

Racing through life: maturation rate plasticity regulates overcompensation and increases persistence

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Abstract. Induced changes in the demographic traits of harvested populations produce ecological responses to mortality that are not generally predicted by traditional models. Strong plasticity in maturation rates—commonly observed among intensely harvested populations—varies the time between birth and reproduction of an individual, thereby affecting a population's growth rate. We developed a general model to explore how density-dependent maturation rates affect both population persistence and overcompensation, the situation in which population abundance increases in response to harvest. We find that plasticity in maturation rates generally dampens or eliminates overcompensation in populations. However stage-specific harvest strategies, rather than those that target a population evenly, could elicit or strengthen an overcompensatory response. Therefore, occurrence of overcompensation in a species may be context-dependent. Our results also demonstrate that faster maturation in response to harvest allows populations with low juvenile survival to persist under much greater harvest pressures and maintain higher levels of adult abundance than when maturation rates are not plastic. Strong compensatory responses in age at maturity can greatly amplify the harvest effort required to reduce or collapse populations with low survival rates. Accounting for this effect can be critical to invasive species control or eradication, as well as to the conservation of ecologically and/or economically important populations.

Key words: density dependence; fisheries; harvest; invasive species control; maturation rate; nuisance species; overcompensation; persistence; phenotypic plasticity; survivorship.

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INTRODUCTION

Species respond to changing environmental conditions either through natural selection on heritable genetic variation or environmentally-induced trait changes through phenotypic plasticity (Ozgul et al. 2009, Shimada et al. 2010, Ellner et al. 2011). In many taxa, both processes influence the age at reproductive maturity, a key demographic factor representing the delay be-

tween recruitment and reproduction (Caswell 1983, Rose et al. 2001). To date, both empirical (Heino et al. 2002) and theoretical (Baskett et al. 2005, van Dooren et al. 2005, de Roos et al. 2006, Bodin et al. 2012) studies have focused on quantifying harvest-driven evolutionary changes in maturation rates across multiple generations. By contrast, phenotypic plasticity in traits allows populations to respond to environmental changes much more rapidly, even within a single

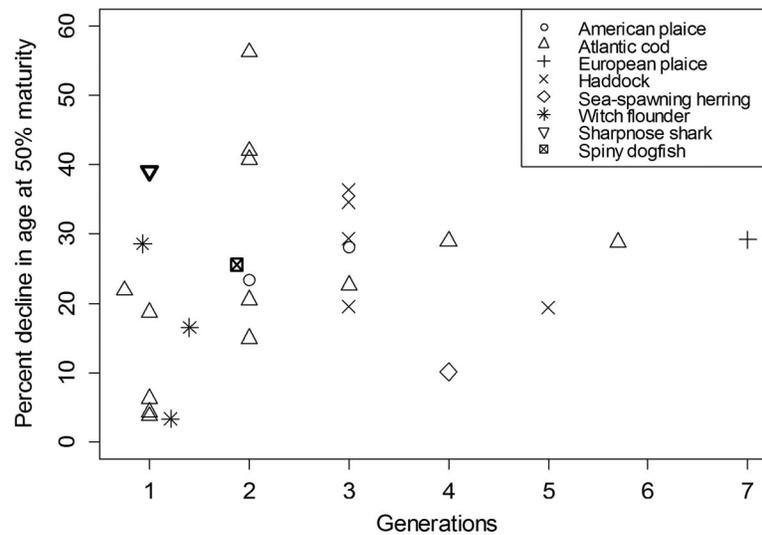


Fig. 1. Reported rates of decline in age at 50% maturity (% decrease per generation) in intensively harvested fish populations. High harvest rates may drive faster maturation through plasticity. Data from Trippel (1995), Carlson and Baremore (2003), Sharpe and Hendry (2009), and Taylor and Gallucci (2009).

generation, and can affect contemporary ecological dynamics (Shimada et al. 2010, Ellner et al. 2011). Although harvest and predation can be dominant factors affecting populations, we know little about how rapid changes in age at maturity affect the population dynamics and management of intensively exploited species (Persson and de Roos 2006).

A growing body of evidence indicates that plasticity in maturation rate is a widespread phenomenon, especially in populations subject to intensive human harvest for commercial purposes. Although time series reporting maturation data are sparse, long-term fisheries surveys commonly report large changes in age at maturity (the inverse of maturation rate) over only a few generations (Fig. 1). For example, Trippel (1995) reported up to two-fold declines in age at maturity for valuable commercial fishes such as Atlantic cod and haddock over periods of 1–3 generations. Similar data from other well-studied, commercially important populations provides a strong indication that maturation rate plasticity can be large and may be widespread.

Recently, extensive research and modelling efforts have aimed to disentangle environmental and evolutionary effects on age and/or size at maturity among fish populations (Grift et al. 2003, Ernande et al. 2004, Poos et al. 2011, Bodin

et al. 2012). These studies consistently find that extensive environmentally-mediated phenotypic plasticity is a key—and in some cases dominant—driver of both short-term fluctuations and long-term changes in age at maturity (Grift et al. 2003, Engelhard and Heino 2004, Dunlop et al. 2007; reviewed in Rose et al. 2001, Lorenzen and Enberg 2002). Long-term studies examining maturation rate plasticity are less common for species with high recruitment, growth, and mortality rates than for commercially important, long-lived, species. However, such life history characteristics have been ascribed to invasive species (Grotkopp et al. 2002, van Kleunen et al. 2010), which have been found to exhibit greater phenotypic plasticity across many traits (Davidson et al. 2011), including growth rates.

Change in conspecific density is one likely mechanism driving plasticity in life history traits of harvested or prey species. As the strength of intraspecific competition often affects resource availability, mortality-driven declines in abundance can result in a compensatory increase in maturation rates over a very short period (Rose et al. 2001, Engelhard and Heino 2004). This response has been observed or suggested in a wide range of taxa, including American plaice (Morgan and Colbourne 1999), sharks (Carlson and Baremore 2003), *Daphnia* zooplankton

(Walsh and Post 2011), and crabs (Zheng, 2008). Compensatory population responses to mortality can also influence the outcome of removal efforts aimed at reducing or eradicating populations of invasive species (Hauser et al. 2006, Edwards and Leung 2009, Pardini et al. 2009, Zipkin et al. 2009).

Overcompensation, in which the removal of individuals unexpectedly results in an increase in population abundance, is an especially undesirable outcome of invasive species control that has been observed in a wide range of taxa with stage-structured life histories, including plants, fish, and invertebrates (reviewed in Abrams 2009, Zipkin et al. 2009, Schröder et al. 2014). A common mechanism of overcompensation shown in both lab and field studies occurs when increased mortality from harvest elicits a large increase in recruitment due to a release from intense intraspecific competition (for a complete review of mechanisms, see Abrams 2009, Schröder et al. 2014). At the same time, harvest-induced increases in maturation rates can reduce the time to reproduction, further increasing population growth. Thus, we might expect rapid increases in maturation rates to amplify the occurrence or magnitude of overcompensation and further exacerbate the negative consequences of removal efforts. Since faster population growth also implies an increased resilience to mortality (Brooks and Lebreton 2001), it is equally important to determine the conditions under which density-dependent maturation affects population size and increases persistence in the face of intense harvest levels.

We developed a suite of stage-structured models that can accommodate a variety of potential density-dependent maturation processes to explore how plasticity in maturation affects the dynamics of exploited populations. We examine a range of harvest intensities and strategies, along with a broad range of probable survivorship values. We also explored the sensitivity of our results to (1) whether maturation rates are limited by juvenile vs. adult abundance and (2) the extent of plasticity in age at maturity. We discuss our findings in the context of both population control and eradication of nuisance species through harvest, and the management of ecologically or economically important species.

METHODS

Model development

We develop a set of models based on the discrete time harvest model in Zipkin et al. (2009) to evaluate how density-dependent maturation impacts population dynamics under constant harvest mortality. The complexity of our models is limited to two discrete life stages, juveniles (J) and adults (A), making them applicable to a wide range of taxa but still simulating the dynamics produced by more complex models with discrete as well as continuous size distributions (de Roos et al. 2007). Time intervals in our models are scaled to the period of the reproductive cycle; thus, juvenile abundance at time $t + 1$ depends on the level of recruitment γ_t as well as the proportion of juveniles at time t which survive (s_J), are not harvested ($1 - h_J$), and do not mature ($1 - m_t$), when $m_t < 1$. Similarly, adult abundance is determined by the surviving juveniles that mature, as well as the proportion of adults which survive (s_A) and are not harvested ($1 - h_A$). Thus, the general structure of all models is

$$\begin{aligned} J_{t+1} &= \gamma_t + J_t(1 - h_J)s_J(1 - m_t) \\ A_{t+1} &= J_t(1 - h_J)s_Jm_t + A_t(1 - h_A)s_A. \end{aligned} \quad (1)$$

Juvenile recruitment (γ_t) is determined by an overcompensatory function described by Ricker (1954), in which the per capita recruitment rate of adults not harvested in the previous time step, $A_t(1 - h_A)$, depends on maximum per capita recruitment α and declines exponentially with adult abundance at time t . We assume that harvest occurs prior to reproduction, a practice seen in both the commercial exploitation of populations and in efforts to control nuisance populations (Brooks and Lebreton 2001). Thus, juvenile recruitment at time $t + 1$ peaks when adult abundance is just below its equilibrium value, which depends on the strength of density dependence in recruitment β , and is given by

$$\gamma_t = A_t(1 - h_A)\alpha \exp\left(-\beta A_t(1 - h_A)\right). \quad (2)$$

This function assumes that intraspecific competition among remaining adults increases with abundance, driving either a decline of per capita adult investment into reproduction, or a reduction in the number of per capita offspring reaching age one through adult cannibalism.

The value of β has no qualitative effect on population dynamics (see Zipkin et al. 2009), so all results are independent of population size. For simplicity, we assume $\beta = 1$ throughout our analysis, although our model can be applied to populations of any size and by adjusting β .

When individuals are young (e.g., larvae or seedlings), low survival likely dominates over density-dependent mechanisms (Cowan et al. 2000), particularly among species with high values of α . However, the resource use of juveniles nearing maturity tends to overlap more with that of adults due to increasing physiological similarities. Growth, and therefore maturation rates, may depend on adult abundance when juveniles are competitively inferior to adults or are displaced to resource-poor habitats (e.g., to avoid cannibalism, Persson and de Roos 2006). We focus on comparing the effects of harvest on populations with fixed maturation rates (i.e., $m_t = \mu$, where $0 < \mu < 1$) to populations where maturation rate increases proportionally with declines in adult abundance. For the latter case, we define m_t as a function ranging in value between m_{\min} (at $A_t = K$) and m_{\max} (at $A_t/K \approx 0$), where K is the equilibrium adult abundance under no harvest (and thus $m_t = m_{\min}$; see Type I curve in Appendix A: Fig. A1)

$$m_t = m_{\max} - (m_{\max} - m_{\min}) \frac{A_t}{K} \quad (3)$$

and

$$K = \beta^{-1} \ln \frac{m_{\min} \alpha}{(1 - s_A)(s_J^{-1} - 1 + m_{\min})}. \quad (4)$$

If juveniles and adults sufficiently separate resource reliance in form, space, or time, maturation may instead be constrained by competition among juveniles (de Roos and Persson 2013). To examine this scenario, we additionally analyze a version of the model in which maturation rates at time t (m_t) are dependent on the number of juveniles, such that J_t is substituted for A_t in Eq. 3. In this case, there are two levels of the equilibrium juvenile abundance at zero harvest (hereafter L)—one stable and one unstable. To standardize results for this scenario with our other simulations, we fitted K in Eq. 3 to be slightly below L (i.e., $m_t = m_{\min}$; Appendix A: Fig. A1). Although the value of L depends on K , we scaled abundance levels in our results to the total

population size at zero harvest; therefore, as long as $K < L$, the effects of density dependent maturation on overcompensation were robust to all the variations in model structure and parameter values presented here. Other variations of the base model we explored tested the sensitivity of our results to nonlinear density dependence of maturation rates (Appendix A), the effect of declining maximum per capita recruitment with faster maturation (Appendix B), and compensatory vs. overcompensatory recruitment (Appendix C).

Model analysis

We examined how a density-dependent maturation rate affected the strength of overcompensation and population persistence across all harvest intensities (i.e., 0, no harvest to 1, 100% harvest). When present, the strength of overcompensation was determined as the highest population size observed across all harvest intensities, relative to abundance at no harvest. Population persistence was evaluated based on (1) the intensity of harvest required to collapse the modeled population (h_c) and (2) the level of harvest at which adult abundance declined by 50% from pre-harvest levels (h_{half}). Constant maturation rates were fixed at $m_t = 0.5$, whereas under density-dependent functional forms, m_t ranged between $m_{\min} = 0.2$ and $m_{\max} = 1$. As maturation rates are likely to be constrained not only by resource availability but also by maximum physiological or developmental rates, we also examined the sensitivity of our predictions about persistence for levels of m_{\max} between m_{\min} and 1.

To examine our results across a range of life histories, we considered four survival regimes: low population-level survival ($s_J = s_A = 0.2$); low juvenile, high adult survival ($s_J = 0.2$, $s_A = 0.8$); high juvenile, low adult survival ($s_J = 0.8$, $s_A = 0.2$); and high population-level survival rates ($s_J = s_A = 0.8$). In all cases, we used a maximum per capita recruitment of $\alpha = 10$. We also compared how alternate harvest strategies targeting a single stage (i.e., $h_J = 0$ or $h_A = 0$) or both life stages (i.e., $h_J = h_A$) affected overcompensation and population persistence.

Our model does not exhibit chaotic behavior under any parameter combinations. Population cycles with a period of two time steps can occur

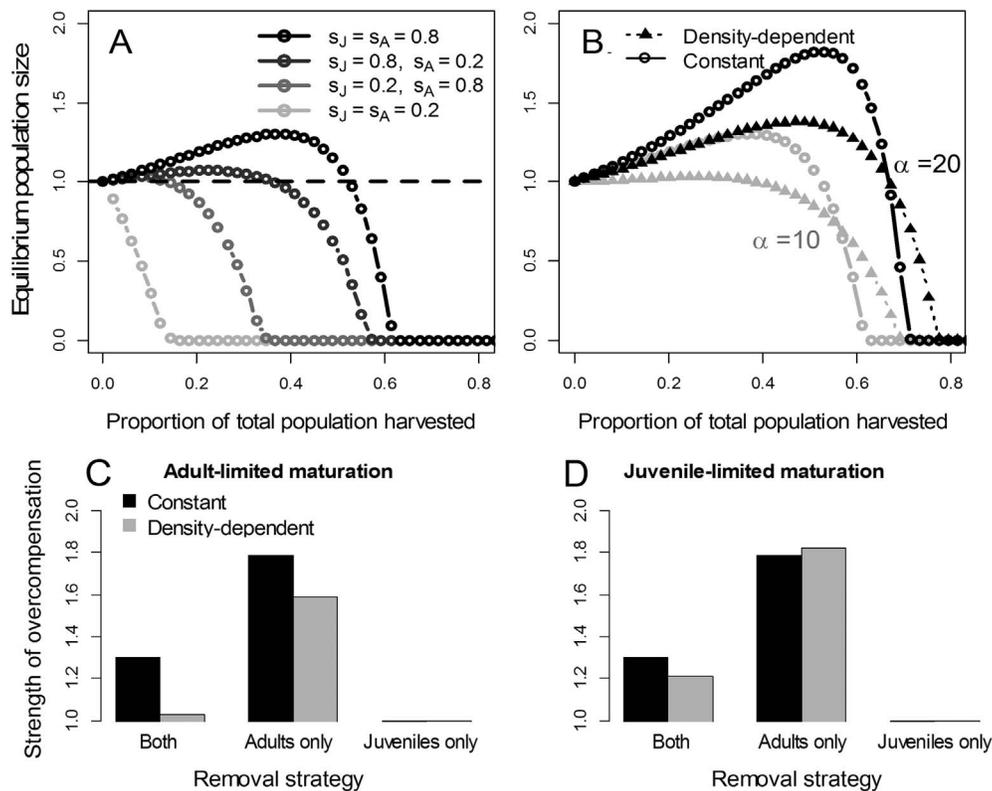


Fig. 2. Overcompensation can be dampened by density-dependent maturation rates. (A) Equilibrium population size over a range of harvest levels and four survival regimes; overcompensation occurs primarily when juvenile survival is high. (B) Effect of constant (open dots) vs. density-dependent (triangles) maturation rates on overcompensation under two levels of maximum per capita recruitment α . (C, D) Effect of adult and juvenile density-dependent maturation rates on overcompensation strength (maximum population size across all harvest levels) when harvest targets one or both stages. Population sizes are scaled to the level of equilibrium abundance in the absence of harvest (equal to 1.0, dashed lines in A and B), with $\alpha = 10$ unless noted otherwise. Density-dependent maturation ranges between $m_{\min} = 0.2$ and $m_{\max} = 1$, while constant maturation is fixed at $m_t = 0.5$.

under density-dependent maturation rates when adult survival is low ($s_A = 0.2$) and the plasticity in maturation rates (i.e., $m_{\max} - m_{\min}$) is high. This occurs because our simplified model assumes that the maturation rate depends only on adult abundance in the previous time step, and periodic cycles disappear when maturation rates depend on abundance over multiple time steps. However, populations are stable throughout the range of results we present. All results are shown for equilibrium population abundances and are independent of initial starting values. For generality, we scaled abundances relative to total population sizes at no harvest.

RESULTS

Overcompensation and stability

As found in empirical studies (Schröder et al. 2014), overcompensation in our model is stage-specific and occurs through a strong increase in juveniles following harvest-driven reductions in adult abundance. As in Zipkin et al. (2009), constant maturation ($m_t = 0.5$) produces an increase in total population size primarily for populations with high rates of juvenile survival (Fig. 2A) and maximum per capita recruitment $\alpha > 4$. In general, the extent to which harvest can produce an overcompensation in abundance strongly depends on α (Fig. 2B), and to a lesser

extent on the adult survival rates.

Compensatory maturation rates (i.e., density dependence in age-at-maturity) greatly reduce overcompensation (Fig. 2B), and higher values of m_{\max} lead to a stronger dampening effect (not shown). Plasticity in maturation is key to producing this effect because removed adults are replaced more quickly when maturation is faster. This dampens overcompensation because (1) the reduced decline in adults leads to a lower peak in juvenile recruitment, and (2) juvenile abundance declines more quickly with increasing maturation rates (since $1 + (1 - s_j - s_j h_j) > 1$ juveniles are needed to replace an adult). This effect is consistent across all survival regimes and persists for other functional forms of density dependence in maturation (Appendix A).

For both constant and density-dependent maturation rates, removal strategies targeting adults amplify overcompensation because total juvenile mortality is reduced (Fig. 2C). No overcompensation is observed under juvenile-targeted harvest ($h_A = 0, h_j > 0$), but such harvest strategies require the removal of virtually all individuals (i.e., $h_j \approx 1$) to collapse the population (Zipkin et al. 2009). Finally, when maturation rate depends on juvenile rather than adult abundance, increases in recruitment maintain high levels of abundance and competition among juveniles, resulting in low rates of maturation. Consequently, the dampening effect of density-dependent maturation on overcompensation (relative to constant $m_t = 0.5$; Fig. 2D) is reduced.

Population persistence and adult abundance

The effect of harvest on population persistence (h_c , the lowest harvest level at which the population collapses) and adult abundance (h_{half} , harvest level at 50% adult decline from $h = 0$) are predominantly determined by natural survival rates, harvest strategy, maximum per capita fecundity, and the maximum maturation rate m_{\max} (Fig. 3). Survival rates of juveniles (vs. adults) have the strongest effect on population persistence and adult abundance since natural adult mortality occurs after newly matured individuals reproduce. Thus, in our model framework, even semelparous populations (i.e., with $s_A = 0$) can be sustained under sufficiently high levels of s_j and α . Although in general populations are less affected by harvest of a

single stage, adult (vs. juvenile) harvest more strongly impacts both persistence and adult abundance because mature individuals are removed before reproduction.

Under a given survival and harvest regime, the two key traits determining how many individuals mature—and thereby population persistence—are per capita recruitment and the rate of maturation. Historically, most population models treat the former trait as density-dependent and assume the latter as fixed (Helser and Brodziak 1998); however, intense harvest can increase density-dependent maturation rates by reducing competition. Faster maturation allows (1) more individuals to survive the juvenile stage and (2) for new recruits to reproduce earlier, increasing the relative abundance of adults. Because adults lost to mortality are replaced more quickly, persistence and adult abundance at a given harvest level increase, particularly when juvenile survival is low. The strength of this effect depends on the maximum maturation rate which the population can attain, and therefore higher values of m_{\max} increase h_c and h_{half} (Fig. 3). This effect is most important for populations with low survival rates (i.e., $s_j = s_A = 0.2$; Fig. 3A), which are prone to collapse even under mild harvest levels.

Because recruitment and maturation are near their maximal values when abundance is low, population persistence increases with m_{\max} regardless of which stage limits density-dependent maturation and whether recruitment is overcompensatory (Appendix B). However, adult abundance is more strongly impacted by harvest in populations with high juvenile survival rates when recruitment is compensatory (vs. overcompensatory; Appendix B). Persistence is also independent of the functional form of density dependence in maturation, although at a given harvest level for $h < h_c$, the functional form can greatly affect adult abundance when juvenile survival is low and maximum maturation rates are high ($m_{\max} > 0.5$), especially if harvest targets adults (Appendix A). Finally, when earlier maturation reduces per capita recruitment (e.g., due to reduced body size at maturity), compensatory maturation may still increase population persistence and adult abundance (Appendix C).

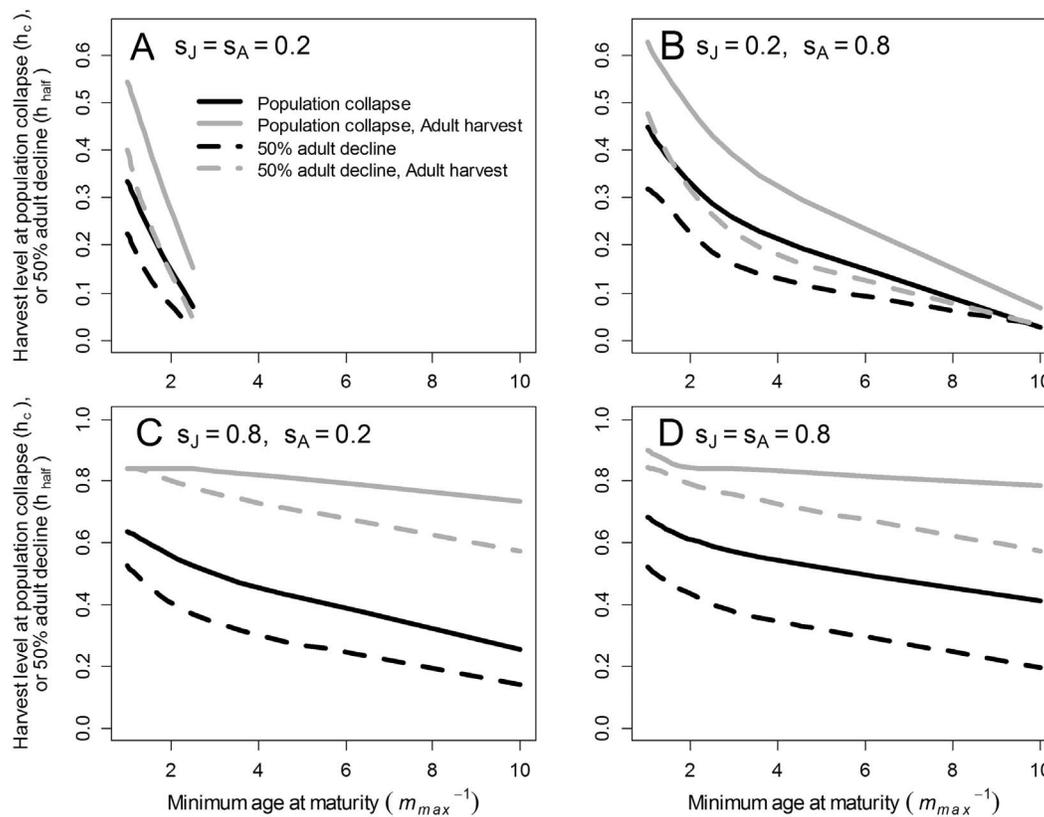


Fig. 3. Effects of maturation plasticity on the harvest level (i) that causes a population collapse (h_c , solid lines) and (ii) at which adult abundance declines by 50% from zero harvest (h_{half} , dashed lines). Total population (black curves) vs. adult-only harvest (grey curves) shown across four survival regimes: (A) low overall survival; (B) low juvenile, high adult survival; (C) high juvenile, low adult survival; and (D) high overall survival rates. Here, the maximum maturation rate m_{max} in simulations is decreased left to right along the x-axes from 1 to $m_{min} = 0.1$. For low survival ($s_J = s_A = 0.2$; panel A), we only show m_{max} between 1 and 0.4 as these populations did not persist when $m_t < 0.4$.

DISCUSSION

Trait plasticity can alter population vital rates at time scales relevant to ecological dynamics. Our results show that compensatory increases in maturation rates in response to increased mortality can dampen or eliminate an overcompensatory population response to harvest, and also allow populations with low juvenile survival to persist under much higher harvest intensities or predation rates than when maturation is fixed. This has important implications for the optimal management and conservation of animal populations, as failure to consider phenotypic plasticity can lead to unintended consequences (Zipkin et al. 2008, Pardini et al. 2009). Below we identify

the life history traits and ecological contexts in which accounting for maturation plasticity is essential for effectively managing both nuisance and commercially important populations.

Implications for nuisance species control

Efforts to mitigate negative impacts of nuisance species commonly attempt to reduce or eradicate populations by removing individuals or introducing and promoting natural predators (Hauser et al. 2006, Edwards and Leung 2009). Ironically, our results suggest that such control efforts are least likely to be successful in nuisance organisms because of their relatively shorter lifespans (higher natural mortality rates), higher growth and maturation rates, and increased

Table 1. Empirical examples of density-related increases in maturation rates and estimated increases in population persistence.

Taxa	Natural annual survival, s_j, s_A	Decrease in age at maturity	Increase in persistence, h_c	Increase in persistence (%)	Source
Round goby	0.4, 0.6	3.0 to 1.0	0.38 to 0.57	52	1
Crayfish (<i>Orconectes rusticus</i> , <i>O. limosus</i>)	0.4, 0.6	2.0 to 1.0	0.45 to 0.57	26	2, 3
Walleye	0.4, 0.6	4.5 to 3.0	0.29 to 0.38	29	4, 5, 6
Yellow perch	0.4, 0.8	3.0 to 2.0	0.42 to 0.49	16	4
Smallmouth bass	0.4, 0.8	4.0 to 3.0	0.37 to 0.42	14	7, 8
Plaice†	0.8, 0.8	6.0 to 4.0	0.47 to 0.53	12	4
Cod†	0.8, 0.8	6.3 to 2.8	0.46 to 0.58	24	4
Haddock†	0.8, 0.8	4.3 to 2.7	0.52 to 0.58	12	4

Notes: Population persistence estimated as the harvest level at population collapse (h_c) under a harvest regime targeting juveniles and adults equally ($h_j = h_A$). For some species (marked †), we selected reasonable survival estimates as stage-specific (i.e., juvenile vs. adult) estimates were unavailable. Due to limited data and large variability in recruitment of these species, we assumed $\alpha = 10$ in all cases to facilitate comparison with Fig. 3. For gobies and crayfish, no studies explicitly link maturation rates to abundance, but faster maturation in more productive environments have been observed; thus, we use a range of maturation rates reported among individuals for crayfish and among studied populations for round gobies. Sources are (1) Corkum et al. (1998); (2) Momot (1984); (3) France (1985); (4) Trippel (1995); (5) Schram et al. (1992); (6) Schueller et al. (2005); (7) Zipkin et al. (2008); (8) V. A. Karatayev, C. E. Kraft, and E. F. Zipkin, *unpublished data*.

growth rate plasticity compared to native species (Grotkopp et al. 2002, van Kleunen et al. 2010, Davidson et al. 2011, Snyder et al. 2014). We find that the increase in population persistence due to plasticity in maturation rates will be greatest when (1) intraspecific competition is an important determinant of age at maturity, (2) maximum maturation rates are high, and (3) natural survival among juveniles is low. In aquatic populations with traits (1) and (2), strong density-dependent declines in age at maturity may correspond to substantial (10–50%) increases in population persistence, especially among invasive species (Table 1). Similar effects are also likely in invasive perennial plants for which fast growth at reduced densities leads to higher age-specific fecundity or vegetative spread (Buckley et al. 2001, Rautiainen et al. 2004).

Populations subject to intense removal or biocontrol may persist indefinitely if harvest efforts fail to attain critical levels for eradication (i.e., h_c). For example, efforts to eradicate a lake-dwelling smallmouth bass population have been unsuccessful for 16 years despite annual harvests removing 20–70% of the total population (Zipkin et al. 2008). In this and other situations, density-dependent maturation rates can increase soon after reductions in abundance. The common assumption that maturation rates are fixed (Helser and Brodziak 1998) at pre-harvest levels is therefore inadequate and underestimates the harvest levels necessary to collapse a population. To account for undesired effects of maturation

plasticity in population control efforts, we recommend first considering the minimum age at maturity and juvenile survival rates reported for a target species. If both of these values are low, it is also important to determine the extent to which intraspecific competition (or cannibalism) regulates maturation. This can be done by looking for negative correlations between age at maturity and stage-specific abundance, total population size, or survival rates in available records from similar populations. In populations with high juvenile survival rates, maturation plasticity may not strongly influence population persistence (Table 1), although eradicating such populations will require intense harvest levels (e.g., >60%) unless per capita recruitment is low (Zipkin et al. 2009).

Recent theoretical studies and removal efforts have also raised concerns that controlling nuisance species through harvest can backfire through an overcompensatory population response to increased mortality (Zipkin et al. 2008, 2009, Abrams 2009, de Roos and Persson 2013). However, despite the prevalence of intense harvest pressure on exploited populations, relatively few empirical examples of overcompensation have been documented (reviewed in Abrams 2009, Schröder et al. 2014). Surprisingly, we find that one explanation for this could be that density dependence in maturation rates dampens overcompensation to the extent that an increase in abundance may be difficult to detect (Fig. 2B). This effect is especially prominent in populations

with high per capita recruitment rates in which harvest elicits a strong increase in abundance when maturation rates are fixed (Zipkin et al. 2009). However, the dampening of overcompensation by density-dependent maturation does not occur universally—for example, even strong plasticity may have little effect when removal efforts target adults, a common strategy in population control (Brooks and Lebreton 2001), or when competition among juveniles limits maturation (Fig. 2D). Combined with high levels of persistence, this makes population control of species with both high survival and recruitment rates especially difficult and emphasizes that overcompensation may be a context-dependent phenomenon.

Implications for commercially harvested populations

Numerous theoretical and empirical studies have described the effect of commercial harvest on size at maturity, a key demographic parameter regulating population biomass (Heino et al. 2002, Baskett et al. 2005, de Roos et al. 2006, Sharpe and Hendry 2009). Although Baskett et al. (2005) found increased persistence with evolutionary increases in maturation, few studies have discussed the effects of maturation plasticity. Treating age at maturity as a fixed trait may be an important shortcoming in managing exploited populations because compensatory maturation reduces both the risk of population collapse and the effects of harvest on adult abundance. As with nuisance species control, we expect these effects to be strongest when a species has high plasticity in age at maturity, experiences low rates of juvenile survivorship, and when juvenile maturation is limited by intraspecific competition (Fig. 3; Appendix A: Fig. A2). Longer time series on age at maturity across harvested populations are more commonly available, which should facilitate the application of these results to commercially important species (e.g., Atlantic cod, haddock; Fig. 1). Additionally, harvest often targets top-level consumers which in turn exert strong predation levels on lower trophic levels. For example, alewife and smelt in the Laurentian Great Lakes experience substantial mortality from intense predation by salmonine fishes (Stewart and Ibarra 1990). Therefore, plasticity-dependent maturation can affect the management of an exploited predatory species through

its effects on persistence in both the harvested population and its prey.

Changes in age at maturity in animal populations have been primarily studied to examine evolutionary effects of long-term harvest or predation (Trippel 1995, Law 2000, Kuparinen and Merilä 2007, Hutchings and Fraser 2008). However, by comparison with evolutionary increases in maturation rates, density-dependent maturation is likely to confer much more rapid increases in persistence that promote population abundance, particularly under variable survival rates. By allowing faster recovery from low densities, maturation rate plasticity may be particularly important in promoting persistence among species with low survival when predator abundance—and therefore predation intensity—is variable. Such conditions typically arise when predator densities vary in response to fluctuating environmental conditions. Examples of this include anoxia-driven mortality of predatory fish (Rao et al. 2014) and inter-seasonal variability in local predator abundance due to migration or patch extinctions (Tiitsaar et al. 2013). Survival variability in such situations highlights the need for a better understanding of the drivers and extent of maturation plasticity in managed populations.

Increases in maturation rates through density dependence have a much smaller effect on the persistence of populations with high survival rates than in shorter-lived species (Fig. 3, Table 1). This is especially relevant to the conservation of long-lived species which also have low tolerance to exploitation (i.e., small h_c) due to low rates of per capita recruitment. In these cases, early maturation confers little advantage because juvenile mortality is low and recruitment, rather than maturation, predominantly limits population growth rate. For example, although long-term increases in maturation rates of the spiny dogfish are a hypothesized result of intense harvest (Taylor and Gallucci 2009), its probability of persistence is unlikely to have changed substantially. Another management concern is that plasticity in maturation rates could result primarily from changes in size at maturity rather than variable growth rates. As fecundity and/or parental care are often associated with adult size (Stearns and Koella 1986, Murawski et al. 2001), declines in per capita

recruitment under intense harvest may reduce persistence even when maturation rates increase (Appendix C: Fig. C1). This emphasizes that increased maturation rates in a population may not always be associated with increased population persistence. Other modifications of the model used here may benefit population management by explicitly considering juvenile age structure to examine population instability arising from fluctuating densities and density-dependent maturation, or by quantifying the importance of maturation rate plasticity on persistence in variable environments.

Conclusions

We showed that increased rates of maturation in response to harvest can dampen or eliminate overcompensatory responses to harvest in species with high survival rates when maturation rates are limited by adult abundance. Nevertheless, we advise removal efforts to avoid exclusively targeting the stage(s) inhibiting recruitment, which typically encompasses mature individuals that are most vulnerable to removal (Zipkin et al. 2008). Identifying the extent to which maturation rates are density-dependent (e.g., m_{\max}) is also important in determining the effect of harvest on adult abundance and the persistence of populations with high juvenile mortality. Given these results and the frequency with which populations demonstrate substantial plasticity in maturation rates, we suggest that models incorporate maturation as a dynamic trait rather than a fixed parameter to better inform management. Overall, compensatory maturation rates can greatly increase the persistence of nuisance or invasive species in control or eradication efforts, and at the same time may in some cases facilitate management efforts designed to sustain economically and/or ecologically important populations.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–C and the Supplement are available online: <http://dx.doi.org/10.1890/ES14-00513.1.sm>