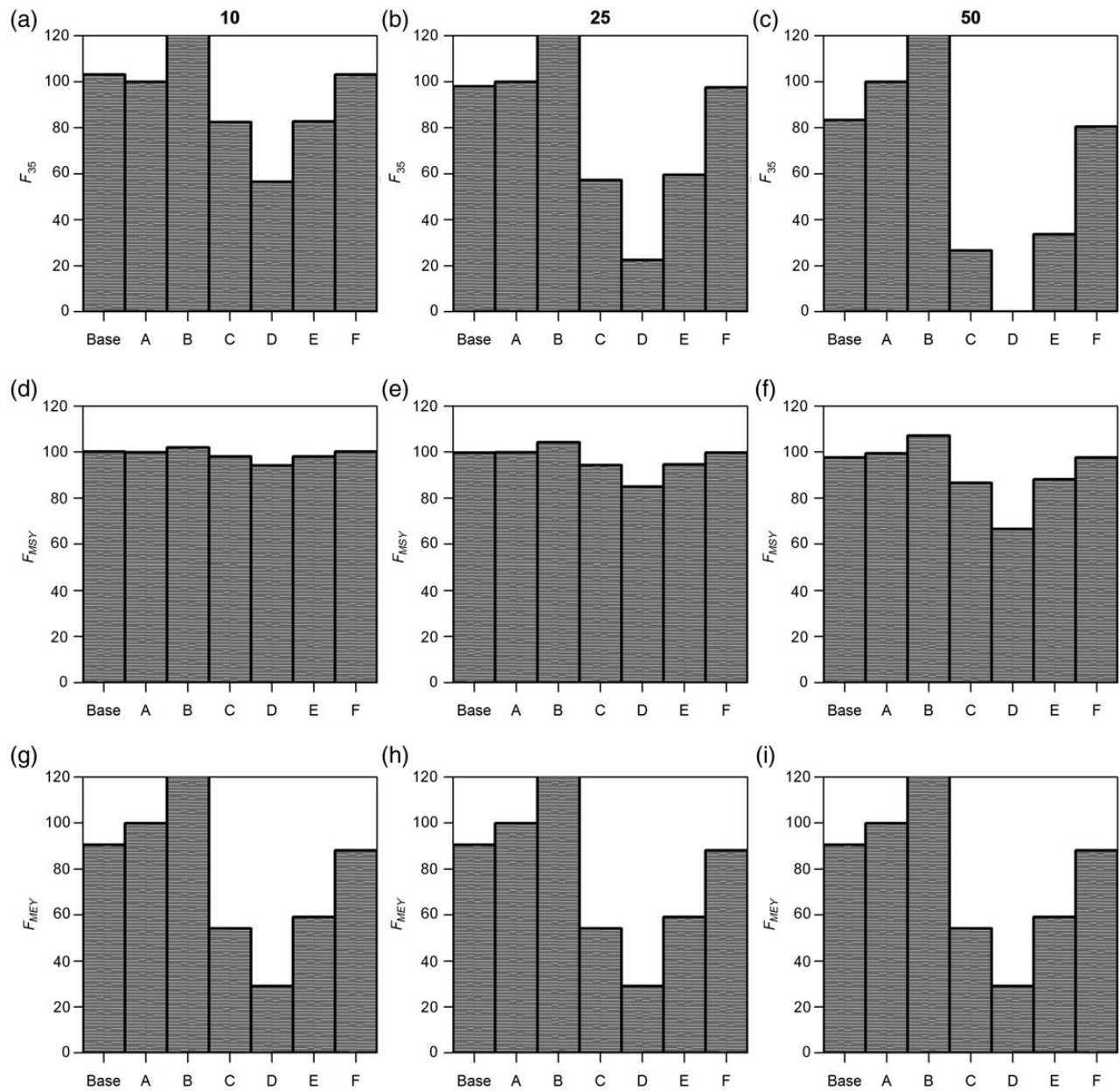
**Figure 8.** Values for three biological reference points ( $F_{35\%}$ ,  $F_{MSY}$ , and  $F_{MEY}$ ) relative to their values in the absence of ocean acidification by case (A–F) for 10, 25, and 50 years into the future. The results in this panel assume that ocean acidification affects natural mortality for 25 mm+ CW crab.

that appropriate experiments be conducted to parameterize the size of effects.

Results confirm expectations from demographic models that effects on the longer life stages have the largest consequences for population productivity. In the context of this paper, effects of ocean acidification on the rate of natural mortality for 25 mm+ CW and juvenile stage crab had by far the largest consequences for biological and economic reference points. In contrast, the consequences of ocean acidification effects on hatching success and larval survival were substantially smaller. As expected, if the effects on hatching success occur before density-dependence, the consequences of reduction in hatching success on biological and economic reference points are reduced. This was confirmed by the results of projections in which the only process affected by ocean acidification was

hatching success and those effects occurred after density-dependence (results not shown). The lack of sensitivity to hatching success is expected from Figure 4a and b, which show that the reduction in hatching success over 50 years is small as is true for larval survival. The consequences of ocean acidification on larval survival differ depending on how the experiments designed to estimate the effects are conducted, with the results when ocean acidification effects occur only during larval development being markedly more optimistic than when such effects occur throughout oocyte and embryo development.

The results of this study complement those of Punt *et al.* (2014b) who used a similar approach to explore the implications of ocean acidification for red king crab in Bristol Bay, Alaska. Unlike this study, Punt *et al.* (2014b) only allowed for ocean acidification effects on juvenile stage crab. They therefore ignored effects on



**Figure 9.** Values for three biological reference points ( $F_{35\%}$ ,  $F_{MSY}$ , and  $F_{MEY}$ ) relative to their values in the absence of ocean acidification by case (A–F) for 10, 25, and 50 years into the future. The results in this panel assume that ocean acidification does not affect natural mortality for 25 mm+ CW crab.

hatching success and larval survival as well as effects on adult crab (although Punt *et al.* (2014b) considered a broader range of instars as juvenile crab so the effect of increased mortality on juvenile crab was higher). The results of this paper suggest that Punt *et al.* (2014b) considered the life history stage that has the largest effect on biological and economic reference points. However, by ignoring the possibility that ocean acidification affects all adult crab, Punt *et al.* (2014b) may have underestimated the consequences of ocean acidification on future stock status and fishery catches.

The results of this study emphasize the need to consider multiple life stages in research on the physiological effects of ocean acidification conditions. Although the consequences of ocean acidification on hatching success was found to be relatively small, at least over a 50-year period (Figures 8 and 9), this could not have been

anticipated *a priori*. The fact that juvenile and adult natural mortality had the largest effect on biological and economic reference points has implications for research priorities. In contrast to the experiments to estimate effects on hatching success and larval survival (30 days in duration), examination of ocean acidification effects on juvenile stage and adult crab requires a large research and infrastructure investment.

We did not quantify the uncertainty associated with the effects of ocean acidification on hatching success and survival and propagate this uncertainty through to values for the biological and economic reference points. Punt *et al.* (2014b) quantified uncertainty associated with ocean acidification effects on juvenile stage crab using a Monte Carlo approach, and combined this uncertainty with the variation in recruitment about the estimated stock–recruitment

relationship. They concluded that the effects of ocean acidification would not be detectable for 20–40 years. Similar results would have been obtained in this study. The model has not explored all possible scenarios. For example, the assumption that density-dependence occurs early in life is common in assessment models, but is not the only possible assumption. For example, density-dependence could occur throughout most of the pre-recruitment stages and in particular during settlement. Although the qualitative results are robust to the timing of density-dependence, quantitatively, the effects of ocean acidification will be reduced if density-dependence occurs after some of the effects of ocean acidification on survival, as is evident from the analyses that explored whether the effect on hatching occurs before or after density-dependence.

The results of this study would be sensitive to some of the assumptions which that could not be explored. In particular, the quantitative, but not qualitative, results would be sensitive to violation of the assumption that the stock–recruitment relationship is of the Beverton–Holt form and that  $F_{MSY} = F_{35\%}$  in the absence of ocean acidification. In addition, the relative mortality of larvae among treatments was based on starvation experiments under the assumption that the pattern of mortality for healthy larvae would be similar. This may explain the model's overestimate of larval survival relative to the experimental data and may suggest that the increase in larval survival rate (Figure 4b) is incorrect. Finally, we assumed that ocean acidification would be the only environmental change as a result of climate change in the North Pacific. As such, we ignored the potential effects of other physical variables (e.g. temperature and water column structure) and biological variables (e.g. primary production and increased acidity due to respiration) and the overall effects these variables would have on crab production, movement, and predator/prey interactions. Future research should attempt to incorporate a more holistic view of the role of expected environmental changes on the biological forcing specific to commercial crab stocks in the North Pacific.

Relative little effort has been directed towards understanding the fishery-related consequences of ocean acidification (Griffith *et al.*, 2011; Malakoff, 2012), particularly for Alaska. Exceptions to this include Kaplan *et al.* (2010) who explored the consequences of ocean acidification for the US West Coast groundfish fishery using the implementation of the ecosystem model Atlantis for the US West Coast (Brand *et al.*, 2007; Kaplan and Levin, 2009), although that analysis was based on catch scenarios rather than actual harvest regimes applied for fisheries management. Mathis *et al.* (2015) applied a risk assessment framework to the impacts of ocean acidification on Alaskan fisheries broadly, by identifying the vulnerability and susceptibility of a range of fisheries across a range of Alaskan regions to the effects of ocean acidification. However, unlike this study (and that of Punt *et al.*, 2014), Mathis *et al.* (2015) did not base their analyses on the population dynamics models developed for the impacted species and fisheries. However, their analysis provides information related to broad policy development. In contrast, while this study does not include the breadth of species and fisheries examined by Mathis *et al.* (2015), it provides results in terms of the quantities (fishing mortality rates, biomass expressed relative to reference points, catches, and revenue) used by fisheries decision makers.

The research strategy follows the plan in Sigler *et al.* (2008) to start with theoretical principles of population biology and use experiments to estimate effects of ocean acidification conditions on early life history parameters as the most effective way to forecast effects of ocean acidification on the abundance of Alaska crab stocks.

This strategy combines biological and economic theory to extrapolate from results obtained in a tightly controlled laboratory setting to conditions that young crab in the Bering Sea may someday experience. Furthermore, the population projections for crab stocks presented in this paper are based on coarse assumptions about future ocean conditions that are necessary in applications that involve scenarios for future carbon emissions to begin to predict effects of ocean acidification on marine ecosystems. The coarsest assumptions can be tested and improved, and striving for a forecasting methodology is a useful objective that can be shared across scientific disciplines. For example, multispecies bioeconomic models are feasible. Bycatch in the fisheries for Alaska red king crab and snow crab appear as independent sources of fishing mortality in the bioeconomic model for Tanner crab presented in this paper. It could be useful and interesting to link population dynamics models for these crab stocks. Inevitably, questions about ecosystem effects arise and addressing those will be difficult.

### Acknowledgements

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