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Permalink

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Journal

Canadian Journal of Fisheries and Aquatic Sciences, 72(3)

ISSN

0706-652X

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Publication Date

2015-03-01

DOI

10.1139/cjfas-2014-0243

Peer reviewed

Quantifying the potential for marine reserves or harvest reductions to buffer temporal mismatches caused by climate change

Lewis A.K. Barnett, Marissa L. Baskett, and Louis W. Botsford

Abstract: Climate change has caused shifts in seasonal timing of climatic events such as the onset of spring upwelling, which can lead to temporal mismatches between fish spawning and production of zooplankton prey. Fishing may exacerbate mismatches through age truncation, particularly when offspring survival is dependent on maternal age, but no-take reserves or harvest reductions might buffer this effect. To quantify the potential for management to buffer synergistic interactions between fishing and climate, we developed a dynamic population model of a harvested species where larval survival depended on spring transition timing and maternal age. We applied this model to rockfishes (*Sebastes* spp.) after verifying empirically that spring transition timing affects their recruitment success. We found that yield and persistence changed more with maternal-age-dependent larval provisioning than maternal-age-dependent spawning timing across a range of spring transition timings, especially with environmental stochasticity. Either implementing reserves or reducing fishing can mitigate impacts on larval survival, but reserves convey the added benefit of decreased sensitivity of yield and persistence to fishing. However, reserve buffering effects decreased with the inclusion of environmental stochasticity.

Résumé : Les changements climatiques ont entraîné des modifications de la période d'occurrence saisonnière d'événements climatiques tels que le début de la remontée printanière des eaux froides, ce qui peut mener à des décalages temporels entre le frai des poissons et la production de proies zooplanctoniques. Si la pêche peut exacerber ces décalages en produisant une troncation des âges, en particulier quand la survie de la progéniture dépend de l'âge maternel, des réserves sans exploitation ou des réductions des prises peuvent atténuer cet effet. Pour quantifier le potentiel d'atténuer par la gestion les interactions synergiques de la pêche et du climat, nous avons élaboré un modèle de dynamique de la population d'une espèce exploitée dans lequel la survie des larves dépend de la période d'occurrence de la transition printanière et de l'âge maternel. Nous avons appliqué ce modèle aux sébastes (*Sebastes* spp.) après avoir vérifié de manière empirique que la période d'occurrence de la transition printanière avait une incidence sur leur succès de recrutement. Nous avons constaté que les variations du rendement et de la persistance étaient plus grandes dans le cas d'un approvisionnement des larves dépendant de l'âge maternel que dans le cas du frai dépendant de l'âge maternel pour une gamme de périodes d'occurrence de la transition printanière, particulièrement en présence d'une stochasticité environnementale. Si la mise en place de réserves et la réduction de la pêche peuvent toutes deux atténuer les impacts sur la survie des larves, les réserves offrent en plus l'avantage de réduire la sensibilité à la pêche du rendement et de la persistance. Les effets d'atténuation des impacts des réserves diminuent toutefois si la stochasticité environnementale est intégrée au modèle. [Traduit par la Rédaction]

Introduction

One of the many challenges of fisheries management is accounting for how climate variability and long-term change might influence productivity of harvested populations (Ianelli et al. 2011), which is expected to occur primarily through changes in recruitment success (Ciannelli et al. 2005). In many fished stocks, recruitment is highly variable on interannual to interdecadal time scales (Hjort 1914; Mueter et al. 2007), and survival in the early life stages prior to settlement and recruitment may be the critical demographic bottleneck that determines cohort size (e.g., Ralston and Howard 1995). Furthermore, recruitment variation can cause instability in populations that are heavily fished (Fogarty et al. 1991).

One mechanism by which climate change affects recruitment is through changes in the timing of seasonal climatic events that promote productivity at lower trophic levels. In particular, the match-mismatch hypothesis (Cushing 1990; a special case of the

critical period hypothesis (Hjort 1914)) posits that population persistence critically depends on the extent of temporal overlap (or “matching”) between the abundance of fish larvae at the developmental stage when feeding is initiated and the abundance of their food source (zooplankton). The frequency and magnitude of mismatches between offspring production and prey availability depend on among-individual heterogeneity in phenology (the seasonal timing of life-cycle events) (Wright and Trippel 2009) and temporal climatic variability (Durant et al. 2007). Mismatches driven by temporal climatic changes have already been observed as a result of global climate change (e.g., in marine plankton communities; Edwards and Richardson 2004). Mismatches driven by among-individual heterogeneity are more difficult to detect and can be due to within-population heterogeneity in many traits, although it is most commonly observed in reproductive timing (Reznick and Braun 1987). Specifically, larger or older mothers sometimes produce offspring earlier in the reproductive season

Received 19 May 2014. Accepted 20 October 2014.

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than smaller or younger mothers, presumably because only larger or older females have adequate energetic stores to begin their seasonal reproductive cycles earlier (Reznick et al. 2006). These biological and climatic drivers of mismatches can interact, as one affects the timing of the environmental change and the other affects the capability of a population to withstand this interannual variability by shaping the distribution of the population's phenology.

By modifying age and size structure, fisheries management policies affect the interaction between biological and climatic drivers of mismatches and therefore the response of populations to climate change. Specifically, the addition of fishing mortality skews the age structure toward younger age classes, an effect that is even stronger when harvest targets large size classes (e.g., Yemane et al. 2008). Given a relationship between maternal size and reproductive timing, fishing-induced age truncation will cause a shifting or narrowing in the distribution of a population's reproductive season. Harvest reductions and spatial closures are the most viable options for mitigating age truncation, because the effectiveness of size limits is limited in most commercial fisheries by discard mortality and lack of gear selectivity (Berkeley et al. 2004b). When harvest rates are reduced evenly across a region (as they would be in conventional fishery management) the spawning age structure expands at all locations, whereas when spatial closures like no-take marine reserves are implemented, the spawning age structure may expand more drastically, but only within the closed area.

Although some researchers have suggested that reserves can provide a buffer against ecological effects of climate change (Heller and Zavaleta 2009; McLeod et al. 2009), whether reserves are an effective tool for fisheries management in a changing climate is an open question. Suggested approaches for reserve management to ameliorate ecological effects of climate change have been primarily qualitative (McLeod et al. 2009). A quantitative understanding requires incorporation of temporal environmental variation in recruitment into population models that can compare the effects of conventional fisheries management and reserve-based management. The few existing models that have incorporated environmental variation suggest that reserves can reduce variability in population size and fishery yield (Sladek Nowlis and Roberts 1999; Mangel 2000; Grafton et al. 2005), indicating a potential role for reserves in buffering population responses to climate change.

Coastal upwelling systems, such as the California Current System (CCS), exemplify all the elements that drive the potential sensitivity of populations to climate-induced mismatches. The importance of variability in climatic phenology was illustrated in 2005, when a long delay in the spring transition to upwelling-favorable conditions was the likely cause of large-scale recruitment failures that were observed in many marine species (e.g., Barth et al. 2007). Climate models have predicted that such delays in the onset of the productive spring upwelling season will become more prevalent in the CCS (Snyder et al. 2003); however, a recent trend toward earlier onset of spring upwelling has been noted in some parts of the region (García-Reyes and Largier 2010). Changes in timing of the onset of upwelling would likely affect fish recruitment, because many species reproduce during late winter and spring, presumably so that their larval phase coincides with upwelling-related food production. Birth date is dependent on maternal age in some fishes of this community (e.g., rockfishes; *Sebastes* spp.), with older mothers having a greater window of time during which they have the capability to produce offspring than do younger mothers (Bobko and Berkeley 2004; Sogard et al. 2008). Some of this phenological breadth has likely been eroded because fishing has caused a shift to smaller sizes and younger ages in harvested rockfishes (Berkeley et al. 2004a; O'Farrell and Botsford 2006b). However, in their model of black rockfish (*Sebastes melanops*), O'Farrell and Botsford (2006b) found that there would not be a significant change in the population size

or fishery yield if the maternal influence on larval provisioning was unaccounted for by managers.

Here we quantify the effect of climate-change-dependent variability in recruitment on population persistence and fisheries yield under different combinations of conventional fisheries management and spatial management using the CCS as a model system. Our approach is to develop trophic-mismatch models that incorporate mismatch-dependent larval survival based on the temporal overlap of seasonal larval fish production and zooplankton production, which begins at onset of spring upwelling. We use this framework to test whether two maternal influences on reproductive phenology, via larval provisioning and via timing of spawning (more specifically parturition or larval release in this particular case study), affect population persistence and fishery yield. We then explore the efficacy of different management approaches for buffering mismatch effects under a range of changes in spring transition timing and we determine whether these outcomes differ when environmental stochasticity is incorporated.

Methods

Study system

Although the modeling framework we develop here could apply to any system in which there is a critical phase of early life during which survival depends on the coincidence of multiple events, we chose to focus on coastal upwelling systems, using the CCS as a case study. Coastal upwelling systems such as the CCS are found on the eastern boundary of all four major ocean basins, where the seasonal upwelling of cold, nutrient-rich water drives primary productivity (Bakun 1996). Within the CCS, we focused on mismatches between organismal and climatic phenology that arise from interannual variability in the timing of the upwelling season and demographic heterogeneity in the timing of offspring production. We used rockfishes as a model taxon to exemplify the phenological component of the process, because researchers have observed maternal-phenotype-dependent offspring traits in this group, including earlier parturition dates (Bobko and Berkeley 2004; Sogard et al. 2008) and larger larval size or larval energy reserve with greater maternal size or age (Berkeley et al. 2004a).

Empirical verification of critical timing assumption

To test our assumption that rockfish recruitment is dependent on the timing of spring transition, we performed an original analysis of SCUBA visual surveys of rockfish recruit density conducted over 19 years (data courtesy of Tom Laidig, NOAA Fisheries; for detailed sampling methods see Laidig et al. 2007). We tested for correlations between mean rockfish recruit density at a given location and the Logerwell et al. (2003) index of spring transition date.

Model overview

We developed a single-species, discrete-time, age-structured model with density-dependent recruitment. We represented spatial variability in fishing by including two discrete patches; one patch was open to fishing, and the other was protected by a marine reserve. We assumed that larvae produced in each patch became well-mixed in the plankton and were redistributed between the patches proportionally to relative patch area (i.e., larval-pool dispersal; Roughgarden and Iwasa 1986). We assumed that there was no adult movement between reserve and unprotected areas. When the area of the reserve patch was zero, the model reduced to a nonspatial model representing conventional fisheries management alone (i.e., there was no longer any spatial heterogeneity in fishing and hence only one patch type).

We incorporated maternal-age-dependent offspring traits in terms of both the larval energy reserve and parturition timing (Figs. 1b–1d). As maternal age increased, parturition (larval release) occurred earlier, and the time to starvation of larvae in the absence of food increased as would be expected from greater oil

Fig. 1. Model structure diagram (a) demonstrating how adults, from age at maturity (\bar{a}) to the maximum age (A), produce larvae whose traits depend on maternal age. Maternal influences are included by specifying that older mothers (grey lines) produce larvae that can resist starvation longer than younger mothers (black lines) (b) and that older mothers can release their batch of larvae earlier in the reproductive season (c). The maternal influence on parturition timing affects the amount of food available to larvae, based on the similarity of birth timing, $r_{a,t}$, to the timing of spring transition and subsequent peak in zooplankton production, t_z (d). The maternal influence on provisioning, d_a , determines the daily larval mortality rate in the absence of zooplankton, thus larval survival (e, f) is a function (described in eq. 2) of the amount of matching between the abundance of zooplankton prey and the period from day of parturition through the early larval phase (illustrated by the shaded region in panel d). Larval survival is also influenced by interannual variability in t_z within the stochastic model (g, h). Panels with dashed lines (b, e, g) show the influence of maternal-age-dependent effects on larval provisioning, while those with dashed-dot lines (c, f, h) represent results with maternal-age-dependent effects on birthdate phenology. In the lower box (e–f), the effect of the labeled maternal influence on larval survival is isolated by removing the alternative maternal influence (e.g., in panel e, $r_{a,t}$ is a constant that is equivalent for mothers of all ages). The vertical grey line indicates the current mean date of maximum zooplankton production, reflecting the general timing of parturition that would result in the least mismatch; thus, climate-induced mismatches increase from this point in both directions along the horizontal axis. Parameter values are as in Table 1.

globule energy reserve provisioning. Larval survival depended on the extent of mismatch between zooplankton production over time during the first major upwelling event and the time from birth through the time when maternally provisioned oil globule energy reserves are completely absorbed (Fig. 1d). Survival from settlement to recruitment was density dependent, represented by scramble competition for shelter on the reef. Once individuals recruited, they experienced constant natural mortality, and for ages greater than the age at entry to the fishery they also experienced fishing mortality. We used this modeling framework to quantify the extent to which mismatches caused by changes in seasonal timing of upwelling can alter the magnitude of fishing mortality that the population can withstand. To determine how each management approach affects persistence and fishery yield in the face of climate change we compared these results between scenarios of nonspatial conventional fisheries management with a constant effort harvest policy and spatial management with reserves and a constant harvest policy in unprotected zones.

Model details

Recruitment depended on the number of competent larvae arriving in a patch and density dependence at the settlement site. We quantified the larvae surviving to the moment just before settlement in patch i at time t ($B_{t,i}$) as the product of the age-dependent fecundity (b_a), the number of individuals at age a ($n_{a,t,i}$), survival of larvae produced by age a mothers ($l_{a,t}$), and the proportion of habitat within each patch (P_i ; given our assumption of a well-mixed larval pool) summed over age from maturity (\bar{a}) to the maximum age (A) and across both patches:

$$(1) \quad B_{t,i} = \sum_{a=\bar{a}}^A \sum_{i=1}^2 b_a n_{a,t,i} l_{a,t} P_i$$

Larval survival ($l_{a,t}$) depended on maternal age and the timing of the first peak in zooplankton production resulting from the onset of the upwelling season in year t ($t_z(t)$) (Table 1). Fecundity (b_a) increased with maternal age (a) given von Bertalanffy growth for increasing length with age, a power function between mass and length, and fecundity proportional to mass (Table 1). The timing of parturition in a given year ($r_{a,t}$) was a step function, dependent on age, with early parturition for ages above a threshold, a_{old} (Table 1; in this base case $r_{a,t}$ was equal to the midpoints of distributions in Fig. 1c). The duration that larvae can survive without food (d_a) increased with age as a negative exponential (Fig. 1b; Table 1). The instantaneous mortality rate in the absence of food was $M_{nf}(a) = -\log(0.5)/d_a$ (derived from d_a by assuming an exponential decay; O'Farrell and Botsford 2006a). We then determined early larval survival by the extent of overlap between zooplankton production over time during the first major upwelling event in year t (defined within each year by a normal distribution with mean $t_z(t)$ and variance σ_z^2) and the transition to exogenous feeding of larvae

from mothers of age a (the interval from $r_{a,t}$ to $r_{a,t} + d_a$, where A is the maximum age and d_a is the maximum duration a larva can survive without consuming prey). Finally, we defined the complete larval survival up to the point prior to settlement as the product of the timing-independent discrete survival probability (S_0) and the mismatch term describing early larval survival:

$$(2) \quad l_{a,t} = \exp \left\{ \int_{r_{a,t}}^{r_{a,t}+d_a} \left[M_{nf} \left(\exp \left\{ \frac{-(\tau - t_z(t))^2}{2\sigma_z^2} \right\} - 1 \right) \right] d\tau \right\} S_0$$

See Appendix A for the detailed derivation of eq. 2.

Combining all of these elements, $B_{t,i}$ is the number of competent larvae arriving in each patch i at time t . Surviving larvae experienced density-dependent survival at settlement according to a Beverton–Holt stock–recruitment function. Thus, we defined recruitment ($R_{t,i}$) as

$$(3) \quad R_{t,i} = \frac{\alpha B_{t,i}}{1 + \beta_i B_{t,i}}$$

where α is the inverse of the slope of the stock–recruitment function near the origin (critical replacement threshold), and the asymptotic maximum number of recruits is α/β_i , a function of the proportion of habitat within each patch (P_i):

$$(4) \quad \beta_i = \frac{\beta}{P_i}$$

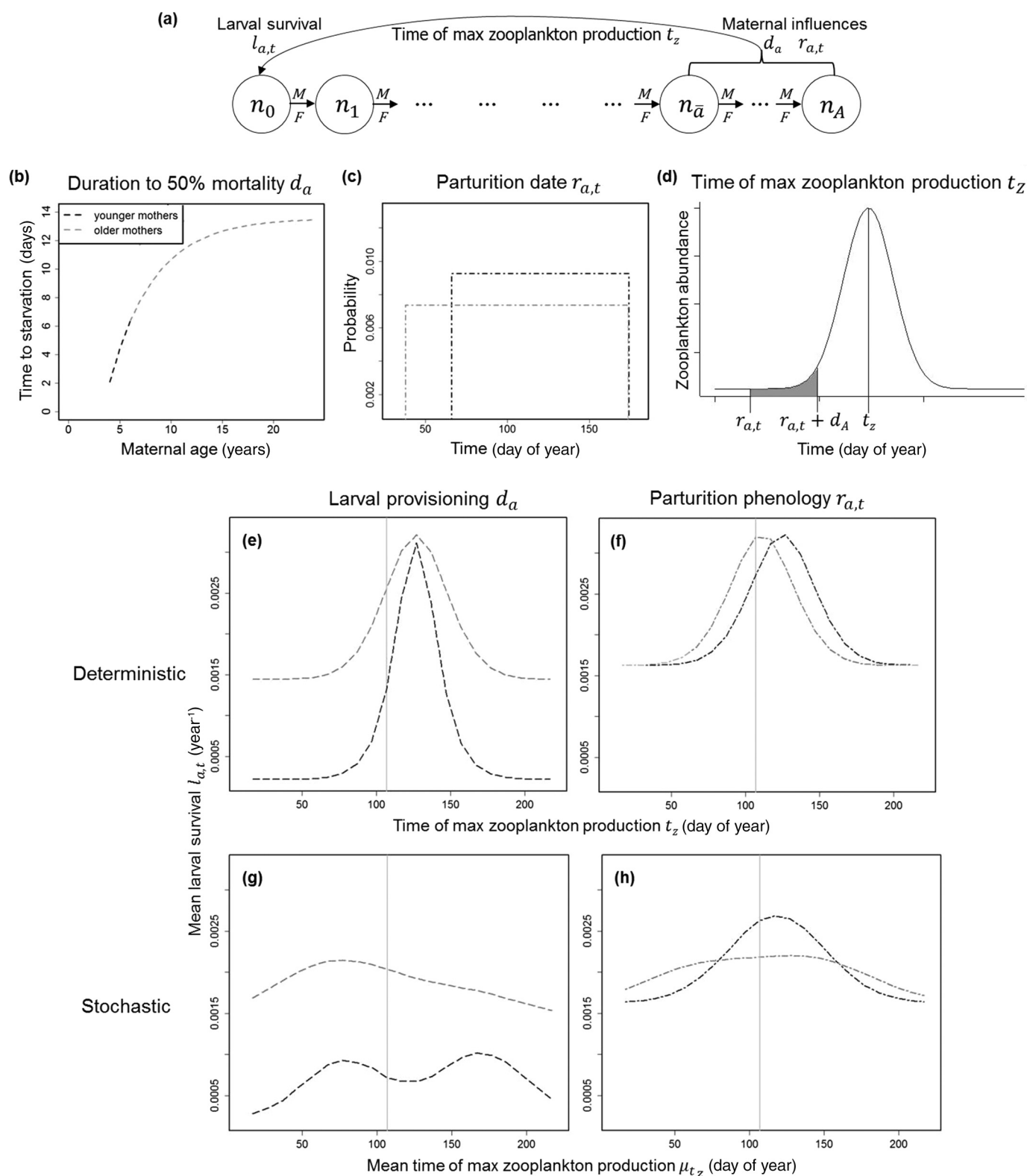
The remaining numbers of individuals at age $a > 0$ were simply reduced at each time step by constant fishing mortality ($F_{a,i}$) and natural mortality M . Therefore, the full model is

$$(5) \quad \begin{cases} n_{0,t+1,i} = R_{t,i} \\ n_{a,t+1,i} = n_{a-1,t,i} \exp[-(M + F_{a-1,i})] \end{cases} \quad 1 \leq a \leq A$$

where fishery selectivity was a knife-edged function. Fishing mortality at a rate \tilde{F} was experienced by individuals in the harvested patch ($i = 1$) after they reached the age at recruitment to the fishery (a_{rec}):

$$(6) \quad F_{a,i} = \begin{cases} \tilde{F}, & a \geq a_{rec} \text{ and } i = 1 \\ 0, & \text{otherwise} \end{cases}$$

We compared two cases of how reserve implementation affects \tilde{F} in the unprotected patch; the case of constant harvest rate, where \tilde{F} did not change with reserve coverage, and the case of compensatory harvest, where \tilde{F} increased proportionally to reserve coverage.



Analysis

To quantify the potential for different management approaches to buffer climatic mismatches, we evaluated and compared (i) metrics of both persistence and yield, (ii) changing harvest rate or implementing reserves, (iii) including or excluding each of the two maternal-age-dependent larval traits, and (iv) deterministic or stochastic spring transition and parturition timing. For the deter-

ministic model, representative of a relatively constant environment, we evaluated persistence and yield under different values of constant spring transition and parturition timing. In comparison, the stochastic model accounts for interannual variation in spring transition and parturition timing. For stochastic parturition timing, we drew independent values of parturition dates from a uniform distribution over a different range for younger

Table 1. Parameter estimates used in model simulations.

Parameter	Symbol	Unit	Value used in model	Source
Maximum age	A	Years	24	Bloeser 1999; Lea et al. 1999
Age at maturity	\bar{a}	Years	4	Wyllie Echeverria 1987
Annual fecundity at age $b_a = cm_a$	b_a	Eggs		MacGregor 1970
	c	Eggs·kg ⁻¹	249	
Natural mortality rate	M		0.2	Key et al. 2005
Mismatch-independent age-0 survival	S_0		0.325×10 ⁻³	
Age at entry to fishery	a_{rec}	Years	7	Key et al. 2005*
Beverton–Holt stock recruitment terms	α		2.60×10 ⁻³	Key et al. 2005
	β		9.46×10 ⁻¹⁰	
Time to 50% starvation mortality $d_a = e + f[1 - \exp(-ga)]$	d_a	Days		Berkeley et al. 2004a
	e	Days	-15.23	
	f	Days	28.79	
	g	Years ⁻¹	0.23	
Date of parturition	r_a	Day of year		Wyllie Echeverria 1987; Berkeley et al. 2004a
Age threshold of earlier parturition date	a_{old}	Years	6	
Midpoint of young mothers			120	
Midpoint of old mothers			106	
Range of young mothers			66–174	
Range of old mothers			38–174	
Date of maximum zooplankton production	t_z	Day of year		
Standard deviation of mean zooplankton peak among years	σ_{t_z}	Days	24	Columbia Basin Research 2011
Max zooplankton production lag		Days	10	Botsford et al. 2006
Mean timing of first zooplankton peak	μ_{t_z}	Day of year	107	Columbia Basin Research 2011; Botsford et al. 2006
Standard deviation of zooplankton production within a year	σ_z	Days	3.7	Botsford et al. 2006
Mass at age $m_a = qL_a^p$	m_a	kg		Key et al. 2005
	q		1.299×10 ⁻⁵	
	p	kg·cm ^{-q}	3.077	
Length at age $L(a) = L_{\infty}\{1 - \exp[-k(a - t_0)]\}$	$L(a)$	cm		Lea et al. 1999
	L_{∞}	cm	341	
	k	Years ⁻¹	0.2256	
	t_0	Years	-0.05	

*Calculated from size at maturity using von Bertalanffy length-at-age relationship.

and older mothers (a broader, earlier range for mothers with age $a \geq a_{\text{old}}$ than for mothers with $a < a_{\text{old}}$; Table 1). For stochastic spring transition timing, in each time step we drew independent values of peak zooplankton production (t_z) from a normal distribution parameterized by the mean (μ_{t_z}) and variability (σ_{t_z}) in spring transition date observed over the past 47 years (i.e., a hyperdistribution; Table 1).

In the deterministic model, we analytically explored the non-spatial case to inform general expectations for model behavior in the numerical simulations. Specifically, we derived the local stability criterion for the zero equilibrium, which determines whether the population will grow at low abundance and therefore persist. This provided intuition for interpreting numerical results by formally describing how population persistence becomes more likely with decreasing critical replacement threshold (α^{-1}), decreasing mortality (M or \tilde{F}), increasing fecundity (b_a), and increasing match-dependent larval survival (l_a). For the numerical analyses, we chose parameter values from the spring-spawning gopher rockfish (*Sebastes carnatus*), because this species has more species-specific life history data available than does the similar copper rockfish (*Sebastes caurinus*), the species for which we verified the relationship between recruitment and spring transition date (see the section entitled “Empirical verification of critical timing assumption”). For parameters in which specific estimates for *S. carnatus* were not available, we used estimates from other rockfish species with similar life histories (Love et al. 2002; Bobko and Berkeley 2004; Key et al. 2008).

One primary persistence metric was F_{persist} , the maximum \tilde{F} that the population could withstand over the long term, evaluated at each extent of mismatch (different values of the timing of peak zooplankton production, t_z). In the deterministic model only two long-term behaviors were possible: approaching a positive equilibrium abundance or zero (the initial population size was well below equilibrium at nearly 15 000 individuals, with numbers at age distributed approximately exponentially with some noise). Therefore, F_{persist} was taken as the greatest \tilde{F} that resulted in an increase toward a positive equilibrium. To determine F_{persist} for each patch in the stochastic model, we calculated the stochastic growth rate (Tuljapurkar 1997; Caswell 2001)

$$(7) \quad \log \lambda_s(i) = \frac{1}{T} \sum_{t=1}^T \log \left(\frac{\sum_{a=0}^{a_{\text{max}}} n_{a,t+1,i}}{\sum_{a=0}^{a_{\text{max}}} n_{a,t,i}} \right)$$

after $T = 5000$ time steps and checked for convergence. This fairly long time horizon ensured that the results reflect quasi-equilibrium conditions rather than initial-condition-dependent transients and allowed a precise estimate of the stochastic growth rate. We then defined F_{persist} as the greatest value of \tilde{F} that resulted in a positive stochastic growth rate. We calculated F_{persist} across a range of values for mean date of peak zooplankton production (μ_{t_z}) to represent possible climate change scenarios. In all scenarios, the

timing of parturition $r_{a,t}$ was independent of the timing of zooplankton production (i.e., we assumed that the phenology does not track climate). While it is a given that F_{persist} will increase with reserve establishment and size owing to protected biomass in reserves, our question concerning the potential for reserves to act as a buffer against climate change effects is how the sensitivity of F_{persist} to the extent of climate-driven mismatch and maternal influences depends on the presence of reserves.

For our yield metric, we use the annual harvested biomass at equilibrium for a given constant fishing mortality rate to ensure comparability of results across scenarios. We calculated equilibrium yield as the product of the age-dependent mean fish mass (m_a) and the number of harvested individuals at each age, summed over all individuals vulnerable to harvest (those of age $a \geq a_{\text{rec}}$ in patch $i = 1$) at time T :

$$(8) \quad Y_T = \sum_{a=a_{\text{rec}}}^A m_a n_{a,T,1} \{1 - \exp[-(M + \tilde{F})]\} \left(\frac{\tilde{F}}{M + \tilde{F}} \right)$$

For the stochastic model, we calculated the mean yield at quasi-equilibrium from 100 realizations of each scenario. Variance among realizations was extremely small and thus is not reported.

While F_{persist} and annual harvested biomass metrics allow separate investigation into each of persistence and yield, in reality the two interact (see Fig. S1¹ for an example of how our yield and persistence metrics are related). To more thoroughly explore the relationship between persistence and yield, we simultaneously computed the equilibrium yield and the corresponding maximum additional larval mortality the population could withstand over the long term (l_{persist}) for a range of values for \tilde{F} . We calculated l_{persist} as the maximum larval mortality (expressed as a proportional increase above a baseline larval mortality rate) that resulted in a population trajectory increasing toward a positive equilibrium abundance, given a particular value of \tilde{F} . Therefore, l_{persist} provides an implicit metric of mismatch that a population can withstand, as compared with the more mechanistic representation in our calculations of F_{persist} and yield for a given \tilde{F} . Given that l_{persist} is an implicit function of the timing of parturition and the timing of maximum zooplankton production, we simplified our analysis of this metric by focusing on only one deterministic set of the two timing parameters as an example.

To evaluate the effect of incorporating maternal-age-dependent larval traits, we first compared computed values of larval survival between old and young mothers at different values of the timing of maximum zooplankton production. Then we made this same comparison across the two maternal-age-dependent traits: the effect on provisioning (e.g., via modification of the oil globule size) and the effect on parturition timing. Carrying these effects through to the context of the complete life cycle, we compared the values of F_{persist} and yield resulting from (i) a full model with both maternal-age-dependent traits to (ii) a model with only maternal influences on parturition timing, (iii) a model with only maternal influences on larval provisioning, and (iv) a model without any maternal influences (i.e., parturition timing and larval provisioning both constant across maternal ages). In the latter case we assumed that the entire observed range of parturition dates is representative of all mothers and specified that the time to starvation of larvae from mothers of all ages is the geometric mean of the observed relationship between larval mortality and maternal age (Table 1). To obtain robust general insights, we focus on quantitative relative differences in F_{persist} and yield among alternative representations of maternal influences or manage-

ment regimes in addition to qualitative differences between the deterministic and stochastic models. The scales of the deterministic and stochastic models differ inherently, and thus the absolute differences of their results are not appropriate to compare.

We performed a sensitivity analysis to identify which factors most influence the magnitude of the effect of mismatches on persistence. We explored sensitivity to one management parameter and four biological parameters that we either expected to significantly influence population growth rate or have large uncertainty in estimation: age at entry to the fishery (a_{rec}), the age threshold that divides the two parturition date distributions (a_{old}), the von Bertalanffy growth coefficient (k), natural mortality rate (M), and the exponent of the length–fecundity relationship (c). Of these, the parameters with the greatest influence on F_{persist} were a_{rec} (Figs. S2a, S2b)¹, M (Figs. S2g, S2h)¹, and c . Overall, the qualitative trends we focus on here are consistent across parameter values, and the sensitivity analysis simply indicates which parameters are most important for precise quantitative predictions.

Results

Empirical verification of critical timing assumption

Rockfish recruitment was consistently correlated with spring transition date across species and sites off the coast of the Mendocino region of northern California. Some of the stronger relationships we found were for yellowtail rockfish (*Sebastes flavidus*) and copper rockfish (*S. caurinus*) (Fig. 2): recruit density and spring transition were negatively correlated for the winter-spawning *S. flavidus* ($r_p = -0.79$; $P < 0.001$) and positively correlated for the spring-spawning *S. caurinus* ($r_p = 0.75$; $P = 0.005$). The latter species is most representative of our model species *S. carnatus* in terms of life history. This corroborated our assumption that the timing of the spring transition substantially affects rockfish recruitment.

Influence of maternal age on response of larval survival to climate change

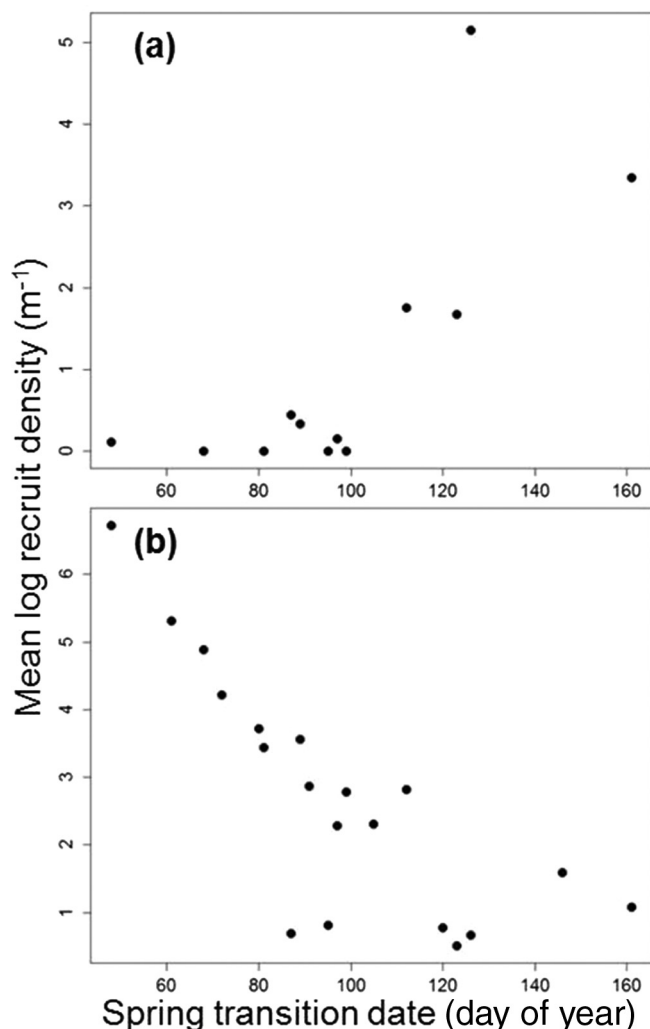
The relationship between maternal age and larval survival depended on the type of maternal-age-dependent larval trait considered and whether the processes leading to mismatches were deterministic or stochastic (Figs. 1e–1h). For the maternal influence on provisioning, larval survival was always greater for the offspring of older mothers, regardless of the state of the climate or deterministic versus stochastic implementation (Figs. 1e, 1g). For the maternal influence on parturition timing, the larvae of older mothers survived at a higher rate than those of younger mothers under only approximately half of the range of climatic conditions (Figs. 1f, 1h). In deterministic simulations, older mothers outperformed younger mothers for earlier spring transitions and vice versa for later spring transitions; in stochastic simulations, older mothers had a flatter distribution such that they outperformed younger mothers at extreme early and late spring transitions, but larvae from younger mothers performed better at intermediate spring transitions (compare Figs. 1e, 1f with 1g, 1h).

Roles of fishing and climate change in affecting persistence and yield

The amount that reduced survival due to increased fishing or increased mismatches reduced the persistence threshold depended on whether the timing of the spring transition and parturition was deterministic or stochastic (Fig. 3). Specifically, compared with deterministic simulations, environmental stochasticity resulted in less sensitivity to mismatches, which produced a broader peak in the relationship between expected mismatch extent and F_{persist} (Fig. 3, compare panel a with panel b)

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0243>.

Fig. 2. Proof-of-concept for the relationships between recruitment of spring-breeding (a) and winter-breeding (b) rockfish relative to spring transition date. Data are for (a) copper rockfish (*Sebastes caurinus*; $r_p = -0.79$; $P < 0.001$) and (b) yellowtail rockfish (*Sebastes flavidus*; $r_p = 0.75$; $P = 0.005$) from 19 years of SCUBA surveys (Laidig et al. 2007) and were provided by Tom Laidig, NOAA Fisheries. Spring transition dates were identified by the Logerwell et al. (2003) method (Columbia Basin Research 2011).

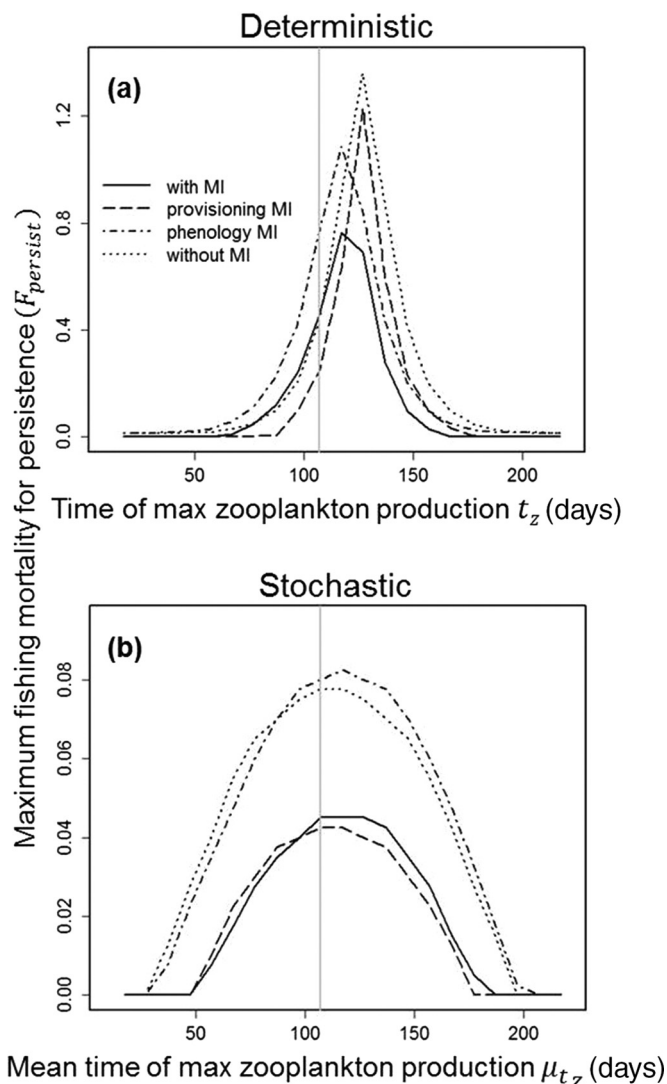


in addition to yield (Fig. 4). The maximum F_{persist} and yield values occurred under conditions wherein the timing of zooplankton production was slightly later than the current climate phenology, an unexpected result given that the midpoint of the parturition date for older mothers was estimated empirically to be nearly equivalent to the mean timing of maximum production in the current climate state. The timing of zooplankton production where the maximum F_{persist} occurs is closer to the midpoint of the parturition date for younger mothers. Thus, the current optimal zooplankton production timing could be later than the historical, unfished optimum owing to age truncation causing an increase in the proportion of total reproductive output from younger mothers.

Influence of including maternal-age-dependent traits in assessment of persistence and yield

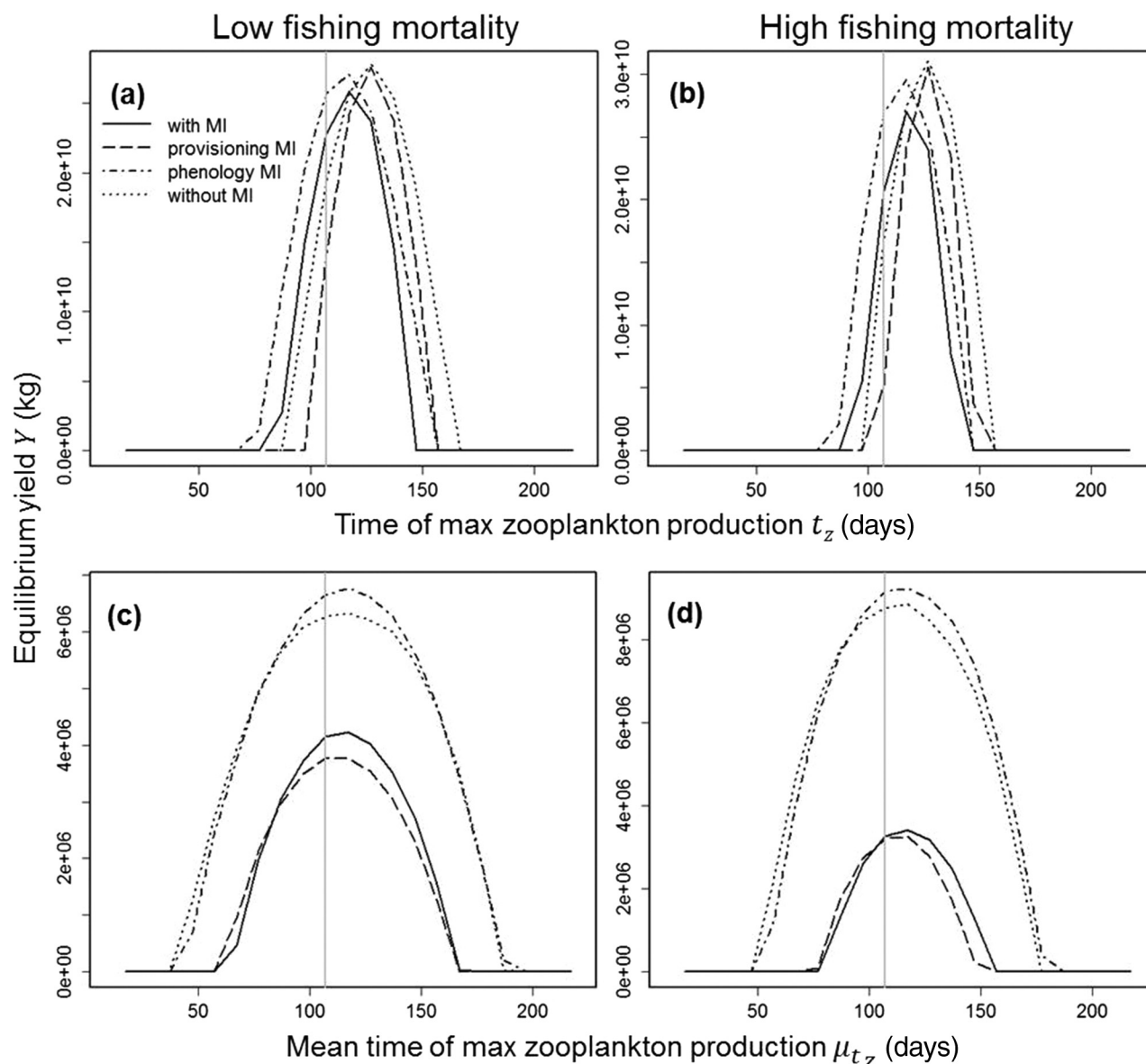
Incorporation of maternal-age-dependent larval traits typically reduced persistence and yield (Figs. 3 and 4, compare four line types). The decrease in F_{persist} and yield when including both phe-

Fig. 3. Maximum fishing mortality for persistence (F_{persist}) given different extents of mismatches arising from climate change. The vertical grey lines indicate the current mean date of maximum zooplankton production, reflecting the general timing of parturition that would result in the least mismatch for older mothers; thus, climate-induced mismatches increase from this point in both directions along the horizontal axis. The solid black lines represent runs with maternal-age-dependent provisioning and phenology, the dotted lines represent runs without any maternal-age-dependent traits, dashed-dot lines represent runs with maternal-age-dependent effects on phenology only, and dashed lines represent runs with maternal-age-dependent effects on provisioning only. Parameter values are as in Table 1.



nology and provisioning maternal influences occurred for later mismatches in the deterministic model (with a slight increase for early mismatches) and for both earlier and later mismatches in the stochastic model, with a greater and more consistent effect overall in the stochastic model (Figs. 3, 4). In the deterministic model the effect of maternal influences on yield is dependent on the type of mismatch (early versus late) because the presence of the timing maternal influence increases (decreases) larval survival when the timing of zooplankton production is early (late) (Fig. 1f). Of the two maternal-age-dependent traits, provisioning drove most of the decrease in F_{persist} and yield in the stochastic model (Figs. 3b, 4c, 4d). While the two maternal influences had clear

Fig. 4. Fishery yield given different extents of mismatches arising from climate change. The vertical grey lines indicate the current mean date of maximum zooplankton production. Black lines of all styles show yields that result from fishing at two arbitrary low (a, c) and high (b, d) rates. The solid lines represent runs with maternal-age-dependent provisioning and phenology, the dotted lines represent runs without any maternal-age-dependent traits, dashed-dot lines represent runs with maternal-age-dependent effects on phenology only, and dashed lines represent runs with maternal-age-dependent effects on provisioning only. Rows correspond to deterministic (a, b) and stochastic (c, d) model outcomes. Note that x-axis scales differ among panels to emphasize within-panel relationships. Fishing mortality rates were (a) $\tilde{F} = 0.1025$, (b) $\tilde{F} = 0.205$, (c) $\tilde{F} = 0.015$, (d) $\tilde{F} = 0.030$. Different values of \tilde{F} were used because the persistence threshold was lower in stochastic implementations than for deterministic implementations. All other parameter values are as in Table 1.



additive effects in the stochastic model, some synergistic effects were apparent in the deterministic model (Figs. 3a, 4a, 4b). Most notably, F_{persist} was substantially lower when both maternal influences were included than would be expected by examining the individual effects of each maternal influence on F_{persist} (Fig. 3a). Increasing fishing intensity narrowed the relationship between yield and spring transition timing across all simulations and decreased peak yield for stochastic simulations, especially with provisioning or both maternal influences (Fig. 4, compare columns). In other words, including maternal influences increased the sensitivity of yield to changes in fishing mortality and spring transition timing.

Effect of reserves on persistence and yield

How the increase in persistence with the inclusion of reserves depended on maternal influences changed with both the direction of mismatch and whether timing events were deterministic or stochastic (comparing F_{persist} as the values of \tilde{F} where equilibrium yields fall to zero in panels of Fig. 5). In the deterministic model, the difference in F_{persist} between reserve and conventional management was greater with maternal influences than without them in the current climate state with little mismatch, yet the relationship was reversed at mismatches resulting from a delay in spring productivity (compare Figs. 5c with 5e). This change in the effect of maternal influences on yield is due to the provisioning

Fig. 5. Comparison of yield as a function of fishing mortality rate, \tilde{F} , between conventional fishery management and reserve management (at 20% coverage) in cases with and without maternal influences for three climate states reflecting the timing of maximum zooplankton production: (a, b) earlier timing ($t_z = 77$), (c, d) no change in timing ($t_z = 107$), and (e, f) later timing ($t_z = 137$). Results of deterministic simulations are in the left column and stochastic simulations in the right column. Note that x-axis scales differ among panels to emphasize within-panel relationships and reflecting differences in F_{persist} among climate states. Parameter values are as in Table 1.

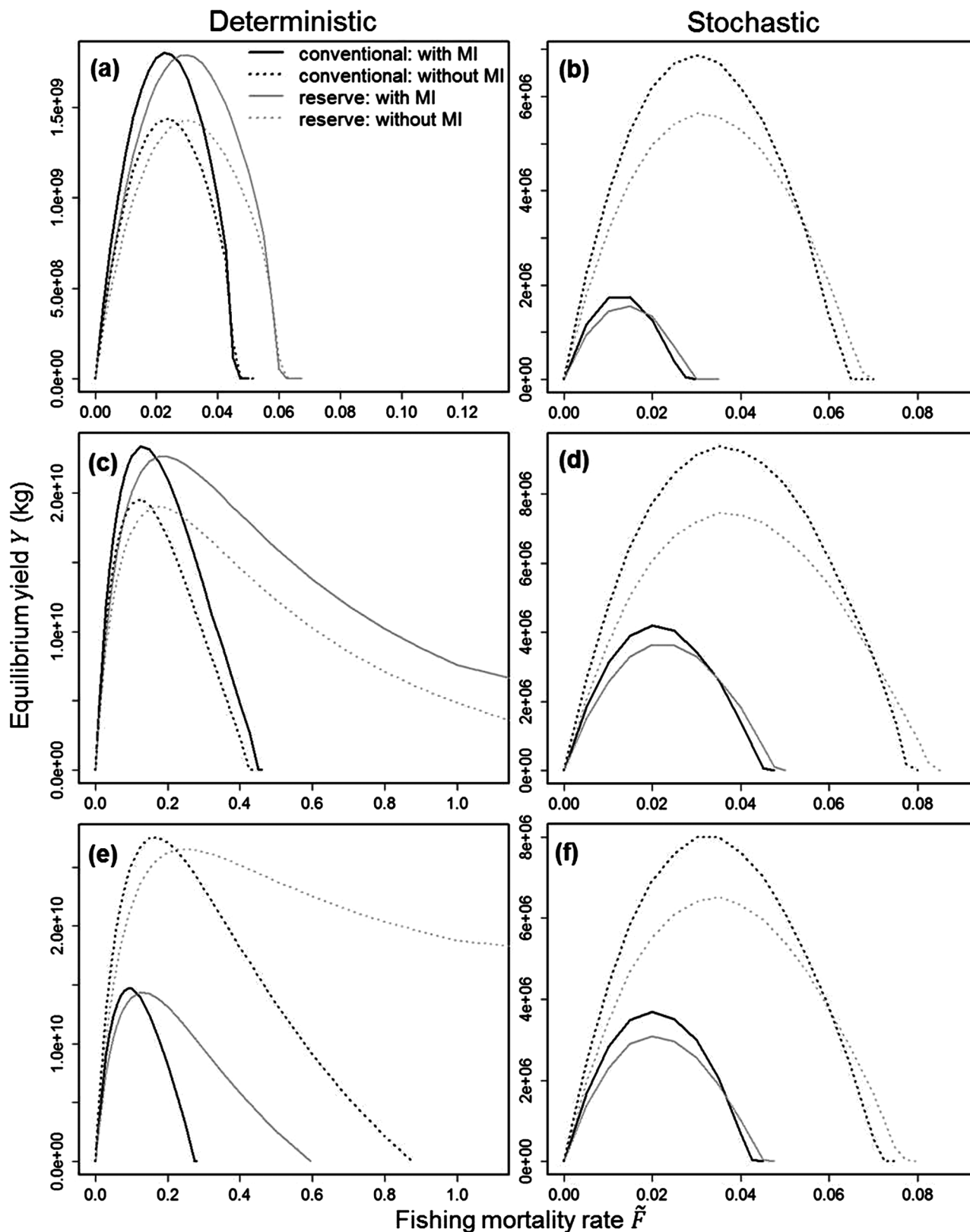
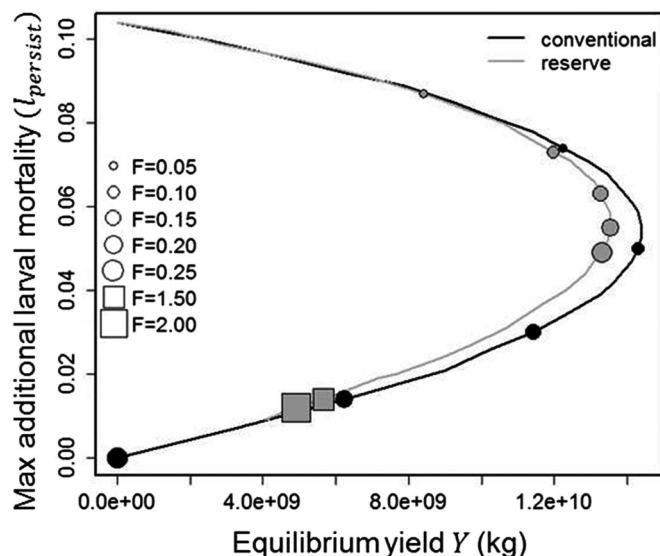


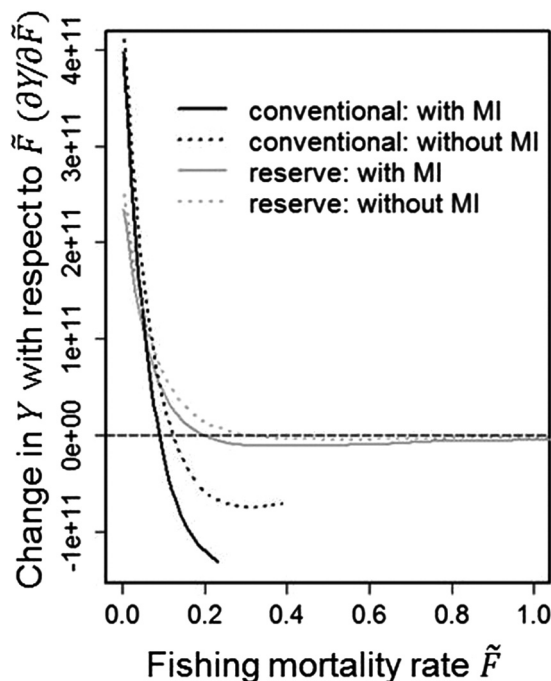
Fig. 6. Comparison of tradeoffs in fishery and conservation benefits between conventional fishery management and reserve management. Relationship between yield and the maximum additional larval mortality the population can withstand l_{persist} (expressed as a proportional increase relative to the baseline larval mortality), with fishing mortality rate, \tilde{F} , increasing along the curves from the top left to bottom left as indicated by the symbols. Results are from the deterministic model with maternal influences on larval provisioning and under environmental conditions approximating the timing of maximum zooplankton production in the current climate state ($t_z = 107$). All other parameter values are as in Table 1.



maternal influence (Fig. 1f). In the stochastic model, the relative increases in persistence with reserve implementation were minor and did not differ between scenarios with or without maternal influences included across a range of mismatches (Figs. 5b, 5d, 5f; notice little difference in the descending slopes of yield curves or F_{persist} values between cases of reserve and conventional management across scenarios with and without maternal influences). The greater effect of maternal influences on persistence in reserve management compared with conventional management in the deterministic versus stochastic model held across different values for reserve coverage (Fig. S3¹). The significant buffering effect of reserves on persistence that occurred across reserve coverage values in the deterministic model (Figs. S3a, S4¹) did not occur until high reserve coverage in the stochastic model (~40%; Figs. S3b, S5¹).

Compared with conventional management alone, incorporating reserves generally led to decreased yield at low exploitation rates but equivalent or increased yield at high exploitation rates (compare line shadings in Figs. 5, 6a), where the range of increased yield was greater in the deterministic than in the stochastic model (Fig. 5). Maternal influences did not affect the relative performance of reserves and conventional management but did affect the absolute yield. In the stochastic model, yield was consistently greater without maternal influences than with maternal influences across a range of climate shifts (Fig. 5, right column). In the deterministic model, yield also decreased with the inclusion of maternal influences for later spring transitions (Fig. 5e); however, yield typically increased with the inclusion of maternal influences for earlier spring transitions (Fig. 5a) and under the current climate state in which there is little mismatch (Fig. 5c). All the above comparative outcomes generally held across a range of values for reserve coverage (Figs. S4, S5¹) and with fishing rate (\tilde{F}) increasing proportionally with reserve coverage (Fig. S6¹, as compared with the harvest outside reserves unchanged with reserve establishment in Fig. 5).

Fig. 7. Sensitivity of equilibrium yield, Y , to fishing mortality rate, \tilde{F} , resulting from conventional or reserve management, with or without maternal influences, across the range of \tilde{F} that produces sustainable yield for each case (i.e., values are truncated at $\tilde{F} = F_{\text{persist}}$). Greater departures from zero in both the positive and negative directions indicate greater sensitivity. Results are from the deterministic model with maternal influences on larval provisioning and under environmental conditions approximating the timing of maximum zooplankton production in the current climate state ($t_z = 107$). All other parameter values are as in Table 1.



The qualitative form of the relationship between yield and l_{persist} (tolerable additional larval mortality) was consistent across management techniques, with only small differences in yield between conventional fishery management and reserve management (Fig. 6a); note that the effort necessary to achieve analogous yields did vary between reserves and conventional management. However, reserve management resulted in much greater values of l_{persist} for a given value of \tilde{F} (compare symbols in Fig. 6) and less sensitivity of yield to variation in \tilde{F} compared with that in conventional fishery management (compare line shades in Fig. 7). Therefore, reserves can provide a buffer against population depletion from overfishing and climatic mismatches (or any other mechanism causing deterministic reductions in larval survival) by decreasing the sensitivity of populations to fishing intensity. Including maternal influences increased the sensitivity of yield to \tilde{F} , with a larger effect of maternal influences under conventional management than with reserves (compare line types of each shade in Fig. 7).

Discussion

We found that mismatches driven by climate change can reduce population persistence and fishery yield and that these effects are exacerbated when maternal influences on larval provisioning are present (Figs. 3, 4). Implementation of reserves and reduction of total fishing mortality via conventional management had qualitatively analogous effects on improving persistence under mismatches (Fig. 5). However, our results suggest that yield is less sensitive to fishing mortality when reserves were implemented (Figs. 5, 6); thus reserves can provide a buffer against uncertainties in management (lack of knowledge about maternal

influences and imprecise control of fishing mortality) and some forms of climate change (increases in larval mortality due to environmental change). Whether this buffering benefit with reserve establishment incurs a cost in yield depends on harvest rate, mismatch extent, and whether maternal influences are present (Figs. 5, 6).

We expected part of the buffering from reserve establishment to occur through the protection of older females with age-dependent larval provisioning and parturition timing. While such maternal influences did affect persistence and yield metrics, they did not affect the amount of buffering from reserves in most cases (Fig. 5). In addition, the inclusion of environmental stochasticity in timing events led to a greater and more consistent decline in persistence and yield with maternal influences (especially with respect to larval provisioning as compared with parturition timing; Figs. 3, 4), but it also reduced the buffering effect of reserves (Fig. 5). In other words, the conditions necessary for a strong, consistent role for maternal influences (environmental stochasticity) also decreased the impact of reserves. Therefore, provisioning maternal influences increase in importance to management with the inclusion of stochasticity, while the capacity for reserves to buffer against climate change effects is more relevant to large directional shifts in mean timing of zooplankton production outside the range of natural environmental variability (as exemplified within the deterministic results). We discuss the roles of maternal influences and environmental stochasticity in more detail below.

Role of environmental stochasticity

Recruitment variability can quantitatively change management predictions such as persistence across a wider range of mismatches under the stochastic versus deterministic simulations here (Fig. 3). Although it has been known for nearly a century that recruitment variability is a dominant factor influencing the dynamics of fish populations (Hjort 1914), this source of environmental variability has rarely been incorporated into marine reserve models. Grafton et al. (2005) demonstrated that reserves can decrease population recovery times from abrupt stock reductions caused by environmental events or anthropogenic actions, reflecting a benefit to persistence probability in the face of rapid change. Earlier implementations demonstrated that interannual catch variability caused by recruitment variability could be dampened only with very extensive reserve coverage (Sladek Nowlis and Roberts 1999; Mangel 2000), and that this environmental variation makes it difficult to determine whether there was a significant change in the risk of overfishing with anything less than an extreme difference in reserve coverage (Mangel 2000). We also identified that the buffering effect of reserves was weakened by environmental stochasticity (Fig. 5). We hypothesize that the buffering effect of reserves is eroded by environmental stochasticity, because under these conditions there is always a chance that mismatches can cause severe recruitment failures, regardless of whether a subset of older individuals is protected within reserves.

Although environmental stochasticity weakened the effect of reserves, it strengthened the effect of maternal influences across a broad range of mismatches (Figs. 3, 4). The strengthening of the role of maternal influences may occur because incorporating environmental stochasticity generates a more consistent difference between the expected survival of larvae from older and younger mothers across mean environmental conditions (Figs. 1e, 1g). With environmental stochasticity there is also a reasonably high potential for young mothers with low provisioning to have nearly zero recruitment in extreme environments (Fig. 1g). Why environmental stochasticity leads to a decreased impact of reserves and an increased impact of maternal influences is likely related to the interplay between the mean response (a more consistent difference between mean larval survival in older and younger mothers) and the variance (complete recruitment failures are only possible

in the stochastic model, because larval survival is always substantially greater than zero in the deterministic model). We hypothesize that the frequency and magnitude of recruitment failures generated by the stochastic model are great enough to disrupt the potential for maternal influences to strengthen the buffering role of reserves.

The role of maternal influences

The merits of explicitly accounting for maternal-age-dependent reproductive traits in management are still mired in debate within the literature (Edwards and Plagányi 2011 and references therein). Indeed, the effects of climate and maternal influences may be already integrated implicitly into assessments of stock productivity when such assessments are informed by recruitment surveys that encompass periods of low adult biomass (Spencer et al. 2014). Explicit inclusion of maternal influences on larval survival does affect estimates of fisheries target (Spencer et al. 2007) and limit (Murawski et al. 2001) reference points. Our results support the finding of Spencer et al. (2014) that biological reference points associated with persistence thresholds (e.g., F_{persist}) are more influenced by the presence or absence of maternal influences than are traditional target reference points (e.g., maximum sustainable yield).

Context dependency of the population-level significance of maternal influences appears in both the theoretical and empirical literature. Empirically, significant effects of maternal age structure on observed recruitment dynamics have been demonstrated for several populations of cod (Scott et al. 1999; Vallin and Nissling 2000; Shelton et al. 2012); however, these effects are not universal among cod populations (Morgan et al. 2007) and are notably absent for Atlantic flatfishes (Morgan et al. 2011). Theory has also provided mixed support for the idea that protecting older individuals provides additional benefits to fisheries beyond the effect of size or age on fecundity. For example, O'Farrell and Botsford (2006a) demonstrated that the maternal influence of larval provisioning on larval survival in black rockfish (*Sebastes melanops*) observed in the laboratory by Bobko and Berkeley (2004) and Berkeley et al. (2004a) had relatively little impact on conventionally managed populations in many conditions, but this conclusion depended on this species' particular maturity schedule and age range of the maternal influence. The age range over which the maternal influence was observed was quite narrow, thus only a small proportion of mothers were mature at ages during which they were predicted to produce larvae with lower provisions. Spencer et al. (2014) found that such maternal influences had a greater effect on estimated fishery reference points of shorter-lived species (contrasting Pacific cod, *Gadus macrocephalus*, and Pacific ocean perch, *Sebastes alutus*). The longevity of our focal species falls between that of *G. macrocephalus* and the two rockfishes, meaning that the results are somewhat — yet inconclusively — consistent with the interpretation that maternal influences have a larger effect for shorter-lived species. More significantly, neither O'Farrell and Botsford (2006a) nor Spencer et al. (2014) directly compared deterministic results to those with environmental stochasticity as we have done here, although the latter study did show that the effect of maternal influences was greater when the environment was more predictable (autocorrelated in time). We found that maternal influences had greater and more consistent impacts on persistence and yield when interannual variability was present, thus the lack of this reality from some previous models may have led to disagreement among studies with respect to the population consequences of maternal influences.

Among traits that depend on maternal age, maternal influences on larval provisioning had a greater effect than those on parturition timing in terms of both the persistence threshold and sensitivity of fishery yield to the magnitude of fishing mortality (Figs. 3, 4). The reason for this greater effect of larval provisioning is likely because increased provisioning increases larval survival in all cli-

mate conditions, whereas earlier parturition timing with age may increase or decrease larval survival depending on the climatic state (compare panels *e*, *g* with *f*, *h* in Fig. 1). The lesser impact of timing maternal influences on persistence and yield might be due in part to our specific assumptions regarding the distribution of parturition dates and the lack of carryover effects beyond the early larval stage (we discuss these possibilities in more detail in the next section, "Evaluation of model assumptions").

Evaluation of model assumptions

For ease of interpretation, we sought to construct the simplest possible model that tests the effect of reserves and harvest reductions on population response to climate change. Thus we needed to make several simplifying assumptions. In particular, we assumed sedentary adults and complete larval mixing in the plankton with evenly redistributed settlement. In reality, adults have movement around home ranges (Jorgensen et al. 2006), and larvae have limited regional dispersal (Buonaccorsi et al. 2004) for species such as our model organism. Representing spatial arrangement explicitly and incorporating more realistic larval dispersal and adult movement could either decrease yield and increase F_{persist} because of increased larval retention or it could have the opposite effect because of increasing adult spillover (Moffitt et al. 2009).

In addition, we assumed that larval traits only affected survival during the early planktonic life stage without considering potential carryover effects (i.e., events that may influence fitness during a later life stage). Including additional processes that occur during settlement, recruitment, and throughout the life cycle may explain why older individuals sometimes release their larvae much earlier in the season than the mean timing of maximum production. For example, there is strong empirical evidence that priority effects in settlement can cause shifts in dominant cover of sessile invertebrates on rocky substrates (Connell 1961), and this may be the case for reef fishes as well (Shulman et al. 1983; Almany 2003). Including such factors can cause changes in the optimal timing of reproduction (Jonzén et al. 2007). Carryover effects initiated by early birth and settlement could increase the importance of maternal influences on parturition timing in our model.

We assumed that there was no change in parturition timing in response to climate change, given that there are no known cues that rockfish could use to anticipate the timing of the spring transition. However, it is certainly possible that adaptive changes through evolution or plasticity could lead to phenological tracking, which would decrease the reported impact of mismatches on population dynamics if populations respond with the correct sign to the correct cues. Although it is now clear that many marine and terrestrial populations are shifting their phenology in response to cues that are affected by climate change (Parmesan and Yohe 2003; Poloczanska et al. 2013), the magnitude of these shifts varies across broad taxonomic groups and it is not yet understood whether these changes are adaptive on average. Empirical investigation of the cues affecting timing of ovarian recrudescence and the heritability of this timing trait are critical to constructing future modeling efforts that incorporate adaptive potential. We expect that a response in organismal phenology to a changing mean environmental state (as might occur through evolution) is unlikely to affect our conclusions given that persistence and yield were affected little by the inclusion of the maternal influence on parturition timing; however, a response that varies interannually (as might occur through plasticity) may change how a population experiences environmental stochasticity, which could have a large impact on our conclusions given the differences observed between our deterministic and stochastic results.

We assumed that the primary benefit to fisheries could be measured by yield, not profit. Considering economic factors such as the cost of fishing can broaden the set of conditions for which implementation of reserves increases profits over conventional

fishery management alone (Sanchirico et al. 2006). Similarly, consideration of economic factors would likely strengthen the evidence for the conservation benefits of reserves. For example, with reserves in place, a real fishery would likely never achieve the extreme fishing mortality rates that it would take to drastically reduce the capacity of a population to withstand an increase in larval mortality (Fig. 6). The cost of fishing would make profits drop to zero before such harvest rates could be reached. We expect that consideration of fishery profit rather than yield would increase the benefits of reserves to the fishery in our model, making reserve management and conventional fishery management quite similar in their potential benefits (as in Hastings and Botsford 1999).

Generality of results across systems

Although we parameterized the models here for rockfishes, the biological elements included in these models are present in a wide variety of ecosystems. For many other organisms, climate change is causing shifts in climatic phenology that are changing the optimal timing of organismal phenology and creating mismatches, with demographic consequences for organisms that cannot shift their phenology to track climatic changes (Parmesan 2006; Durant et al. 2007). Even in cases where species respond to changes in climate phenology, mismatches can occur; for example, shifts in migration phenology of butterflies have caused mismatches because the flowering timings of their host plants have not changed (Visser and Both 2005). In addition, offspring traits dependent on maternal age are found in a diverse array of animals; for example, intra-annual timing of birth in many birds (Møller et al. 2006), mammals (Nussey et al. 2005), and fishes (Wright and Trippel 2009). The exacerbation of mismatches caused by age truncation is not exclusive to fishery harvest, as age truncation occurs in most game species as a result of hunting (Milner et al. 2007; Fenberg and Roy 2008) and in nongame species (e.g., birds, mammals, and arthropods) though habitat fragmentation and spread of diseases or parasites (Major et al. 1999; Jessup et al. 2004; McMeniman et al. 2009). Given the commonalities between these disparate taxa and those inhabiting the temperate upwelling system we focused on, our result that management through spatial refugia can mitigate climate-driven mismatches may be generalizable to many systems that share these physical and biological attributes.

Acknowledgements

Funding was provided by the California Sea Grant College Program under grant R/FISH-211 to L.W.B., American Fisheries Society Marine Fisheries Section to L.A.K.B., American Fisheries Society Cal-Neva Chapter to L.A.K.B., and University of California Davis. L.A.K.B. thanks Tom Laidig for providing the rockfish recruitment data. We thank two anonymous referees for helpful comments.

References

- Almany, G.R. 2003. Priority effects in coral reef fish communities. *Ecology*, **84**(7): 1920–1935. doi:10.1890/0012-9658(2003)084[1920:PEICRF]2.0.CO;2.
- Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. University of California Sea Grant (in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico), San Diego, USA.
- Barth, J.A., Menge, B.A., Lubchenco, J., Chan, F., Bane, J.M., Kirincich, A.R., McManus, M.A., Nielsen, K.J., Pierce, S.D., and Washburn, L. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proc. Natl. Acad. Sci. U.S.A.* **104**(10): 3719–3724. doi:10.1073/pnas.0700462104. PMID:17360419.
- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, **85**(5): 1258–1264. doi:10.1890/03-0706.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, **29**(8): 23–32. doi:10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2.

- Bloeser, J.A. 1999. Diminishing returns: the status of West Coast rockfish. Pacific Marine Conservation Council.
- Bobko, S.J., and Berkeley, S.A. 2004. Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). Fish Bull. 102: 418–429. doi:10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2.
- Botsford, L.W., Lawrence, C.A., Dever, E.P., Hastings, A., and Largier, J. 2006. Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. Deep Sea Res. Part II Top. Stud. Oceanogr. 53(25–26): 3116–3140. doi:10.1016/j.dsr2.2006.07.011.
- Buonaccorsi, V.P., Westerman, M., Stannard, J., Kimbrell, C., Lynn, E., and Vetter, R.D. 2004. Molecular genetic structure suggests limited larval dispersal in grass rockfish, *Sebastes rastrelliger*. Mar. Biol. 145(4): 779–788. doi:10.1007/s00227-004-1362-2.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Mass.
- Ciannelli, L., Bailey, K.M., Chan, K.-S., Belgrano, A., and Stenseth, N.C. 2005. Climate change causing phase transitions of walleye pollock (*Theragra chalcogramma*) recruitment dynamics. Proc. R. Soc. B Biol. Sci. 272(1573): 1735–1743. doi:10.1098/rspb.2005.3136.
- Columbia Basin Research. 2011. Columbia River data access in real time [online]. http://www.cbr.washington.edu/data/trans_data.html [accessed 1 March 2011].
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology, 42(4): 710–723. doi:10.2307/1933500.
- Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26: 249–293. doi:10.1016/S0065-2881(08)60202-3.
- Durant, J.M., Hjermann, D.O., Ottersen, G., and Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. Clim. Res. 33(3): 271–283. doi:10.3354/cr033271.
- Edwards, C.T.T., and Plagányi, É.E. 2011. Protecting old fish through spatial management: is there a benefit for sustainable exploitation? J. Appl. Ecol. 48(4): 853–863. doi:10.1111/j.1365-2664.2011.01961.x.
- Edwards, M., and Richardson, A.J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430(7002): 881–884. doi:10.1038/nature02808. PMID:15318219.
- Fenberg, P.B., and Roy, K. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Mol. Ecol. 17(1): 209–220. doi:10.1111/j.1365-294X.2007.03522.x. PMID:17868288.
- Fogarty, M.J., Sissenwine, M.P., and Cohen, E.B. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends Ecol. Evol. 6(8): 241–246. doi:10.1016/0169-5347(91)90069-A. PMID:21232469.
- García-Reyes, M., and Largier, J. 2010. Observations of increased wind-driven coastal upwelling off central California. J. Geophys. Res. 115(C4): C04011. doi:10.1029/2009jc005576.
- Grafton, R., Kompas, T., and Lindenmayer, D. 2005. Marine reserves with ecological uncertainty. Bull. Math. Biol. 67(5): 957–971. doi:10.1016/j.bulm.2004.11.006. PMID:15998490.
- Hastings, A., and Botsford, L.W. 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science, 284(28 May 1999): 1537–1538. doi:10.1126/science.284.5419.1537.
- Heller, N.E., and Zavaleta, E.S. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol. Conserv. 142(1): 14–32. doi:10.1016/j.biocon.2008.10.006.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. Proc. Verb. Reunions, 20: 1–228.
- Ianelli, J.N., Hollowed, A.B., Haynie, A.C., Mueter, F.J., and Bond, N.A. 2011. Evaluating management strategies for eastern Bering Sea walleye pollock (*Theragra chalcogramma*) in a changing environment. ICES J. Mar. Sci. 68(6): 1297–1304. doi:10.1093/icesjms/fsr010.
- Jessup, D., Miller, M., Ames, J., Harris, M., Kreuder, C., Conrad, P., and Mazet, J.K. 2004. Southern sea otter as a sentinel of marine ecosystem health. EcoHealth, 1(3): 239–245. doi:10.1007/s10393-004-0093-7.
- Jonzén, N., Hedenström, A., and Lundberg, P. 2007. Climate change and the optimal arrival of migratory birds. Proc. R. Soc. B Biol. Sci. 274(1607): 269–274. doi:10.1098/rspb.2006.3719.
- Jorgensen, S.J., Kaplan, D.M., Klimley, A.P., Morgan, S.G., O'Farrell, M.R., and Botsford, L.W. 2006. Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home range. Mar. Ecol. Prog. Ser. 327: 157–170. doi:10.3354/meps327157.
- Key, M., MacCall, A.D., Bishop, T., and Leos, B. 2005. Stock assessment of the gopher rockfish (*Sebastes carnatus*). California Department of Fish & Game.
- Key, M., MacCall, A.D., Field, J., Aseltine-Neilson, D., and Lynn, K. 2008. The 2007 assessment of blue rockfish (*Sebastes mystinus*) in California. Pacific Fishery Management Council, Portland, Ore.
- Laidig, T.E., Chess, J.R., and Howard, D.F. 2007. Relationship between abundance of juvenile rockfishes (*Sebastes* spp.) and environmental variables documented off northern California and potential mechanisms for the covariation. Fish Bull. 105: 39–48.
- Lea, R.N., McAllister, R.D., and VenTresca, D.A. 1999. Biological aspects of near-shore rockfishes of the genus *Sebastes* from central California: with notes on ecologically related sport fishes. State of California, The Resources Agency, Department of Fish and Game.
- Logerwell, E.A., Mantua, N., Lawson, P.W., Francis, R.C., and Agostini, V.N. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fish Oceanogr. 12(6): 554–568. doi:10.1046/j.1365-2419.2003.00238.x.
- Love, M.S., Yoklavich, M., and Thorsteinson, L. 2002. The rockfishes of the north-east Pacific. University of California Press, Berkeley, Calif.
- MacGregor, J.S. 1970. Fecundity, multiple spawning, and description of the gonads in *Sebastes*. USFWS Spec. Sci. Rep. 596.
- Major, R.E., Christie, F.J., Gowing, G., and Ivison, T.J. 1999. Age structure and density of red-capped robin populations vary with habitat size and shape. J. Appl. Ecol. 36(6): 901–908. doi:10.1046/j.1365-2664.1999.00457.x.
- Mangel, M. 2000. Irreducible uncertainties, sustainable fisheries and marine reserves. Evol. Ecol. Res. 2: 547–557.
- McLeod, E., Salm, R., Green, A., and Almany, J. 2009. Designing marine protected area networks to address the impacts of climate change. Front. Ecol. Environ. 7(7): 362–370. doi:10.1890/070211.
- McMeniman, C.J., Lane, R.V., Cass, B.N., Fong, A.W.C., Sidhu, M., Wang, Y.-F., and O'Neill, S.L. 2009. Stable introduction of a life-shortening *Wolbachia* infection into the mosquito *Aedes aegypti*. Science, 323(5910): 141–144. doi:10.1126/science.1165326. PMID:19119237.
- Milner, J.M., Nilsen, E.B., and Andreassen, H.P. 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conserv. Biol. 21(1): 36–47. doi:10.1111/j.1523-1739.2006.00591.x. PMID:17298509.
- Moffitt, E.A., Botsford, L.W., Kaplan, D.M., and O'Farrell, M.R. 2009. Marine reserve networks for species that move within a home range. Ecol. Appl. 19(7): 1835–1847. doi:10.1890/08-1101.1. PMID:19831073.
- Møller, A.P., Flensted-Jensen, E., and Mardal, W. 2006. Rapidly advancing laying date in a seabird and the changing advantage of early reproduction. J. Anim. Ecol. 75(3): 657–665. doi:10.1111/j.1365-2656.2006.01086.x. PMID:16689948.
- Morgan, M.J., Shelton, P.A., and Brattey, J. 2007. Age composition of the spawning stock does not always influence recruitment. J. Northwest Atl. Fish. Sci. 38: 1–12. doi:10.2960/J.v38.m584.
- Morgan, M.J., Perez-Rodriguez, A., and Saborido-Rey, F. 2011. Does increased information about reproductive potential result in better prediction of recruitment? Can. J. Fish. Aquat. Sci. 68(8): 1361–1368. doi:10.1139/f2011-049.
- Mueter, F.J., Boldt, J.L., Megrey, B.A., and Peterman, R.M. 2007. Recruitment and survival of northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. Can. J. Fish. Aquat. Sci. 64(6): 911–927. doi:10.1139/f07-069.
- Murawski, S.A., Rago, P.J., and Trippel, E.A. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES J. Mar. Sci. 58(5): 1002–1014. doi:10.1006/jmsc.2001.1097.
- Nussey, D.H., Clutton-Brock, T.H., Elston, D.A., Albon, S.D., and Kruuk, L.E.B. 2005. Phenotypic plasticity in a maternal trait in red deer. J. Anim. Ecol. 74: 387–396. doi:10.1111/j.1365-2656.2005.00941.x.
- O'Farrell, M.R., and Botsford, L.W. 2006a. The fisheries management implications of maternal-age-dependent larval survival. Can. J. Fish. Aquat. Sci. 63(10): 2249–2258. doi:10.1139/f06-130.
- O'Farrell, M.R., and Botsford, L.W. 2006b. Estimating the status of nearshore rockfish (*Sebastes* spp.) populations with length frequency data. Ecol. Appl. 16(3): 977–986. doi:10.1890/1051-0761(2006)016[0977:ETSONR]2.0.CO;2. PMID:16826996.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Syst. 37(1): 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.
- Parnesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421: 37–42. doi:10.1038/nature01286. PMID:12511946.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., and Burrows, M.T. 2013. Global imprint of climate change on marine life. Nat. Clim. Change, 3(10): 919–925. doi:10.1038/nclimate1958.
- Ralston, S., and Howard, D.F. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. Fish. Bull. 93: 710–720.
- Reznick, D.N., and Braun, B. 1987. Fat cycling in the mosquitofish (*Gambusia affinis*): fat storage as a reproductive adaptation. Oecologia, 73(3): 401–413. doi:10.1007/BF00385257.
- Reznick, D., Schultz, E., Morey, S., and Roff, D. 2006. On the virtue of being the first born: the influence of date of birth on fitness in the mosquitofish, *Gambusia affinis*. Oikos, 114(1): 135–147. doi:10.1111/j.2006.0030-1299.14446.x.
- Roughgarden, J., and Iwasa, Y. 1986. Dynamics of a metapopulation with space-limited subpopulations. Theor. Popul. Biol. 29(2): 235–261. doi:10.1016/0040-5809(86)90010-9.
- Sanchirico, J.N., Malvadkar, U., Hastings, A., and Wilen, J.E. 2006. When are no-take zones an economically optimal fishery management strategy? Ecol. Appl. 16(5): 1643–1659. doi:10.1890/1051-0761(2006)016[1643:WANZAE]2.0.CO;2. PMID:17069360.
- Scott, B., Marteinsdottir, G., and Wright, P. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. Can. J. Fish. Aquat. Sci. 56(10): 1882–1890. doi:10.1139/f99-125.
- Shelton, A.O., Munch, S.B., Keith, D., and Mangel, M. 2012. Maternal age, fecun-

- dity, egg quality, and recruitment: linking stock structure to recruitment using an age-structured Ricker model. *Can. J. Fish. Aquat. Sci.* **69**(10): 1631–1641. doi:10.1139/f2012-082.
- Shulman, M.J., Ogden, J.C., Ebersole, J.P., McFarland, W.N., Miller, S.L., and Wolfe, N. 1983. Priority effects in the recruitment of juvenile coral reef fishes. *Ecology*, **64**(6): 1508–1513. doi:10.2307/1937505.
- Sladek Nowlis, J., and Roberts, C.M. 1999. Fisheries benefits and optimal design of marine reserves. *Fish. Bull.* **97**: 604–616.
- Snyder, M.A., Sloan, L.C., Diffenbaugh, N.S., and Bell, J.L. 2003. Future climate change and upwelling in the California Current. *Geophys. Res. Lett.* **30**(15): 1823. doi:10.1029/2003GL017647.
- Sogard, S.M., Berkeley, S.A., and Fisher, R. 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. *Mar. Ecol. Prog. Ser.* **360**: 227–236. doi:10.3354/meps07468.
- Spencer, P., Hanselman, D., and Dorn, M. 2007. The effect of maternal age of spawning on estimation of F_{msy} for Alaska Pacific ocean perch. In *Biology, assessment, and management of North Pacific rockfishes*. Edited by J. Heifetz, J. DiCosimo, A.J. Gharrett, M.S. Love, V.M. O'Connell, and R.D. Stanley. Alaska Sea Grant, University of Alaska Fairbanks. pp. 513–533.
- Spencer, P.D., Kraak, S.B.M., and Trippel, E.A. 2014. The influence of maternal effects in larval survival on fishery harvest reference points for two life-history patterns. *Can. J. Fish. Aquat. Sci.* **71**(1): 151–161. doi:10.1139/cjfas-2013-0253.
- Tuljapourkar, S. 1997. Stochastic matrix models. In *Structured population models in marine, freshwater and terrestrial ecosystems*. Edited by S. Tuljapourkar and H. Caswell. Chapman and Hall, New York. pp. 59–88.
- Vallin, L., and Nissling, A. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*: implications for stock structure effects on recruitment. *Fish. Res.* **49**(1): 21–37. doi:10.1016/S0165-7836(00)00194-6.
- Visser, M.E., and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B Biol. Sci.* **272**(1581): 2561–2569. doi:10.1098/rspb.2005.3356.
- Wright, P.J., and Trippel, E.A. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish. Fish.* **10**(3): 283–304. doi:10.1111/j.1467-2979.2008.00322.x.
- Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. *Fish. Bull.* **85**(2): 229–250.
- Yemane, D., Field, J.G., and Leslie, R.W. 2008. Indicators of change in the size structure of fish communities: a case study from the south coast of South Africa. *Fish. Res.* **93**(1–2): 163–172. doi:10.1016/j.fishres.2008.03.005.

Appendix A. Derivation of larval survival function

Here we derive the function describing larval survival (eq. 2). From the instant of birth to the end of the early larval phase, the number of larvae ($B(\tau)$) decreases at a rate that depends on the instantaneous rates of mortality with (M_f) and without (M_{nf}) food and the amount of that food is present ($f(t_z)$):

$$(A1) \quad \frac{dB(\tau)}{dt} = -[M_{nf}(a) - M_f f(t_z)]B(\tau)$$

Given our assumption that food production over time follows a normal distribution, we calculate this quantity at any given instant τ as the solution of the probability density function for a normal distribution with mean $t_z(t)$ and variance σ_z :

$$(A2) \quad f(t_z) = \frac{1}{\sigma_z \sqrt{2\pi}} \exp\left\{-\frac{[\tau - t_z(t)]^2}{2\sigma_z^2}\right\}$$

We define an environment-independent discrete survival probability (S_0) that describes survival from the end of the early larval phase to the instant before settlement. Thus the total larval survival in each year t is the product of S_0 and the exponential of the

environment-dependent instantaneous mortality rate during the early larval stage (the integral of the term in brackets in eq. A1 over the interval from the time of parturition ($r_{a,t}$) to the end of the early larval phase ($r_{a,t} + d_A$):

$$(A3) \quad l_{a,t} = \exp\left\{\int_{r_{a,t}}^{r_{a,t}+d_A} \left[M_{nf}(a) - M_f \left(\frac{1}{\sigma_z \sqrt{2\pi}} \times \exp\left\{ \frac{-[\tau - t_z(t)]^2}{2\sigma_z^2} \right\} \right) \right] d\tau \right\} S_0$$

To ensure that the term in brackets in eq. (A3) goes to zero when there is no mismatch and approaches M_{nf} at extreme values of mismatch, we specify

$$(A4) \quad M_f = M_{nf}(a) \sigma_z \sqrt{2\pi}$$

Substituting the right-hand side of eq. A4 in for M_f in eq. A3 and simplifying produces the complete form of the larval survival equation as specified in eq. 2 of the main text:

$$(A5) \quad l_{a,t} = \exp\left\{\int_{r_{a,t}}^{r_{a,t}+d_A} \left[M_{nf}(a) \left(\exp\left\{ \frac{-[\tau - t_z(t)]^2}{2\sigma_z^2} \right\} - 1 \right) \right] d\tau \right\} S_0$$

Appendix B. Equilibria and stability of the nonspatial deterministic mismatch model

Here we find an analytical equilibrium solution for the model when assuming that juvenile and adult mortality are constant with time. It can be shown that the expression for recruitment at the nonzero equilibrium (R_e) is

$$(B1) \quad R_e = \frac{\sum_{a=0}^{a_{\max}} b_a \sigma_a l_a - \alpha^{-1}}{\sum_{a=0}^{a_{\max}} b_a \sigma_a l_a}$$

where b_a is the fecundity, σ_a is the proportion of individuals that survive from recruitment to age a , l_a is survival of larvae produced by age a mothers, and α^{-1} is the critical replacement threshold. Given the Beverton–Holt form, this equilibrium (eq. B1) is locally stable if

$$(B2) \quad \sum_{a=0}^{a_{\max}} b_a \sigma_a l_a > \alpha^{-1}$$

that is, reproduction outweighs mortality at low population abundance and population replacement is achieved. Another way to interpret this result is that the zero equilibrium is locally unstable when the condition in eq. B2 is met; therefore, this is the persistence criterion. As anticipated, stability decreases as the critical replacement threshold (α^{-1}) decreases, fecundity (b_a) increases, M or \bar{F} decreases (increasing σ_a), or match-dependent larval survival (l_a) increases.