Abalone populations are most sensitive to environmental stress effects on adult individuals

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ABSTRACT: Marine organisms are exposed to stressors associated with climate change throughout their life cycle, but a majority of studies focus on responses in single life stages, typically early ones. Here, we examined how negative impacts from stressors associated with climate change, ocean acidification, and pollution can act across multiple life stages to influence long-term population dynamics and decrease resilience to mass mortality events. We used a continuous-size-structured density-dependent model for abalone (*Haliotis* spp.), calcifying mollusks that support valuable fisheries, to explore the sensitivity of stock abundance and annual catch to potential changes in growth, survival, and fecundity across the organism's lifespan. Our model predicts that decreased recruitment from lowered fertilization success or larval survival has small negative impacts on the population, and that stock size and fishery performance are much more sensitive to changes in parameters that affect the size or survival of adults. Sensitivity to impacts on subadults and juveniles is also important for the population, though less so than for adults. Importantly, likelihood of recovery following mortality events showed more pronounced sensitivity to most possible parameter impacts, greater than the effects on equilibrium density or catch. Our results suggest that future experiments on environmental stressors should focus on multiple life stages to capture effects on population structure and dynamics, particularly for species with size-dependent fecundity.

KEY WORDS: Ocean acidification · Population dynamics · Environmental stress · Abalone · *Haliotis* spp. · Adult survival · Fisheries management

1. INTRODUCTION

Marine ecosystems are subject to multiple sources of environmental stress, many increasing in intensity with climate change and human activity. Organisms are exposed to higher temperatures, altered water chemistry, decreased oxygen levels, disrupted hydro-dynamic patterns, pollution from toxins and terrestrial run-off, and heightened noise levels, to name some of the most prominent examples (Walther et al. 2002, Parmesan & Yohe 2003, Perry et al. 2005, Harley et al. 2006, Fabry et al. 2008, Cheung et al. 2009, Hoegh-Guldberg & Bruno 2010, Doney et al. 2012). These

stressors can have pronounced effects across the entire life history of a species (e.g. Gibson et al. 2011, Pankhurst & Munday 2011), increasing the vulnerability of its population to extraction (Perry et al. 2010) and catastrophic events (e.g. corals and hurricanes; Andres & Rodenhouse 1993, Roff & Mumby 2012, Mora et al. 2016). Mass mortality events caused by extreme environmental events are expected to increase under climate change (Jentsch et al. 2007, Hegerl et al. 2011), including temperature spikes (e.g. Dayton & Tegner 1984, Garrabou et al. 2009, Wernberg et al. 2013, Arafeh-Dalmau et al. 2020) and prolonged hypoxic conditions (Diaz 2001, Grantham

et al. 2004, Chan et al. 2008, Vaquer-Sunyer & Duarte 2008, Laffoley & Baxter 2018).

Determining the long-term effects of environmental stressors on marine populations is critical for conservation and sustainable management. For logistical reasons, research on stress effects has often focused on early life stages (e.g. Sheppard Brennand et al. 2010, Nakamura et al. 2011, Pineda et al. 2012, Rosa et al. 2013); however, early stages are not always the most sensitive (e.g. hypoxia and warming for clams, Clark et al. 2013, 2016; warming for copepods, Tangwancharoen & Burton 2014; warming for fish, Messmer et al. 2017). The combined effect of 2 or more stressors may be stronger than expected from each stressor individually, as documented for decreased oxygen and pH for fish (DePasquale et al. 2015) and sea urchins (O'Donnell et al. 2009, Sheppard Brennand et al. 2010), warming and decreased oxygen for krill (Tremblay & Abele 2016), and warming and salinity for oysters (Rybovich et al. 2016, Lowe et al. 2017). The trait most sensitive to an environmental stressor at the individual level might not have the largest effect on overall fitness and population dynamics, as with cadmium and nematode fecundity (most sensitive) and delayed maturity (most important to fitness; Kammenga et al. 1996).

One major component of climate change with the potential to act throughout the lifespan of a marine species is ocean acidification (OA), caused by the increasing ocean uptake of CO_2 and concurrent changes in seawater chemistry. OA is expected to greatly impact the structure and function of marine ecosystems (Teixidó et al. 2018), although the precise effects are species-specific and difficult to predict (Orr et al. 2005, Fabry et al. 2008, Doney et al. 2009, 2012, Gaylord et al. 2015). Research on the potential species-level effects of OA (Kroeker et al. 2013) has revealed significant decreases in growth and reproductive success across a wide variety of organisms (e.g. snails and sea urchins, Shirayama & Thornton 2005; mussels and oysters, Gazeau et al. 2007; corals, Hoegh-Guldberg & Bruno 2010; seagrasses and marine algae, Koch et al. 2013), caused primarily by reduced calcification rates and delayed larval development. However, due to the limitations of laboratory experimentation, most understanding of the impacts of OA stress comes from studies focusing on the larval and juvenile stages, despite the fact that species are exposed to OA throughout their life cycles. The full effects of OA, as well as other stressors, across an individual's life history and, more critically, how these changes affect population-level dynamics are still not well understood.

Taking OA as an example of a pervasive environmental stressor with increasing, potentially negative effects, we identified mollusks as a group of particular importance, given their role as grazers or predators in creating biogenic habitat, their commercial value, and their sensitivity, as calcifying organisms, to increased acidity (Parker et al. 2013). As with other groups, mollusk OA research has primarily focused on the effects of acidification on larvae and juveniles (e.g. Havenhand et al. 2008, Byrne et al. 2010, Crim et al. 2011, Moulin et al. 2011, Yu et al. 2011). Although it has been hypothesized that the direct negative impact may be stronger at early life history stages (Kroeker et al. 2013), this hypothesis has rarely been tested, and it is still unclear how experimental results translate into population-level changes. To address these gaps, we use a size-structured integral projection model (IPM) to explore population sensitivity to negative impact across an animal's life history, a type of analysis common in management (Lande 1988, Akçakaya 2000, Caswell 2000, Gerber & Heppell 2004). This approach has been successfully used to inform conservation of animals such as sea turtles (Crouse et al. 1987), tortoises (Doak et al. 1994), whales (Caswell et al. 1999), amphibians (Vonesh & De la Cruz 2002), and ducks (Hoekman et al. 2002) subject to poaching, bycatch, increased temperature, and other stressors, but this is the first study that specifically uses an IPM to analyze sensitivity of an abalone population and fishery performance with respect to environmental stresses.

We chose abalone (*Haliotis* spp.) as representative calcifying organisms because of their commercial and conservation importance. Abalone are found globally, and the collective market value of both abalone fisheries (6500 metric tons, mt) and aquaculture (~129 000 mt, Cook 2016) was between US $2 and 3 billion in 2015 (assuming a flat value of $20 kg^{-1}). Additionally, multiple North American abalone species are either of concern (pink *H. corrugata*; green *H. fulgens*; California Department of Fish and Game 2005) or endangered (black *H. cracherodii*; white *H. sorenseni*; NOAA 2001, 2009), and all California fisheries were closed in the 1990s because of rapid population declines (Karpov et al. 2000). Similarly, several species and fisheries have declined worldwide due to a combination of overfishing and environmental causes, including in South Africa (Hauck & Sweijd 1999, Raemaekers et al. 2011), New Zealand (Breen et al. 2003, McKenzie & Smith 2009), Mexico (Morales-Bojórquez et al. 2008), and Australia (Ferguson et al. 2017), with global fishery output falling by almost two-thirds (Cook 2016). Although some studies have investigated

the effects of lowered pH on abalone larval development (Crim et al. 2011), juvenile growth (Harris et al. 1999, Kim et al. 2013), and fertilization success (Boch et al. 2017), little is known about the potential effects of OA on adult fitness or overall population health.

In prior experimental work, we determined that fertilization success for red abalone *H. rufescens* is negatively affected when gametes are exposed to pH values below 7.5 (Fig. 1; Boch et al. 2017). Although the observed effect is strong, it is impossible to assess in the laboratory how overall abalone population dynamics might be affected by this decline, or similar temperature- or oxygen-mediated impacts on very early life stages. For example, a 50% drop in fertilization success might produce only minimal population effects if spawning adults are abundant and the number of new recruits is limited primarily by density-dependent processes. Conversely, a population experiencing occasional recruitment failure due to low density, i.e. the Allee effect, may decline to extinction (Allee 1932). In addition, there are many other life history parameters which may be sensitive to OA. Reduced calcification rates may produce individuals with thinner shells, for example, potentially increasing vulnerability to predators and lowering juvenile or adult survival rates. Prioritizing shell strength might slow overall growth rate, delaying time to maturity and reproductive output. Thus, stressors such as OA may impact multiple stages and processes, and it is difficult in a laboratory setting to assess how negative impacts interact to affect overall population persistence and dynamics.

To address these questions, we used a continuous-size-structured abalone population model from Aalto et al. (2019) to explore the population-level effects of deleterious changes to life-history parameters across multiple life stages in a simulated abalone fishery. First, we assumed a sustainably managed fishery and focused primarily on how declines in each parameter would affect a theoretical equilibrium biomass and catch, under a scenario of gradual ocean acidification. We additionally simulated a sudden mass mortality event to explore whether the long-term effects of a stressor such as OA could affect short-term resilience to catastrophe by delaying or preventing population and fishery recovery. Finally, we combined small simultaneous changes in recruitment, growth, and survival parameters to determine if negative interactive effects would exceed the expected additive outcome. We discuss the results in the context of the potential relative impacts of sudden mass mortality events and combined stresses from other environmental drivers
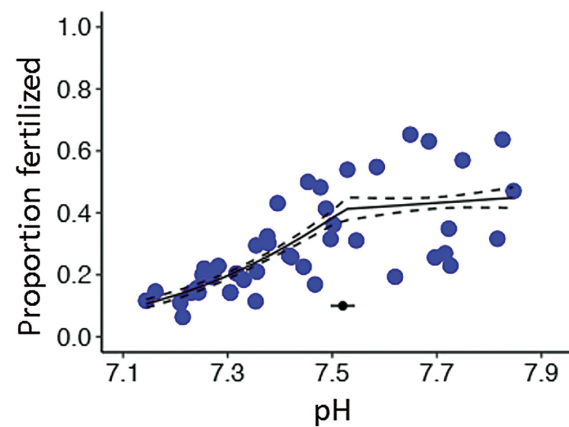

Fig. 1. Abalone fertilization response to low pH (from Boch et al. 2017). The solid black line represents a segmented model fit; dashed lines represent 95% confidence limits. The *y*-axis represents proportional fertilization success, and the *x*-axis represents the measured pH in each experimental sample. The small black solid circle represents the break-point estimate, with error bars showing SE

thought to be rapidly changing in the Anthropocene, such as temperature and decreased oxygen.

2. METHODS

2.1. Model description

We used the IPM (Ellner & Rees 2006) from Aalto et al. (2019) to simulate recruitment, survival, and growth of green abalone *Haliotis fulgens*, a species ranging from central southern California, USA, to southern Baja California, Mexico, under increasing OA. The IPM allows continuous size structure, rather than using discrete size or age classes, which is necessary when modeling the impact of small life history parameter changes on a species with size-dependent survival and fecundity. All model parameters and equations are given in the Supplement at www.int-res. com/articles/suppl/m643p075_supp.pdf. We modeled annual abalone growth using a probabilistic non-negative Gompertz growth function (Fig. 2a; Bardos 2005) developed to match the highly variable abalone growth dynamics seen in the field (Troynikov et al. 1998). Both abalone survival (Fig. 2b) and egg production (Fig. 2c) increase exponentially with length. Following Button's (2008) empirical study and other research on abalone breeding (Shepherd & Partington 1995, Gascoigne & Lipcius 2004, Zhang 2008, Catton et al. 2016), we assumed the existence of an Allee effect and modeled breeding success as an increasing and saturating function of spawner density that ranged
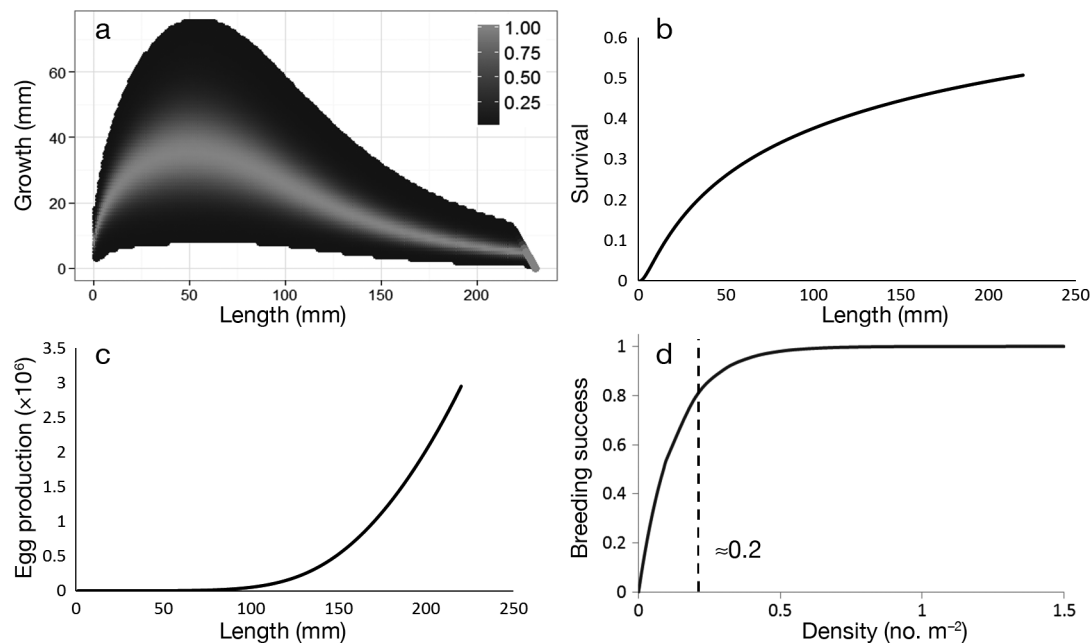
Fig. 2. Population dynamic elements of the annual abalone growth model. (a) Growth by size. The horizontal and vertical axes indicate starting length and amount of growth, respectively. Growth is distributed across a range, with brightness indicating relative proportion of the size class growing a specific amount. (b) Survival proportion based on length. (c) Fecundity (total egg production for mature individuals) based on length. (d) Allee effect. Relative breeding success based on density of adults. The dashed line indicates the density associated with roughly 80% breeding success, the default value for the baseline model

between 0 and 1, with a threshold density below which recruitment begins to fail (Fig. 2d). Multiple studies have found that low-density abalone populations have difficulty recovering even after a fishery closure (e.g. Tegner 1993, Rothaus et al. 2008, Coates et al. 2013, 2014), suggesting that Allee effects are potentially important to recovery of depleted abalone stocks following a mass mortality event.

We assumed a closed system with density-dependent settlement, with no net effect on local recruitment from offshore larval input or loss, and annual fluctuations in relative settler survival rate due to year-to-year environmental variability. We set the carrying capacity to produce an unfished density of ~0.2 ind. m^{-2} based on the work of McShane (1991) and Daume et al. (2004) and consistent with field data (Rogers-Bennett et al. 2004, Micheli et al. 2008).

We modeled catch as a constant proportion h of commercial size abalone harvested annually, representing a constant level of effort. We set h to the fishing pressure required to produce 2/3 of the maximum sustainable yield (F_{MSY}), as determined by prior simulation with no OA effects. This is a precautionary reference point that was commonly used in the past in fisheries management (Jennings et al. 2001), and is generally considered a good compromise between maximizing sustainable yields and minimizing risk of collapse.

2.2. Analysis

We established baseline catch and population values by running 200 simulations for 300 timesteps (years) to ensure that the population reached equilibrium (because the standard deviations for equilibrium biomass and catch were <1% of mean values for each scenario and much smaller than the difference from parameter changes, additional runs would produce little benefit). The 8 parameters tested (Table 1) governed different aspects of abalone life history: for recruitment, we used larval production (combined gamete production, fertilization success, and larval development) and Allee sensitivity; for survival, we used juvenile survival, subadult survival, and adult survival; and for growth, we used growth rate, maximum size, and size at maturity. To test the importance of each potential OA effect, we systematically decreased each parameter by up to 20% in 1 or 2.5% intervals, depending on the sensitivity of the parameter (or increased, in the case of size at maturity), ran 200 simulations (300 yr each) for each value, and compared the new equilibrium catch and population to the baseline values without OA effects to determine the relative change. We used linear regression to estimate change in biomass density or catch as a

Table 1. Abalone growth model response slopes for changes in 8 life history parameters

Aspect of life history	Model parameter	Slope of regression		
		Density	Catch	Recovery likelihood
Recruitment				
Larval production	e_w, σ_E, or σ_S	0.11	0.11	1.00
Allee sensitivity	a_{agg}	0.047	0.048	1.00
Survival				
Juvenile, <50 mm	α_J	4.05	4.01	4.65
Subadult, ≥50 mm, <L_{mat}	α_Y	4.68	4.77	5.39
Adult, ≥L_{mat}	α_M	9.39	10.90	10.12
Growth				
Size at maturity	L_{mat}	−1.66	−0.31	−0.5
Maximum size	L_n	9.99	11.30	11.15
Growth rate	G	9.77	10.19	9.64

single-parameter results. We chose larval production as the 'recruitment' term and growth rate as the 'growth' term. Because sensitivity to changes in adult survival was high and similar in strength to changes in growth rate, combining 5% declines in both would guarantee extinction. Consequently, we used juvenile survival as the representative survival term. We added size at maturity as an alternative to growth rate because its behavior was different from the other growth parameters, although the 2 parameters are inter-related if maturity is primarily based on age. All simulations were run using the programming language R v. 3.4.4 (R Development Core Team 2018).

function of change in parameter, with a steeper slope indicating greater sensitivity. Similarly, we evaluated the effect on population resilience by running each simulation to equilibrium, simulating a catastrophic hypoxic upwelling event with 50% mortality (similar to mortality levels observed by Micheli et al. 2012), and continuing to run each simulation until the population either recovers or, if sufficiently below the Allee threshold, goes extinct. Finally, we investigated possible interactive effects by testing different combinations of 2 parameters from 3 general life history aspects (recruitment, survival, and growth) and comparing the combined effect of a 5, 7.5, or 10% decrease in both parameters with the additive effect predicted by the 2

3. RESULTS

The equilibrium spawning stock biomass density (slightly greater than abalone fishery stock size, because $L_{minH} > L_{mat}$, where L_{minH} is minimum length at harvest) was most sensitive to parameters which directly affected the size and number of adult abalone (Table 1, Fig. 3). Specifically, these parameters were maximum size (L_n), growth rate (G), and adult survival α_M (length ≥L_{mat}). The next most sensitive were subadult survival α_Y (length ≥50 mm and <L_{mat}), juvenile survival α_J (length <50 mm), and size at maturity (L_{mat}). Finally, the population was least sensitive to the recruitment parameters larval production (e_w) and Allee sensitivity (a_{agg}). The same sensitivity pattern was seen for catch (Table 1, Fig. 4a) and recovery likelihood (Table 1, Fig. 4b). Recovery likelihood showed greater overall sensitivity to the potential OA effects, meaning that for most parameter changes, the decrease in recovery likelihood (Fig. 4b) was greater than the decrease in equilibrium density (Fig. 3) or catch (Fig. 4a). In particular, recovery likelihood had a more pronounced non-linear response to most parameter impacts (excepting larval production and Allee sensitivity), caused by the non-linearity of the underlying Allee effect governing population recovery (Fig. 2d). Although a polynomial fit was significantly better for some of the parameters, depending on the metric, we used linear regression exclusively to facilitate comparison.
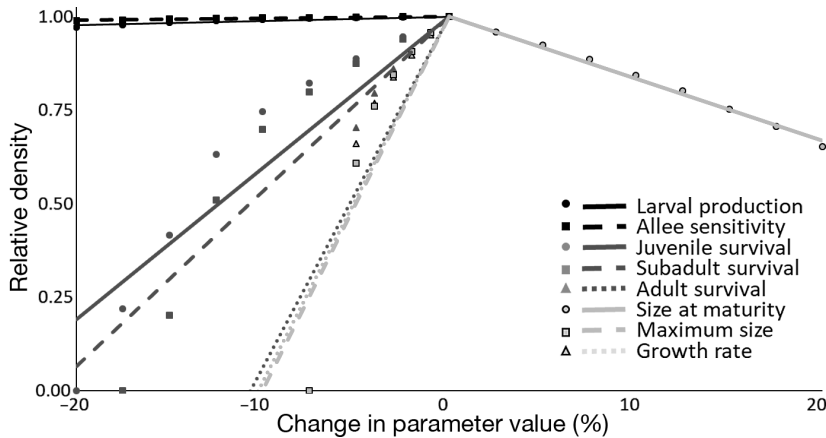

Fig. 3. Sensitivity of equilibrium population density to changes in life history parameters. The y-axis represents relative equilibrium population density compared to the baseline case (default parameter value), and the x-axis represents percentage deviation from default parameter values. The lines represent standard regressions for each parameter tested (see Table 1 for slope values)
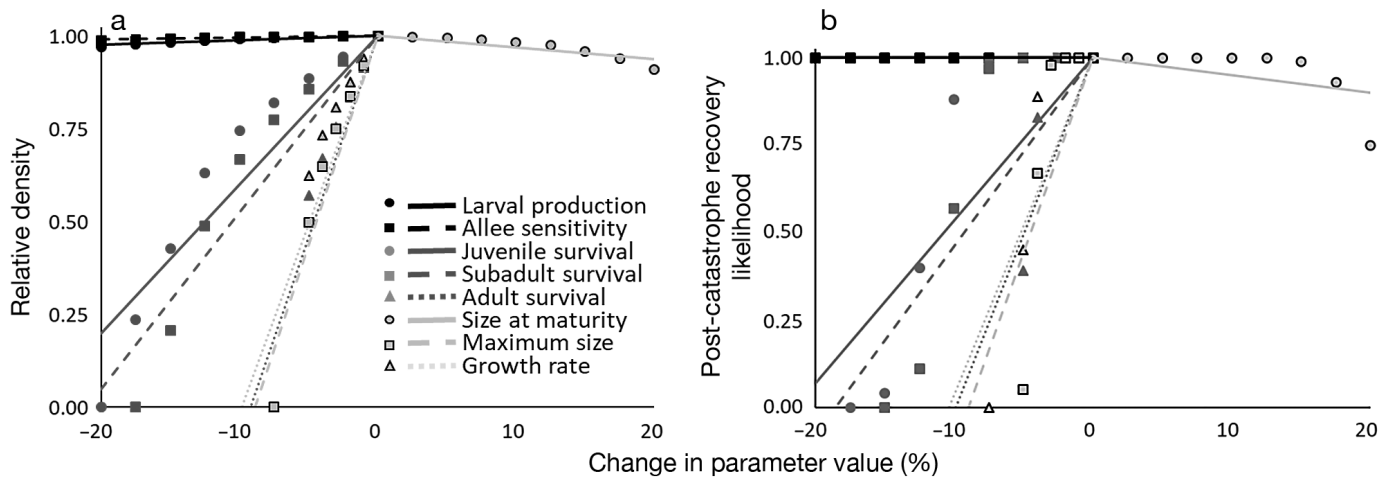
Fig. 4. Sensitivity of equilibrium catch and recovery likelihood to changes in life history parameters. The axes and regression lines are the same as in Fig. 3. (a) Equilibrium catch. (b) Recovery likelihood following a 50% mortality event. The default population carrying capacity is set to be at the 80% Allee effect threshold (i.e. due to the Allee effect, recruitment is 80% of maximum at equilibrium density). Note the significant non-linear response for some of the parameter changes, although linear trendlines are shown for ease of comparison
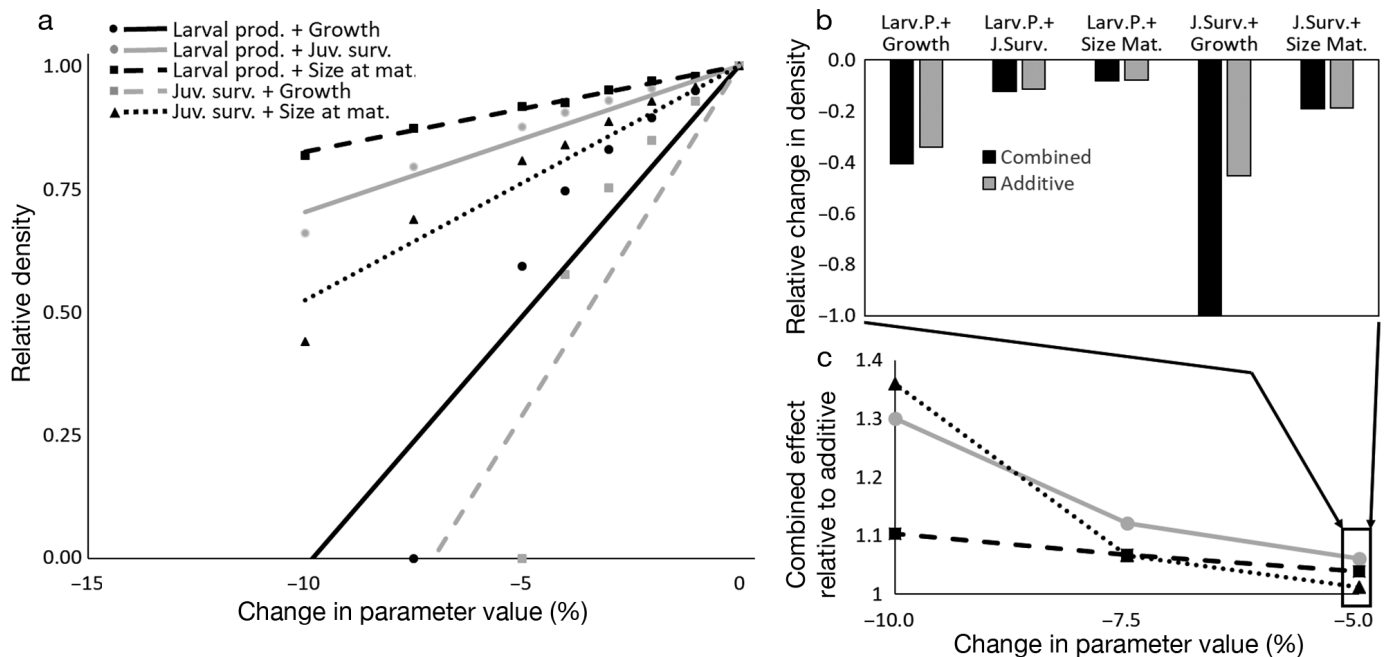

Fig. 5. Interactive effects of parameter combinations in the abalone growth model. (a) Sensitivity of equilibrium population density to simultaneous changes in 2 life history parameters. The axes and regression lines are the same as in Fig. 3; prod.: production; juv.: juvenile, surv.: survival, mat: maturity. (b) Comparison between combined ocean acidification effects and predicted additive effect. The *y*-axis indicates the relative decrease in population density compared to baseline for each multiple-stressor model and the same stressors combined additively. The results shown are for a 5% change in each parameter (−5% for larval production, growth rate, and juvenile survival; +5% for size at maturity). Larv. P.: larval production, J. surv.: juvenile survival; Size mat.: size at maturity. (c) Proportional magnitude of interactive effect. The *x*-axis indicates the change in parameter value, as in panel (a). The *y*-axis shows the combined effect on density relative to the additive effect, with values >1.0 indicating a positive interactive effect. Points and lines are the same as in (a), although the lines simply link points. Note that for 2 of the combined parameter scenarios, the population went extinct for values <−5%

All of the parameter combinations showed positive interactive effects, with abundance in the combined effect scenarios decreasing 1.02–1.39 times as much

as the predicted additive effects (Fig. 5a). For a 5% reduction, the biggest interactive effect was seen for any combination which included growth rate (1.23–

2.24 times; Fig. 5b). All 3 parameter combinations which did not cause extinction at higher stress effect levels (those without growth rate decreases) showed the biggest interactive effect at −10% (1.10–1.39 times; Fig. 5c). Note that we used the simulated OA impact values for each model, not the predicted values from linear regression, to avoid over-estimating the additive impact because of non-linearity in parameter sensitivity.

4. DISCUSSION

Our modeling analysis suggests that, for a calcifying marine mollusk, population level impacts of environmental stressors, such as OA, are driven by differential responses of later life stages, highlighting the importance of considering the sensitivity of the entire life cycle of the species and identifying and focusing analysis on the most sensitive stages. Specifically, the model predicts that population size is most sensitive to parameters which directly affect the creation and survival of large, fecund adults. This is consistent with studies that have highlighted the key role of 'big old fat fecund female fish' in population persistence and fisheries management (Longhurst 2002, Palumbi 2004, Micheli et al. 2012, De Leo & Micheli 2015), and prior sensitivity analysis identifying adult survival as the most critical factor for red and white abalone management and conservation (Rogers-Bennett & Leaf 2006). Similarly, gorgonian population persistence was found to be most sensitive to adult survival, not fecundity (Gotelli 1991, Linares et al. 2007), although sensitivity to recruitment failure varied by species (Hughes & Tanner 2000).

Because fecundity scales exponentially with abalone size, decreasing the growth rate, maximum size, or adult survival has a disproportionate impact on overall larval production across the entire lifespan of an individual. Conversely, relaxation of density-dependent competition for space and resources during recruitment and in the early life stages may partially compensate for the potential reduction in mean fecundity or fertilization success caused by OA. These results highlight the importance of increasing our understanding of how environmental stress affects the creation and survival of large, fecund adults in harvested marine invertebrate populations in order to more effectively manage and conserve these important components of marine biodiversity under climate change scenarios. Regardless of the potential environmental stressor, future empirical studies should focus on the possible long-term, cumulative ef-

fects on growth and survival of late immature stages and adults over the entire lifespan, and examine effects on multiple parameters and how they combine to influence adult survival and reproductive output.

On the other hand, the risk of recruitment failure caused by non-linear, negative density-dependent breeding (i.e. the Allee effect) could interact powerfully with catastrophic events. A 33% decrease in equilibrium abundance (following, for example, a 5% decline in growth rate; light gray dotted line, Fig. 3) could translate into a 60% likelihood of extinction following a moderate mass mortality event (Fig. 4b). Given that extreme events such as heat waves, hypoxia, and harmful algal blooms are expected to increase with climate change (Jentsch et al. 2007, Hegerl et al. 2011), adjusting fishing effort for this decrease in resilience, for example, by lowering fisheries mortality, F, below the standard MSY-based reference point to maintain a biomass 'buffer' against catastrophe, could be critical to sustainable management (Wagner et al. 2007, Game et al. 2008).

Even small deleterious effects can have unexpectedly large population-level impacts if they act synergistically across several life history parameters, creating interactive effects more damaging than the sum of the individual changes. Our simulation found that the loss of equilibrium abundance was 23–220% worse than the cumulative expected loss when a 5% decrease in growth rate was combined with a similar decrease in another life history parameter. Because these detrimental effects acted simultaneously on different life stages, their combined effect across an individual's lifespan was greater than parameters with overlapping effects (for example, both larval production and size at maturity generally lower lifetime fecundity). Although studies have identified multiple early life processes which are impacted by stressors such as OA (e.g. both larval settlement and growth in corals; Albright & Langdon 2011), our analysis stresses the importance of cumulative interactive effects across the individual's lifespan. In our simulations, multiple co-occurring small effects across key survival, growth, and fecundity parameters can largely amplify the demographic consequences of a reduction of each parameter individually, disrupting fishery sustainability, or even push a recoverable decline into extinction. In the case of abalone, our study showed that the non-linearity of the response to multiple stress effects across the individual's lifespan is more extreme than for the single effect scenarios, with a shift from −4 to −5% (juvenile survival + growth rate) or −5 to −7.5% (larval production + growth rate) dropping equilibrium abundance

from ~60% to 0. Combined effects could result from a single stressor affecting multiple parameters or the overall effects of changes in more than one environmental driver.

Prior research has focused on measuring responses of individual organisms to stresses such as OA, but determining the actual impacts requires considering changes within the full ecological context (Gaylord et al. 2015). This includes population dynamics, species interactions, interactions with other environmental stressors, resilience in the face of catastrophe, and the potential for adaptation through genetic plasticity or selection. Here, we assumed that environmental stress could cause declines in life history parameters of between 5 and 20% (well within the range of observed responses to OA; Kroeker et al. 2013), and projected those changes across a full population over time. Our model predicts that population size and persistence are much more sensitive to adult growth and survival, parameters that are difficult to study in a laboratory setting, than the more tractable early life history parameters such as fertilization success and larval survival, although extreme stress scenarios resulting in near-complete reproductive failure or close to 100% larval mortality are expected to have population impacts. It is well recognized that extreme events, such as hypoxic crises (Diaz 2001, Vaquer-Sunyer & Duarte 2008, Laffoley & Baxter 2018), heatwaves (Garrabou et al. 2009, Arafeh-Dalmau et al. 2020), and disease outbreaks (Ward & Lafferty 2004, Miner et al. 2006, 2018), can eliminate a large fraction of a managed population. Our analysis shows that environmental stressors that do not cause mass mortality but a progressive reduction in fertilization success may lead to recruitment failure in species with negative density dependence. Much less recognized in the literature is the fact that even small changes in key demographic parameters, such as growth rate and adult survival as shown in our study, have a cumulative effect over the entire lifespan of an individual that is comparable to that caused by major catastrophic events. Therefore, future studies of the impact of OA and other environmental stressors should not dismiss the long-term consequences of small changes caused by climate change. Our study also casts light on the interactive, non-linear effect of small, multiple, co-occurring stressors, which might have profound consequences on the persistence of populations of commercial or conservation value, especially when the effects are additive or synergetic and not compensative. Consequently, our results suggest that current research may underestimate the effects of environmental stressors, at least for marine invertebrates with size-dependent fecundity and especially when multiple impacts are involved. These predictions can help guide future laboratory and field research towards a more comprehensive understanding of how changing marine conditions can alter not only individual fitness, but population structure, resilience, and key ecosystem services such as fisheries sustainability.

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