The Effects of Selective Harvest on Japanese Spanish Mackerel (*Scomberomorus niphonius*) Phenotypic Evolution

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Japanese Spanish mackerel (*Scomberomorus niphonius*) is an important fish species in the China Seas with wide distribution, extensive migration, and high economic value. This species has been yielding high fisheries production despite experiencing continuously high fishing pressure and the conversion from gillnet to trawl harvesting. Meanwhile, changes in life-history traits have been observed, including earlier maturation and smaller size at age. Here, we build an individual-based eco-genetic model parameterized for Japanese Spanish mackerel to investigate the population's response to different fishing scenarios (fishing by trawl or by gillnet). The model allows evolution of life-history processes including maturation, reproduction and growth. It also incorporates environmental variability, phenotypic plasticity, and density-dependent feedbacks. Our results show that different gear types can result in different responses of life-history traits and altered population dynamics. The population harvested by gillnet shows weaker response to fishing than that by trawl. When fishing ceases, gillnet-harvested population can recover to the pre-harvest level more easily than that harvested by trawl. The different responses of population growth rate and evolution to different fishing gears demonstrated in this study shed light on the sustainable management and utilization of Japanese Spanish mackerel in the over-exploited China Seas.

Keywords: fisheries-induced evolution, eco-genetic model, gear selectivity, life history traits, fisheries management

INTRODUCTION

Fishing is recognized as a potential evolutionary force, described as a "large-scale size-selective experiment on life-history evolution" (Rijnsdorp, 1993; Stokes and Law, 2000). Usually, commercial fisheries harvest large-sized individuals, because fisheries management regulations are enacted to protect small individuals and larger-sized individuals tend to have higher economic values (Holland and Sutinen, 1999; Salas et al., 2004; Andersen et al., 2012). Consequently, smaller-sized individuals survive better from selective harvest, and earlier-matured individuals are more likely to reproduce. When these affected traits possess genetic variability, the resultant harvest selection will alter the population's gene frequencies. Conclusive evidence for adaptive evolution has been

obtained through controlled experiments [reviewed by Conover and Baumann (2009); Díaz Pauli and Heino (2014)]. Controlled experiments show that the removal of larger individuals from a population leads to changes in phenotypic traits, typically leading to reduced body size and smaller size at maturation (Edley and Law, 1988; Conover and Munch, 2002; van Wijk et al., 2013). In the wild, evidence for FIE is less conclusive because it can be difficult to disentangle fisheries-induced evolution (FIE) from phenotypically plastic or demographic changes (Ricker, 1981; Rijnsdorp, 1993; Heino and Dieckmann, 2008; Heino et al., 2015). FIE experiments in the laboratory also revealed dramatic shifts in allele frequencies, loss of genetic diversity, and increases in linkage disequilibrium at specific locations in the genome (van Wijk et al., 2013; Uusi-Heikkilä et al., 2017; Therkildsen et al., 2019). However, the magnitude and frequency of FIE may be quite small in the wild (Andersen and Brander, 2009). A recent study analyzed genome-wide data obtained from two exploited Atlantic cod populations and found little evidence of rapid evolution (Pinsky et al., 2021).

In order to understand the mechanisms of FIE and guide empirical work, eco-genetic models have emerged as indispensable tools. Eco-genetic models permit the incorporation of salient genetic detail such as a population's genetic variances and covariances and the corresponding heritabilities, as well as the probabilistic inheritance and phenotypic expression of quantitative traits (Dunlop et al., 2009a). Eco-genetic models integrate principles of life-history and quantitative genetics theories to account for life-history and genetic variability and have been used to explore the eco-evolutionary consequences of harvesting on fish populations (e.g., Baskett et al., 2005; Marty et al., 2015; Mollet et al., 2016). Such eco-genetic models focus on the evolution of life-history traits, their correlation structure, bioeconomic consequences, and the effects of different exploitation strategies. These models have generated insights into the influence of FIE on populations (Dunlop et al., 2009b, 2015; Enberg et al., 2009; Marty et al., 2015), differences in selection pressures caused by different gear types (Jørgensen et al., 2009), and the bioeconomic consequences of FIE (Eikeset et al., 2013; Zimmermann and Jørgensen, 2015). These insights provide guidance to managers to help mitigate adverse effects of FIE and achieve the sustainable management of fisheries resources (Dunlop et al., 2009a; Jørgensen et al., 2009; Heino et al., 2013; Laugen et al., 2014; Mollet et al., 2016).

Theoretical modeling affirms that decreasing fishing mortality can weaken the evolutionary response to harvest (Law and Grey, 1989; Ernande et al., 2004; Marty et al., 2015; Kuparinen et al., 2016). But reducing fishing effort in a fishery is generally known to be difficult (Hilborn and Walters, 1992), considering its short-term social and economic effects, which makes managing fishing gear and their size-selectivity an attractive alternative avenue (Law, 2000; Jørgensen et al., 2009; Zimmermann and Jørgensen, 2017). The selectivity of fishing gears is determined by gear type (Watson et al., 2006) and properties of individual gear, such as mesh size (Hamley, 1975). Trawls, seines and stow nets with sigmoid size-selectivity curves target big individuals. Gillnets with bell-shaped selectivity curve exclude fish below or above a target size range. The difference of selection landscape between sigmoid and bell-shaped selectivity curves causes different responses of life-history traits to fishing (Jørgensen et al., 2009; Mollet et al., 2016; Zimmermann and Jørgensen, 2017).

Japanese Spanish mackerel is an epipelagic, neritic species, widely distributed throughout the subtropical and temperate waters of the western North Pacific and playing an important role in the commercial fisheries of China. Since the 1950s, Japanese Spanish mackerel has been extensively exploited; however, its catch has shown an increasing trend, maintaining above 4×10^5 t in recent years (Ministry of Agriculture and Rural Affairs, 1998–2020). Japanese Spanish mackerel was mainly exploited by gillnets from the 1950s to 1970s. Since then, the catch proportion harvested by gillnets has declined, and trawl has become the main harvesting gear (Qiu et al., 2009). The sustained high catch of Japanese Spanish mackerel under continuous fishing pressure by trawl fisheries is contrary to the common pattern that commercial fish populations tend to decline after an extended period of fishing pressure (Law, 2000; Hutchings, 2005). At the same time, the population characteristics of Japanese Spanish mackerel have changed, including age structure dominated by 1- and 2-year-old individuals, earlier maturation, and prolonged spawning season (Qiu and Ye, 1996; Mu et al., 2018). So it will be worth studying the influence of different gear types on the evolution of life-history traits, the effects of life-history evolution on population characteristics, and the possibility of reversing evolution by managing fishing gear and its size-selectivity.

Here, we constructed an individual-based eco-genetic model (Dunlop et al., 2009b) parameterized for Japanese Spanish mackerel in the China Seas and investigated two contrasting scenarios—evolutionary and non-evolutionary—in order to assess the consequences of genetic trait evolution under exploitation with different gears. Specifically, by comparing the evolutionary and non-evolutionary scenarios during the exploitation phase as well as the subsequent moratorium period, we can address the role of FIE in population dynamics under different fishing gear types. The main objectives of this study are to (a) explore the role of evolution during population exploitation and moratorium phases, (b) identify the influence of different gear types and levels of fishing mortality on the adaptive evolution, and the response of genetic traits to trawl- and gillnet-harvesting, and (c) provide guidance to mitigate the adverse effects of FIE.

MODEL DESCRIPTION

We constructed an individual-based eco-genetic model to study the influence of selective harvest on evolution of life-history traits for Japanese Spanish mackerel. The model combines the quantitative genetics of evolving life-history traits with individual-level ecological processes of growth, survival and reproduction, as well as with population-level ecological processes such as density dependence and environmental variability.

In our model, each individual is characterized by five traits, which affect its life history through growth rate, maturation schedule, and reproductive investment. The expression of these

genetic traits can be influenced by environmental variation. Eventually, the phenotypic traits are determined by the value of genetic traits and environmental variation together. The individuals grow, mature, reproduce, and die from natural or fishing mortality. When many such interacting individuals share a common ecological environment, population dynamics emerge. The factors affecting population dynamics are present as density dependence and environmental stochastic fluctuations, which act on recruitment and growth conditions. In this competitive and stochastic environment, some genetic traits improve an individual's chances to survive and produce offspring more than others and are therefore more likely to be transmitted to future generations.

Genetic Traits and Their Expression

Each individual i in year t possesses five inherited quantitative genetic traits: juvenile growth rate $g(i, t)$, growth investment at maturation onset $\alpha(i, t)$, rate of decay in post-maturation growth investment $\chi(i, t)$, intercept $\gamma(i, t)$, and slope $s(i, t)$ of probabilistic maturation reaction norm (PMRN; Heino et al., 2002; Dieckmann and Heino, 2007). The genetic trait $g(i, t)$ affects its resource acquisition, while $\alpha(i, t)$ and $\chi(i, t)$ determine the trade-off between somatic growth and reproductive investment. The genetic traits $\gamma(i, t)$ and $s(i, t)$ specify an individual's maturation schedule through the PMRN intercept γ and slope s.

Given that the actual distribution of genetic variation among our five inherited quantitative genetic traits is unknown for Japanese Spanish mackerel, we assumed the same coefficient of genetic variation ($CV_G = 12\%$) for all evolving traits. CV_G is given by,

$$CV_G = 100 \sqrt{\sigma_G^2}/\bar{T} \tag{1a}$$

Where σ_G^2 is the genetic variance of the initial population, and $\bar{T}$ is the mean value of genetic trait.

All initial individuals are assigned with trait values from a normal distribution with a mean equal to the population-level genetic value and a coefficient of genetic variation of 12%. Offspring inherit the genetic traits of their parents from a normal distribution with mean equal to the mid-parental value and variance σ_o^2; the latter is assumed to held constant through time at half the genetic variance σ_G^2 of the initial population, i.e., $\sigma_o^2 = 0.5\sigma_G^2$ (Dunlop et al., 2009b). The phenotypic variance σ_P^2 of genetic traits was determined by assuming that individual-level phenotypic can be described by a Gaussian distribution with a mean equal to the individual's genetic trait value and a constant environmental variance σ_E^2, with the latter calculated by assuming a conservative heritability h^2 of 0.2 in the initial population; thus $\sigma_P^2 = \sigma_G^2 + \sigma_E^2$. The relationship among σ_E^2, σ_G^2, and h^2 is given by,

$$\sigma_E^2 = \sigma_G^2(h^{-2} - 1) \tag{1b}$$

Besides expression noise, population-level density dependence also can affect the juvenile growth rate $g(i, t)$,

$$g(i, t) = \frac{g(i)}{1 + \rho B(t)} \tag{1c}$$

Where $B(t)$ is the population biomass in year t and ρ is the strength of density dependence in growth.

Life-History Processes

In addition to the five genetic traits $[g(i, t), \alpha(i, t), \chi(i, t), \gamma(i, t), s(i, t)]$, an individual i in year t is also characterized by its phenotypic life-history traits including age $a(i, t)$, length $l(i, t)$, age at maturation $a_m(i)$, and fecundity $Q(i, t)$. All these life-history traits determine the life-history processes including somatic and gonadic growth, maturation, reproduction and mortality.

Energy Allocation to Somatic and Gonadic Growth

Energy allocation between growth and reproduction is described following the biphasic seasonal growth model (Quince et al., 2008). Before maturation, an individual allocates all net energy, which is assumed to scale with its somatic weight $w(i, t)$ as $w^\beta(i, t)$, where β denotes the allometric exponent, to somatic growth. For adults, net energy is allocated between somatic and gonadic growth after a fraction $p(i, t)$ of the productive season and $p(i, t)$ is given by,

$$p(i, t) = \begin{cases} 1 & \text{for } a(i, t) < a_m(i, t) \\ \alpha(i) \, \chi(i)^{a(i,t)-(a_m(i)+1)} & \text{for } a(i, t) \geq a_m(i, t) \end{cases} \tag{2a}$$

Where $\alpha(i)$ gives the proportion of the growing season in the first adult year that is devoted to somatic growth, and $\chi(i)$ measures the annual decrease of this proportion in the adult stage. Both parameters range from 0 to 1 (Quince et al., 2008). This is consistent with von Bertalanffy adult growth.

We assume an allometric exponent β of 2/3 (Kozlowski and Wiegert, 1986; Kozłowski and Wiegert, 1987; Lester et al., 2004) and relationship between somatic weight and body length of $w = \Omega l^3$. An individual length-at-age trajectory is given by,

$$l(i, t) = l(i, t - 1) + p(i, t) g(i, t) \tag{2b}$$

Before maturation, the gonad weight equals 0. After maturation, it is a function of body length at the end of each productive season,

$$G(i, t) = 3\gamma\Omega l^2(i, t)(1 - p(i, t)) g(i, t) \tag{2c}$$

Where γ is the ratio of the wet-weight energy density of somatic tissue to gonad tissue.

Maturation

We model the maturation process using the PMRNs (Heino et al., 2002; Dieckmann and Heino, 2007). The probability that an immature individual matures in a given year probabilistically depends on its age and size. We assume a linear PMRN with a constant width. The PMRN is thus determined by its intercept γ and slope s. The maturation probability is then given by the logistic equation:

$$m(i, t) = \frac{1}{1 + \exp(-\frac{l(i,t)-l_{p50}(i,t)}{\delta})} \tag{3a}$$

Where $l(i, t)$ is the length of individual i in year t, and $l_{p50}(i, t)$ defines the reaction-norm midpoints, i.e., the body length at which the probability of maturing reaches 50%, calculated as $l_{p50}(i, t) = y(i) + s(i) a(i, t)$. The parameter δ is determined by the PMRN envelope width w,

$$\delta = \frac{w}{logit(p_{up}) - logit(p_{low})} \qquad (3b)$$

With $logit(p) = \ln\left(\frac{p}{1-P}\right)$, where p_{up} and p_{low} specify the lower and upper probability bounds, respectively, chosen for defining the PMRN width (in our model, we chose quartiles $p_{up} = 0.25$ and $p_{low} = 0.75$).

We use a stochastic process of Bernoulli trials to model an individual maturation process. If a number randomly drawn from a uniform distribution between 0 and 1 is smaller than $m(i, t)$, maturation takes place.

Reproduction

An individual's fecundity is defined by dividing its gonad weight by an egg weight, $Q(i, t) = G(i, t)/w_{egg}$. The total number of newborns in each year, N_0, is density-dependent and determined by a Beverton–Holt recruitment function (Beverton and Holt, 1957) that depends on the total fecundity $\sum_i Q(i, t)$ of the population.

$$N_0(t) = \frac{\eta_1 \sum_i Q(i, t)}{1 + \eta_2 \sum_i Q(i, t)} e^{-\varepsilon_R(t)} \qquad (4)$$

Here, $e^{-\varepsilon_R(t)}$ describes population-level inter-annual environmental variability in recruitment modeled as a lognormal process, where $\varepsilon_R(t)$ is normally distributed, which represents the influence of environmental fluctuations (e.g., temperature or larval food supply) on recruitment. The parameter η_1 specifies the survival of recruits when total fecundity is low, while η_2 measures the strength of density dependence; the asymptotic number of recruits at high total fecundity is given by η_1/η_2 (Quinn and Deriso, 1999).

The female parent of newborns is selected in proportion to female gonad size through a stochastic process of Bernoulli trials. Firstly, we determine the female which has the largest gonad weight. And then, a number is drawn randomly from a uniform distribution between 0 and this maximal gonad weigh. If this number is less than the gonad weight of the drawn individual, this individual will be selected as female parent. The other parent will be selected randomly from amongst the mature males. Eventually, all newborns will be assigned two parents through the random draws. Therefore, an individual having higher fecundity will, on average, produce more offspring (Marty et al., 2015).

For each female in the population, the model records the number of offspring that survive to reach maturity. Then we calculate the average number of offspring that reach maturity for each cohort R_0, which represents the average lifetime reproductive output of females in a cohort. For each cohort we calculate the population growth rate per unit time as $r \approx \frac{\ln[R_0]}{G}$, where G is the generation time, estimated by the mean age at maturation for the cohort (Kuparinen and Hutchings, 2012; Dunlop et al., 2015).

Natural and Fishing Mortality

Natural mortality consists of three components: (i) size-independent mortality d_0 originating from diseases, senescence, parasites or any stochastic source of mortality; (ii) size-dependent predation mortality d_s that decreases with the increase in body size according to,

$$d_s(i, t) = c_s \exp\left(-\frac{l(i, t)}{l_s}\right) \qquad (5a)$$

Where c_s denotes the (hypothetical) maximum instantaneous predation mortality rate at size zero and l_s is the size at which the predation mortality is decreased by the factor $1/e$; and (iii) a growth-dependent mortality,

$$d_g(i, t) = c_g \exp\left(\frac{g(i, t)}{g_0}\right) \qquad (5b)$$

With c_g denoting the minimum instantaneous growth-dependent mortality rate and g_0 the growth rate at which the growth-dependent mortality is increased by factor e. Growth-dependent mortality accounts for the trade-off between growth and survival. Faster growth is achieved at the cost of less energy being available for maintenance (Ernande et al., 2004) and/or a higher exposure to predation (Abrams, 1991; Werner and Anholt, 1993; Walters and Korman, 1999) through more active foraging.

In addition to the natural mortality components, individuals may also experience fishing mortality at an instantaneous rate H. Fishing is size-selective with gillnet-like or trawl-like fishing selectivity curves (**Figure 1**). Gillnet-like selectivity curve k_G is defined as:

$$k_{G,t}(a, m) = e^{-\left(\frac{l(a,m) - L_{max}}{2 \cdot (s_\gamma \cdot L_{max})^2}\right)^2} \qquad (6a)$$

Where L_{max} specifies the size at which the selectivity curve peaks and fish become fully vulnerable to fishing. To increase comparability, we introduce a modified trawl-like selectivity curve k_T by replacing the descending leg of the curve by a constant equal to the maximum selectivity:

$$k_{T,t}(a, m) = \begin{cases} k_{G,t}(a, m), & L_t(a, m) < L_{max} \\ 1, & L_t(a, m) \geq L_{max} \end{cases} \qquad (6b)$$

The instantaneous fishing mortality rate is determined by this selectivity $0 < k \leq 1$ and the maximum instantaneous harvest rate H,

$$d_F(i, t) = k(a, m) \cdot H \qquad (6c)$$

The total instantaneous mortality rate is then given by,

$$Z(i, t) = d_0 + d_s(i, t) + d_g(i, t) + d_F(i, t) \qquad (7)$$

The resultant individual-specific annual probability of dying is $D(i, t) = 1 - \exp(-Z(i, t) \cdot 1 \text{ year})$, which again is realized through Bernoulli trials.
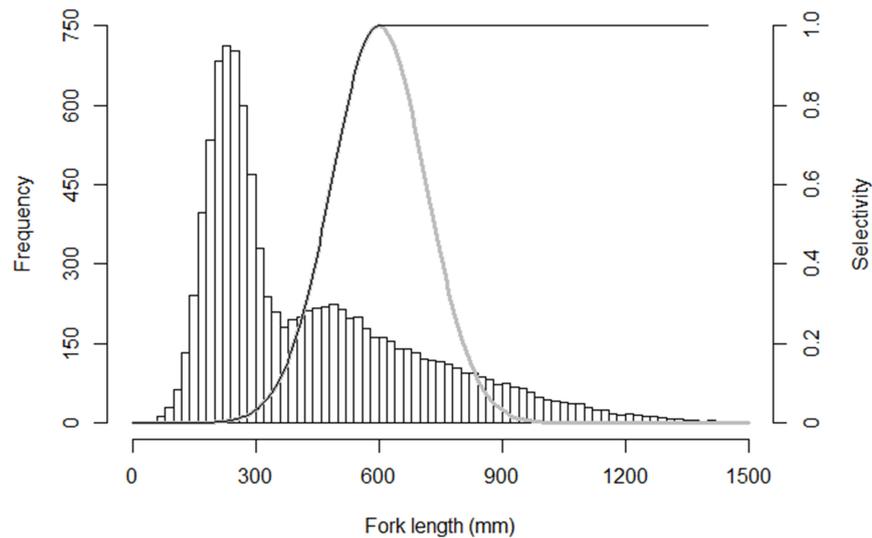
FIGURE 1 | Fork length distribution of Japanese Spanish mackerel populations and size-selectivity curves used to impose selection on Japanese Spanish mackerel life histories. At maximum selectivity, fish of that size are harvested at the rate specified by the parameter H. The bell-shaped size-selectivity curve is for gillnet. The peak of the Gaussian function is at 600 mm. In each case the standard deviation is 1.5% of the mean. Sigmoid trawl selectivity was modeled based on the same probability distribution as for gillnet, maximum selectivity for all fish with lengths larger than that at the peak selectivity.

Model Parameterization and Model Runs

We model a Japanese Spanish mackerel population with parameters taken from the historical survey data. Whereas some parameters are unknown or cannot be estimated from available data, we assume these values to ensure that the emergent model properties qualitatively and quantitatively resemble the natural patterns (Grimm et al., 2005). To do so, we first run our model to reach an equilibrium with likely parameter values and compare the output with data available. Parameters were adjusted until the modeled patterns (e.g., growth curves, age and size distributions, and fecundity) resemble the real patterns observed for Japanese Spanish mackerel, and all parameters are shown in **Table 1**.

After running for 5,000 years without harvesting, the population approaches a demographic and evolutionary equilibrium, that is, all genetic traits and the correlations among them have converged close to an evolutionarily stable strategy. We display all results from this time onward. Model is then run without fishing for 100 extra years. Harvesting then starts and lasts another 100 years, followed by a 100 years' moratorium. All results presented are averages of 30 replicate models runs, carried out with different random seeds.

Evolutionary and Non-evolutionary Model

Given the unknown evolvability of the evolving traits in Japanese Spanish mackerel population, following Houle (1992) and Dunlop et al. (2009b), we set the CV_G at either 0% (i.e., purely ecological dynamics with no evolution) or 12% (i.e., with a high evolvability), respectively, to construct the non-evolutionary and evolutionary scenarios. The comparison between the non-evolutionary and evolutionary scenarios can help understand the influence of gear types on life-history

evolution qualitatively, and the role of evolution in population exploitation and recovery phase.

RESULTS

Dynamics of Population Biomass and Population Traits in Evolutionary and Non-evolutionary Scenarios

The response of population biomass to fishing is determined by harvest patterns and evolutionary assumptions (**Figure 2**). With the trawl-harvesting, increasing fishing intensity magnifies the evolutionary response of population biomass, which can be seen by comparing time series of total biomass for the evolving population with its hypothetical non-evolving counterpart (**Figures 2A,C,E**). When fishing begins, biomass of evolving population declines dramatically at the early phase of harvest, and then rebounds; this rebound is more obvious at high fishing pressure (**Figure 2E**). When fishing ceases, biomass of evolving population increases rapidly at the early phase of moratorium, but then the pace of recovery slows down and the biomass does not recover to the pre-harvest level during a 100-year moratorium. In contrast, biomass of non-evolving population does not rebound during the fishing period, but it quickly recovers to the pre-harvest level during the moratorium.

Compared to trawl fishing, populations exposed to gillnet fishing show weaker but qualitatively similar biomass responses to fishing and its termination (**Figures 2B,D,F**). The responses are weaker also when evolution is allowed. Importantly, however, the biomasses of the evolving populations do not systematically differ from their hypothetical non-evolving counterparts (**Figures 2B,D,F**). In other words, there is no

TABLE 1 | Model parameters.

Parameter group	Description	Value	Symbol	Unit	Equations	Source
Genetics	Heritability	0.2	h^2	–	1b	(1)
	Coefficient of genetic variation	0.12	CV_G	–	1a	(1)
Evolving traits	Growth rate	400	$g(i)$	mm year^{-1}	1a, 1c, 2b, 2c, 5b	(2)
	Growth investment at maturation onset	0.6	$\alpha(i)$	–	1a, 2a	(3)
	Rate of decay in post-maturation growth investment	0.6	$\chi(i)$	–	1a, 2a	(3)
	PMRN intercept	600	$y(i)$	mm	1a	(3)
	PMRN slope	10	$s(i)$	mm year^{-1}	1a	(3)
Growth	Strength of density dependence in growth	1×10^{-7}	ρ	g^{-1}	1c	(3)
	Production exponent	2/3	β	–		(3)
	Constant in allometric weight-length relationship	2×10^{-5}	Ω	g mm^{-3}	2c	(4)
	Initial length	4.5	l_0	mm		(2)
Maturation	PMRN envelope width	200	ω	mm	3b	(3)
	Lower bound of PMRN envelope	0.25	p_{up}	–	3b	(5)
	Upper bound of PMRN envelope	0.75	p_{low}	–	3b	(5)
Reproduction	Ratio of somatic to gonadic wet-weight energy densities	0.62	γ	–		(6)
	Weight of an egg	4×10^{-3}	W_{egg}	g		(6)
	Maximum survival probability of recruits	3×10^{-4}	η_1	–	4	(7)
	Strength of density dependence in recruitment	5×10^{-9}	η_2	–	4	(7)
	Noise coefficient of recruitment	1 (0.1)	$\varepsilon_R(t)$	–	4	(8)
Natural mortality	Size-independent instantaneous natural mortality rate	0.3	d_0	year^{-1}	7	(9)
	Maximum instantaneous predation mortality rate	0.6	c_s	year^{-1}	5a	(9)
	Scaling factor of predation mortality rate	200	l_s	mm	5a	(9)
	Minimum instantaneous growth-dependent mortality rate	0.02	c_g	year^{-1}	5b	(9)
	Scaling factor of growth-dependent mortality rate	200	g_0	mm year^{-1}	5b	(9)
Fishing mortality	Gillnet selectivity parameter	0.015	s_y	–	6a	(2)
	Length at which the selectivity curve peaks	600	L_{max}	mm	6b	(2)
	Maximum instantaneous harvest rate	[0.2, 0.8]	H	year^{-1}	6c	

–, dimensionless parameters.
(1) within the range reported by Gjedrem (1983); Mousseau and Roff (1987), Houle (1992), and Carlson and Seamons (2008); (2) values taken from You et al. (2014) and slightly modified when necessary; (3) values chosen such that the life-history characteristics resemble those of Japanese Spanish mackerel (e.g., Liu et al., 1982; Qiu and Ye, 1996; Mu et al., 2018); (4) values obtained from http://www.fishbase.org; (5) definition of PMRN width based on quartiles; (6) set such that individual fecundity is in the range reported by Qiu and Ye (1994, 1996); (7) set to create a population of large yet computationally manageable size (ca. 10,000–12,000 individuals) in which recruitment is roughly one half of the asymptotic level η_1/η_2; (8) values taken from Marty et al. (2015); (9) total natural mortality within the range reported by Chen et al. (2018).
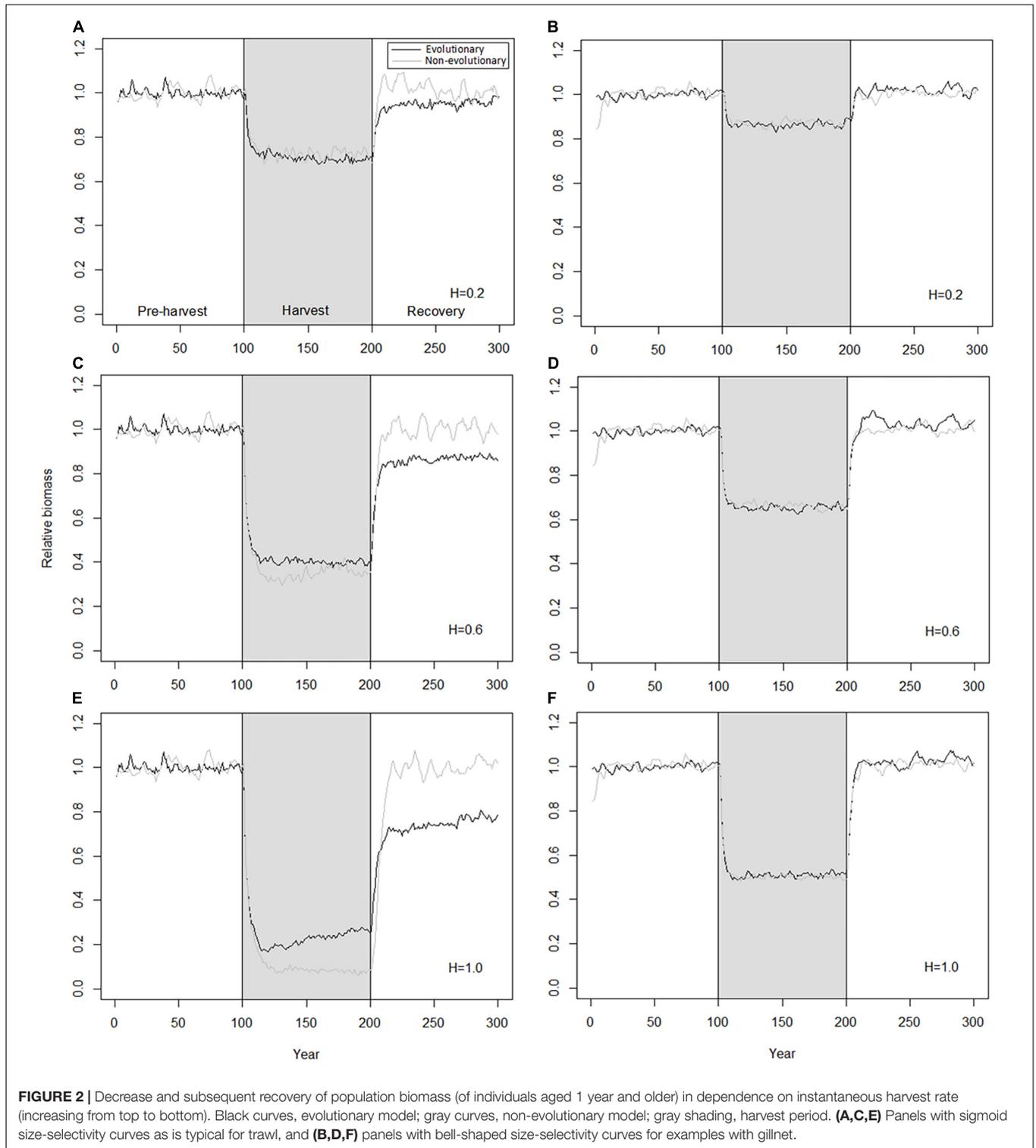
rebound during the fishing period, nor lack of recovery during the moratorium.

Parallel with changes in population biomass, also population- and individual-level phenotypic traits are changing. In absence of evolution, these changes reflect only demographic changes and equilibrate quickly to a new level after changes in fishing pressure (**Figure 3**), similarly as already seen for population biomass (**Figure 2**). Traits in evolving trawl-harvested populations show rapid initial responses similar to those seen for non-evolving populations, but also somewhat slower, sustained trait changes (**Figure 3**). These sustained changes occur during both harvest and recovery periods but are reversed and slower during the harvest period. Because of the slow change during the moratorium, population traits are not restored to their pre-harvest levels during the time horizon considered here (100 years). Notably, while the differences in traits between evolving and non-evolving populations are at their greatest in the end of the harvest period, even after 100 years of recovery, evolving populations that adapted to harvesting are characterized by earlier maturation at smaller sizes, but also by

higher productivity, higher fecundity, and higher proportion of mature individuals, compared to the pre-harvest levels or those seen in the recovered non-evolving population.

Differences in Responses to Harvest Between Trawl-Harvested and Gillnet-Harvested Populations Under the Same Maximum Fishing Mortality

When the trawl-harvested and gillnet-harvested populations are exposed to fishing with the same maximum instantaneous harvest rate (here 0.6 yr^{-1}), all genetic traits show stronger responses to trawl-harvesting than to gillnet-harvesting (**Figure 4**), with the exception of growth rate (**Figure 4E**). The difference is the starkest for the PMRN intercept, which declines by about 30% under trawl-harvest, but increases by about 5% under gillnet-harvest (**Figure 4A**). In contrast, the PMRN slope, growth investment at maturation onset, and the ratio of decay in post-maturation growth investment show less drastic declining

FIGURE 2 | Decrease and subsequent recovery of population biomass (of individuals aged 1 year and older) in dependence on instantaneous harvest rate (increasing from top to bottom). Black curves, evolutionary model; gray curves, non-evolutionary model; gray shading, harvest period. **(A,C,E)** Panels with sigmoid size-selectivity curves as is typical for trawl, and **(B,D,F)** panels with bell-shaped size-selectivity curves for examples with gillnet.

trends during the early phase of fishing (**Figures 4B–D**). Contrary to other genetic traits, growth rate increases during the fishing phase, and furthermore, does not show markedly divergent responses between the trawl-harvest and gillnet-harvest (**Figure 4E**).

Compared to the genetic traits, population traits show more consistently large harvest-induced divergence between trawl-harvested and gillnet-harvested populations (**Figure 5**). During the moratorium, because genetic changes in individual-level genetic traits are relatively modest in gillnet-harvested

FIGURE 3 | Decrease and subsequent recovery of population traits under 0.6 of instantaneous harvest rate by trawl. Black curves, evolutionary model; gray curves, non-evolutionary model; gray shading, harvest period. **(A)** Mean age at maturation; **(B)** fork length at 50% maturation; **(C)** productivity; **(D)** population size; **(E)** relative population total fecundity; **(F)** proportion of mature individuals.

populations (**Figure 4**), traits in these population are able to quickly recover near to their pre-harvest levels. In contrast, trawl-harvested populations show consistently large responses during the harvest period and only partial recovery during the moratorium (**Figure 5**). Notable exceptions to this pattern are population size and population fecundity: in trawl-harvested populations the former recovers to its preharvest level (**Figure 5D**), while the latter overshoots to a level that exceeds its pre-harvest level by about 10% (**Figure 5E**). For these same cases, the gillnet-harvested populations fail to reach a full recovery.

FIGURE 4 | Dynamics of the mean genotypic values of evolving traits before, during and after harvest. Harvest (gray shading) starts at $t = 100$ years and stop at $t = 200$ years. Dynamics are shown for two harvest patterns: $H = 0.6$ year^{-1} for trawl (solid points) and $H = 0.6$ year^{-1} for gillnet (hollow points). **(A)** PMRN intercept y; **(B)** PMRN slope s; **(C)** Growth investment α at maturation onset; **(D)** Annual ratio χ of decay in post-maturation growth investment; **(E)** Juvenile growth rate g.

The large differences in the evolutionary responses between the trawl-harvested and gillnet-harvested populations are probably largely driven by the much lower overall harvest-induced mortality in the gillnet-harvested populations than in the trawl-harvested populations: the former experience near-maximal levels of mortality only over a narrow range of sizes, whereas the latter have a prolonged exposure. To make a fairer comparison between these two fishing gear types, we conduct

below comparisons where total catch instead of maximum fishing mortality is standardized.

Differences in Responses to Harvest Between Trawl-Harvested and Gillnet-Harvested Populations Under the Same Biomass Removal

When the same amount of biomass is removed from the population, the evolutionary responses to different fishing gears again diverge (**Figure 6**), but the difference are less than under the same maximal fishing mortality (**Figure 4**). While the responses under gillnet harvesting are similar as before (catch standardization was done using gillnet catch as the baseline), responses under trawling are greatly reduced. The response is larger for trawling compared to gillnet fishery only for the PMRN intercept (**Figure 6A**) and is similar (genetic PMRN intercept, genetic annual ratio of decay in post-maturation growth investment; **Figures 6B,D**) or less (growth investment at maturation, genetic growth rate; **Figures 6C,E**). Recovery is modest, except for growth investment at maturation after trawl fishing and for genetic growth rate after gillnet fishing.

The population traits also respond differently to trawl- and gillnet-harvesting (**Figure 7**). As for the genetic traits, catch-standardization results in a weaker response than maximum fishing mortality standardization under trawl but not under gillnet fishing. Nevertheless, the effect of trawl fishing is larger than that of gillnet fishing for three population traits, mean age at maturation, length at 50% maturity, and productivity (**Figures 7A–C**). For the other three traits, the response after fishing is larger, but the differences diminish following the 100-year recovery.

Importance of the Level of Instantaneous Harvest Rate

When fishing intensity increases, the responses of genetic traits under both trawl- and gillnet-harvesting generally, but not always, increase (**Figure 8**). However, the large differences between fishing gears and between traits are evident. Among all combinations of gears and traits, the PMRN intercept shows the highest degree of response to trawl-harvesting, declining by almost 40% after 100-year harvest under the instantaneous harvest rate of 1.0 yr^{-1}. In contrast, under the same harvest rate with gillnet-harvesting, the PMRN intercept increases by about 5%. Similar pattern, but of lesser magnitude, is observed for the growth investment at maturation onset and annual ratio of decay in post-maturation growth investment; note, however, that the response for the latter is markedly non-linear. The response in the growth coefficients is qualitatively similar under both trawl- and gillnet-harvesting, although the effect is saturating for the trawl harvesting. The responses of the PMRN slope under trawl- and gillnet-harvesting show no obvious trends as the fishing intensity increases.

Compared with genetic traits, the population traits show much stronger responses to increasing harvest intensity (**Figure 9**). The absolute magnitude of the responses is always larger under trawl-harvesting than under gillnet-harvesting. Moreover, the responses are qualitatively similar between trawl- and gillnet harvesting for all but one population trait, fork length at 50% maturation, which shows responses of opposing signs. With the remarkable exception of productivity for both gears and fork length at 50% maturation for gillnet harvesting, the responses are generally negative.
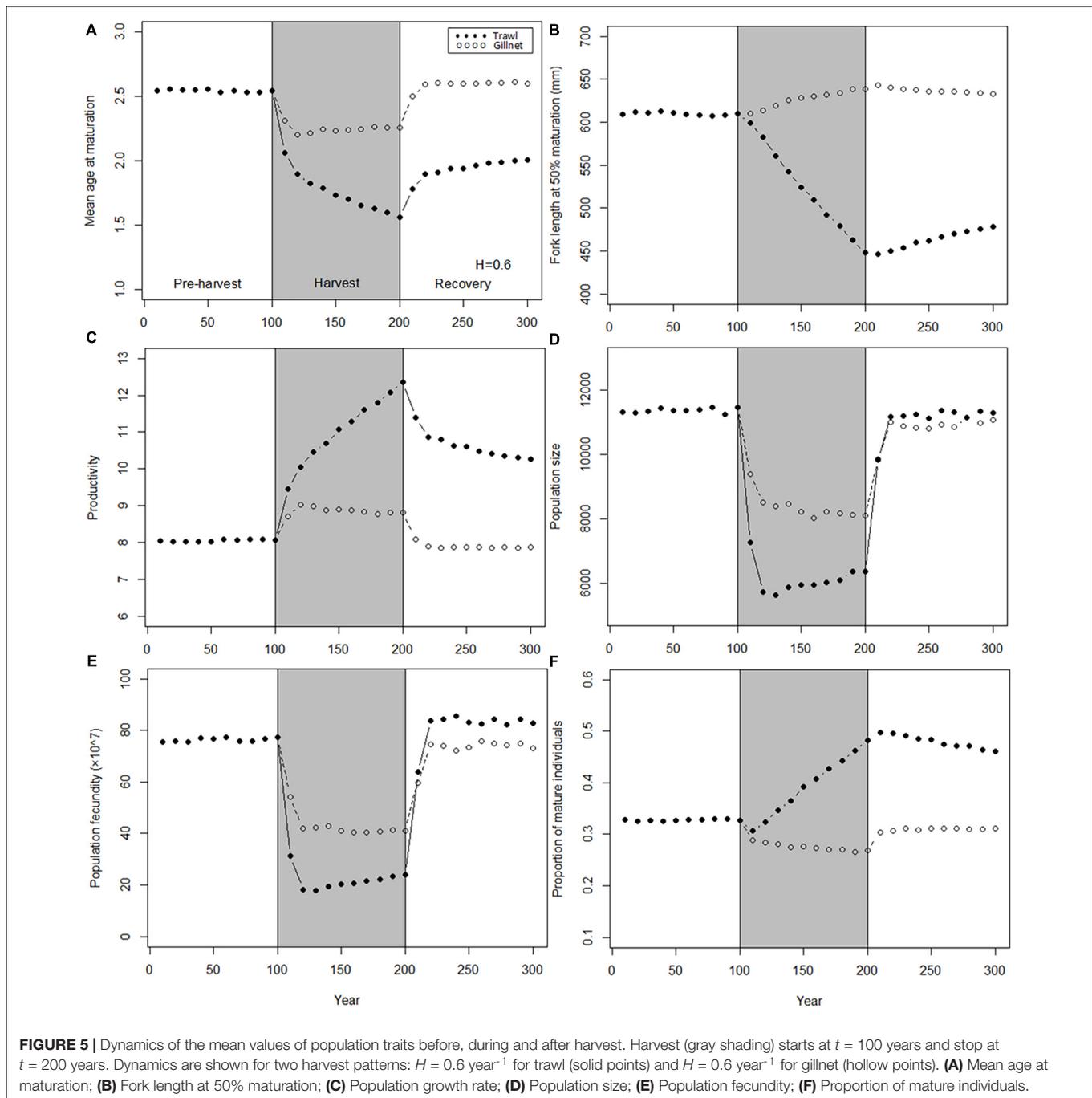
DISCUSSION

Dynamics of Fisheries-Induced Population Declines and Population Recovery Under Selective Harvest

Prior to exploitation, the population will approach a demographic and evolutionary equilibrium with stable population traits. When harvest begins, mature and large individuals are removed from the population, resulting in rapid demographic changes and subsequent changes in genetic traits that take place at slower, generational time scale. Changes in population-level characteristics reflect changes at both time scales.

When fishing is ceased, individuals that would have previously been harvested survive and influence population dynamics. This is observed as a sharp increase in biomass at the beginning of moratorium, but also as rapid changes in population traits. These effects result from the restoration of an age and size structure in which previously fished size groups are dying off at a slower rate. This demographic restoration is mainly observed in terms of very rapid initial recoveries of most of the population characteristics shown in **Figures 3**, **5**, **7**. The recovery of genetic traits occurs at a much slower and more constant rate (**Figures 4**, **6**). As the total biomass increases, also density-dependent effects begin to alter the phenotypic composition of the population by affecting individual rates of growth and reproduction until the population dynamic reaches a new demographic equilibrium.
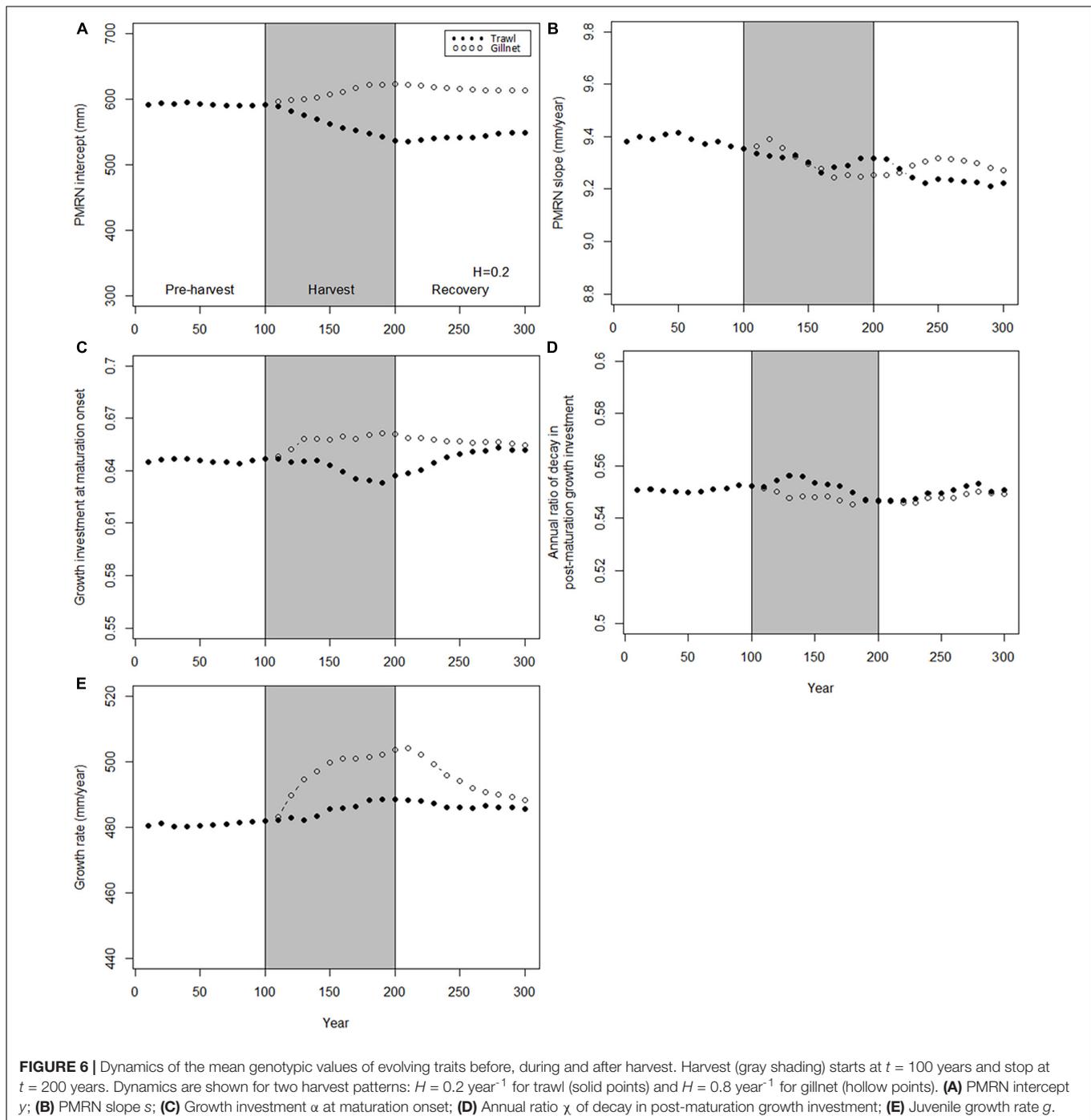
Studies have shown that FIE is not always negative for exploited population (Christie et al., 2018; Ahti et al., 2020). Especially for the populations under high fishing mortality, adaptation may allow population biomass to increase while fishing still continues at the same, high intensity (**Figure 2E**). A more extreme scenario is that of an evolutionary rescue, where a population that does not adapt (or is not adapting fast enough) would be driven to extinction, but under FIE, the population survives high fishing intensity owing to the survival of favorable genotypes (Jusufovski and Kuparinen, 2020; Kuparinen and Uusi-Heikkilä, 2020). Non-evolutionary populations collapse under high-intensity fishing pressure, while evolutionary populations can still maintain a certain biomass level under high-intensity fishing pressure (Kaitala and Getz, 1995; Heino, 1998; Dunlop et al., 2015). In this study, when the instantaneous harvest rate $H = 1.0$, the biomass of non-evolutionary population is significantly lower than that of evolutionary population, and the difference between the biomass will gradually increase with the increasing fishing pressure (**Figures 2**, **3**). At the beginning of moratorium, the biomass and population characteristics of the evolutionary population

FIGURE 5 | Dynamics of the mean values of population traits before, during and after harvest. Harvest (gray shading) starts at t = 100 years and stop at t = 200 years. Dynamics are shown for two harvest patterns: H = 0.6 year^{-1} for trawl (solid points) and H = 0.6 year^{-1} for gillnet (hollow points). **(A)** Mean age at maturation; **(B)** Fork length at 50% maturation; **(C)** Population growth rate; **(D)** Population size; **(E)** Population fecundity; **(F)** Proportion of mature individuals.

gradually decrease in the recovery phase, and cannot return to pre-harvest levels within 100 years, especially with trawl fishing. This is attributable to the earlier maturation and smaller size at age, despite fecundity and population size return back to pre-harvest levels. This difference between evolutionary and non-evolutionary population change process could be used as a reference to judge whether the population evolves under the fishing effects.

Selection can be manipulated to help populations, and is a demographic process that can alter birth and death rates,

and so it can have an immediate influence on population dynamics (Boukal et al., 2008; Hendry et al., 2011). The exploited population is directly affected by harvest selection, rather than indirectly affected through human-induced environment. Current studies have concluded that both phenotypic plasticity and genetic changes lead to the phenotypic changes observed in the population (Dieckmann and Heino, 2007; Crispo et al., 2010). When exploitation is reduced, the population may initially recover fast (Kaitala and Getz, 1995; Heino, 1998; Enberg et al., 2009). This beneficial aspect of FIE is not guaranteed though,
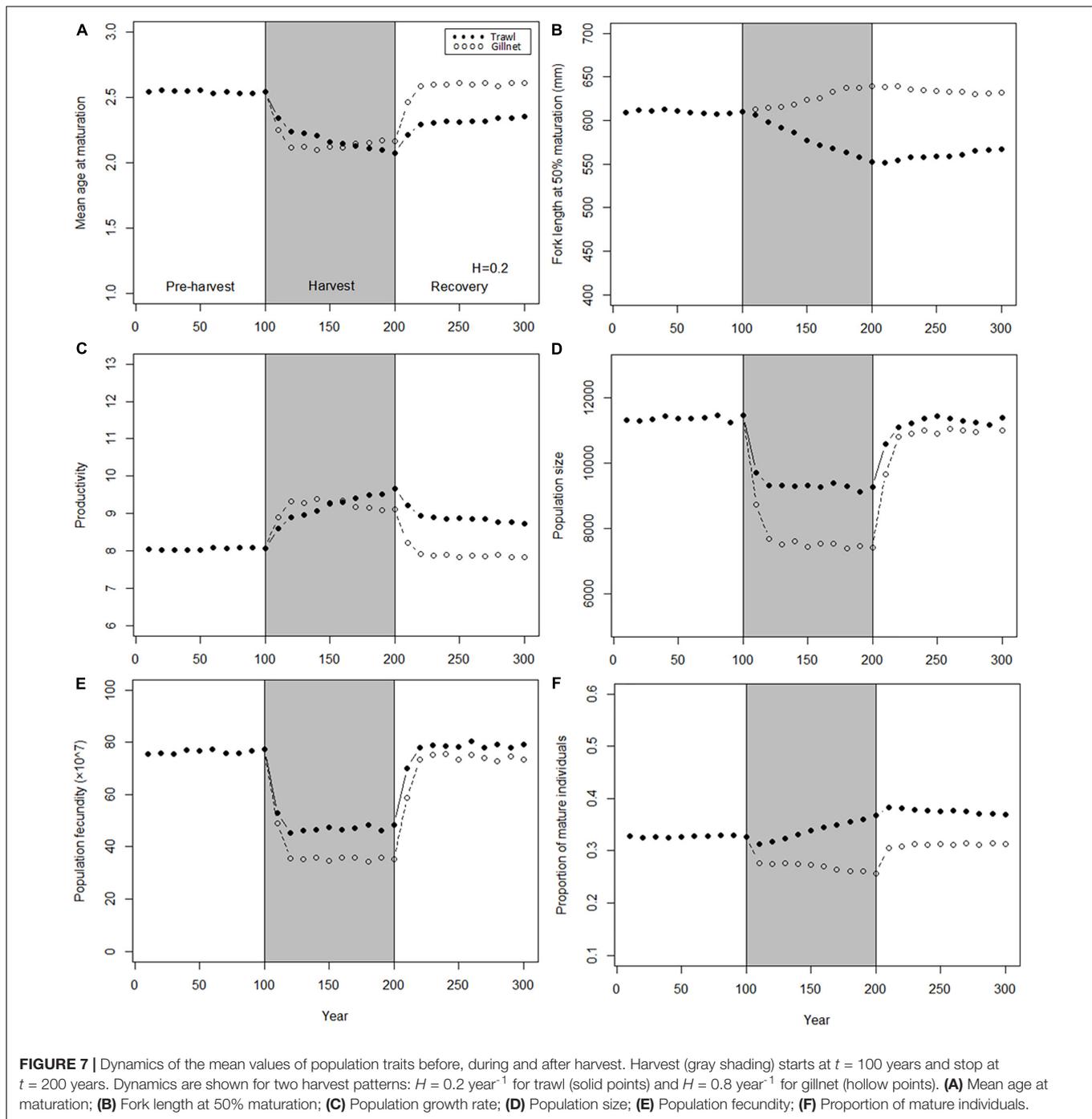
FIGURE 6 | Dynamics of the mean genotypic values of evolving traits before, during and after harvest. Harvest (gray shading) starts at $t = 100$ years and stop at $t = 200$ years. Dynamics are shown for two harvest patterns: $H = 0.2$ year^{-1} for trawl (solid points) and $H = 0.8$ year^{-1} for gillnet (hollow points). **(A)** PMRN intercept y; **(B)** PMRN slope s; **(C)** Growth investment α at maturation onset; **(D)** Annual ratio χ of decay in post-maturation growth investment; **(E)** Juvenile growth rate g.

and under 70% harvest rate adaptive evolution can lead to yellow perch (*Perca flavescens*) extinction (Dunlop et al., 2015).

Differences in Evolution Under Size-Selective Trawl- and Gillnet-Harvesting

Fishing mortality levels and gear types influence the size structure of fish stocks and the evolution of life-history traits over time. Evolutionary change occurs even if fishing mortality is low, but

the magnitude of response markedly differs between trawl and gillnet selectivity (**Figures 8**, **9**), which implies that a suitable management strategy based on gear selectivity could reduce the effect of FIE. The different response of genetic traits to fishing depends on which size group is preserved to reproduce next generation (Roff, 1992; Heino and Kaitala, 1999; Lester et al., 2004).
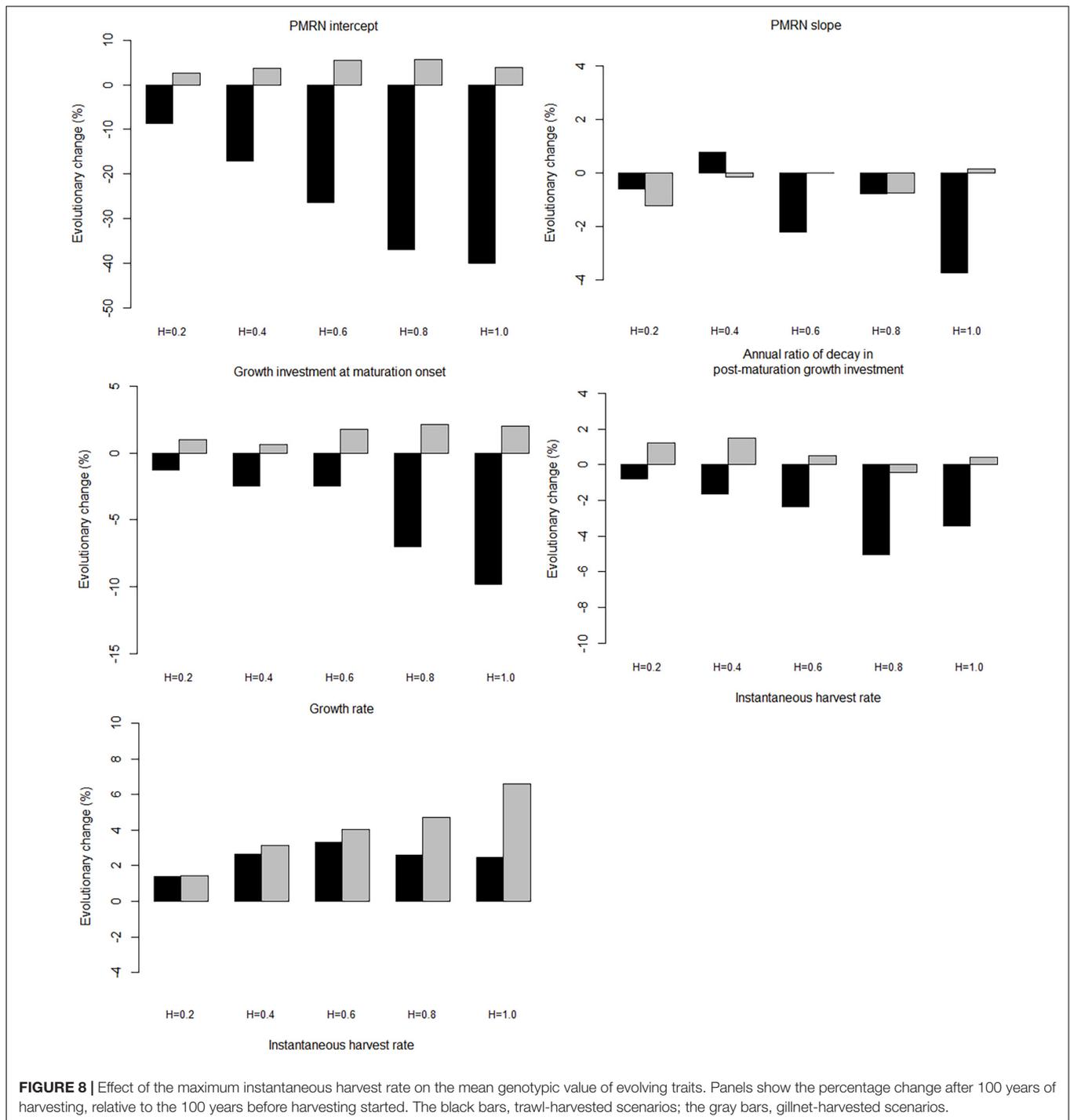
The exploited population will show different evolutionary trends to different fishing gears over decades of fishing. Under

FIGURE 7 | Dynamics of the mean values of population traits before, during and after harvest. Harvest (gray shading) starts at t = 100 years and stop at t = 200 years. Dynamics are shown for two harvest patterns: H = 0.2 year^{-1} for trawl (solid points) and H = 0.8 year^{-1} for gillnet (hollow points). **(A)** Mean age at maturation; **(B)** Fork length at 50% maturation; **(C)** Population growth rate; **(D)** Population size; **(E)** Population fecundity; **(F)** Proportion of mature individuals.

the gillnet-harvesting, individuals that manage to pass the size range vulnerable to fishing have high survival and can grow big and fecund, eventually producing high numbers of offspring that carry their parents' genetic traits. But with trawl-harvesting removing large and fecund individuals, the offspring are mainly reproduced by small-sized mature individuals.

Under trawl-harvesting, fishing induces decreased PMRN, larger genetic growth capacity, less growth investment at maturation, and slower rate of decay in post-maturation growth
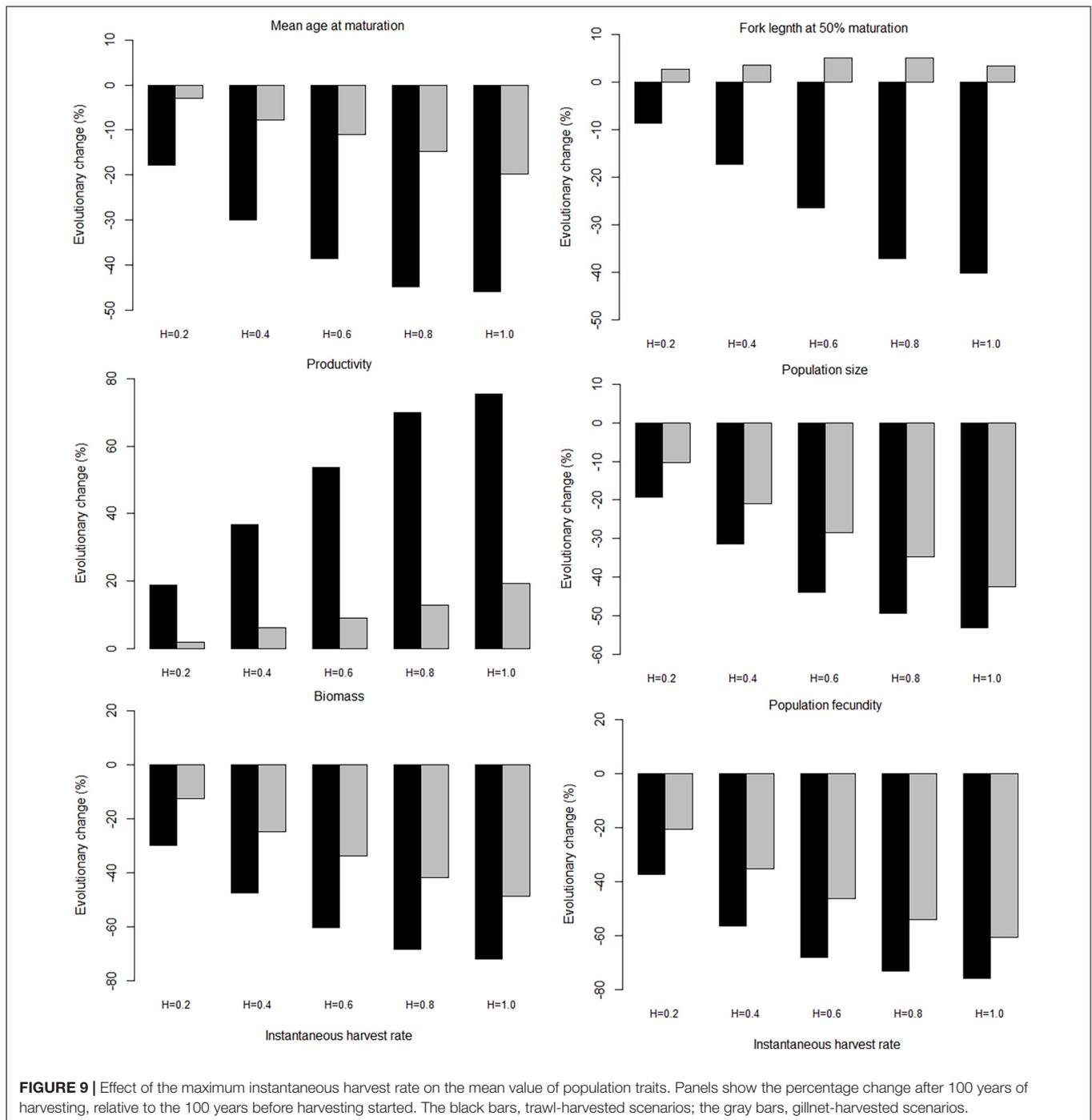
investment (**Figure 4**). The changes in these genetic traits cause the population to mature earlier, grow faster, and invest more energy into reproduction, which is consistent with the observations in Japanese Spanish mackerel fishery since the 1980s. But when the population is harvested by gillnet, PMRN intercept, growth investment at maturation, and genetic growth capacity show slightly increasing trend (**Figures 4A,C,D**), which makes the population to mature later and to grow faster by investing more energy into somatic growth. Even when the

FIGURE 8 | Effect of the maximum instantaneous harvest rate on the mean genotypic value of evolving traits. Panels show the percentage change after 100 years of harvesting, relative to the 100 years before harvesting started. The black bars, trawl-harvested scenarios; the gray bars, gillnet-harvested scenarios.

same amount of biomass is removed from the population, the population responds differently to trawl- and gillnet-harvesting (**Figures 6, 7**). The remaining individuals influence the recovery process of genetic traits and population traits. Compared with trawl-harvested population, the population traits under gillnet-harvesting recover faster to pre-harvest levels (**Figure 7**).

Furthermore, genomic analysis can complement conclusions from evolutionary modeling. The whole-genome sequence

analysis of Atlantic cod (*Gadus morhua*) suggest that phenotypic change in these populations is not constrained by irreversible loss of genomic variation, which have implications for both the model and experimental research of fisheries-induced evolution (Pinsky et al., 2021). Broadly speaking, our results agree with earlier results by Jørgensen et al. (2009) and Mollet et al. (2016) that while no exploitation is evolutionarily neutral, dome-shaped exploitation patterns can offer both high long-term yields and

FIGURE 9 | Effect of the maximum instantaneous harvest rate on the mean value of population traits. Panels show the percentage change after 100 years of harvesting, relative to the 100 years before harvesting started. The black bars, trawl-harvested scenarios; the gray bars, gillnet-harvested scenarios.

low evolutionary impact. The model by Mollet et al. (2016), albeit for a demersal fish species (North Sea plaice), is broadly similar to ours, involving similar evolving traits (apart from having a more rigid scheme for reproductive investment) and modeling approach (individual-based eco-genetic modeling). The model by Jørgensen et al. (2009) is also for a demersal fish (Northeast Arctic cod), but one with relatively rare distinction between spawner and feeder fisheries (only mature fish are caught in the former, while both immature and mature are caught in the latter). The

modeling framework is also different, involving fully flexible evolution of energy allocation between growth and reproduction but no evolution of genetic growth capacity. Note that the evolution of growth is an important part of the evolutionary response to fishing in both our model and in that by Mollet et al. (2016). The model is an optimization model that can predict long-term outcomes but no transient behaviors. Nevertheless, the model runs that are most comparable to ours, ones without spawner fishery, suggest that dome-shaped selectivity has better

chances of conserving the population's original life history than sigmoid selectivity.

Management Implications for Japanese Spanish Mackerel in Response to Evolution

An important commercial fish species in the China Seas, the annual catch of Japanese Spanish mackerel is more than 0.1 million tons (Sun, 2009). The current dominant management measures include minimum landing size limit, minimum mesh size of fishing gear, total allowable catch, "Double-control" system (the control of both the total number of marine engine-powered fishing vessels and their total engine power), and summer moratorium in China. The summer moratorium aims to protect the main spawning period of marine fish in the China Seas and stops fishing for about 4 months each year. Controlling the mesh size of fishing gear can help protect small-sized individuals such that they survive to grow and reproduce the next generation.

The life-history traits of Japanese Spanish mackerel have changed since the 1980s, including changes in age at maturation, size at age, and spawning season. As our model has shown, adaptive evolution is expected to occur under a long-term harvest, resulting in the loss of genotypic diversity and low rate of recovery for genetic traits. Therefore, there is a need to incorporate management measures that would minimize unwanted evolutionary impacts of fisheries. Our study focusses on the individual eco-genetic model of Japanese Spanish mackerel, and does not consider the processes of species interaction, and predation. In order to explore the FIE of multiple species, primary productivity and species interaction should be considered in future modeling studies. In addition, we set different instantaneous mortality to harvest, this determines the changes of harvest, which is consistent with biomass. The sensitivity analysis is performed using different mesh sizes, and the derivation of the selectivity curves of Japanese Spanish mackerel depend on the actual studies on Japanese Spanish mackerel (You et al., 2014; **Supplementary Tables 4**, **5**). The impact of fishing selectivity under varying mesh sizes on FIE would be considered in the further work.

The rate of evolution in an exploited population depends on the size groups that are removed by fishing, which are ultimately determined by the size selectivity of gears and the intensity of harvest (Therkildsen et al., 2019; Crespel et al., 2021). In order to control the negative effects of FIE, low fishing mortalities have been suggested as a general remedy (Heino, 1998; Law, 2000; Laugen et al., 2014). Our results agree with this prediction (**Figures 8**, **9**). Meanwhile, our results also suggest that changing converting exploitation pattern from sigmoid to bell-shaped selectivity, by allowing large and fecund

individuals to survive and reproduce, could be an alternative avenue to reduce the evolutionary responses to fishing. Japanese Spanish mackerel have experienced heavy exploitation and showed an obvious evolutionary shift. Therefore, limiting the exploitation intensity and controlling fishing gear could weaken or even reverse the evolutionary trend. In particular, harvesting the population with gillnets could reduce the evolutionary response to fishing and promote a more sustainable utilization of fisheries resources. When gillnet harvesting is used to extract similar yields as trawling, it appears less evolutionarily benign than comparisons using similar maximum exploitation rates. Moreover, evolutionary and plastic responses to harvest are affected by more complex processes than those considered in any single-species model, such as the one considered here. Fishing affects the dynamics of target populations, changes interspecific processes, such as predation-prey interactions, and alters natural mortality rates (Law, 2000; Heino and Godø, 2002; Pope et al., 2021). So, an ecosystem approach is required to explore this kind of complex dynamics (Blanchard et al., 2005; Jørgensen and Fiksen, 2006).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

PS designed and conducted the model structure. YS and RS conducted the model building and data analysis. PS, YT, and MH wrote and edited the manuscript, while all other authors have reviewed and revised it. All authors have given final approval of the manuscript.

FUNDING

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.844693/full#supplementary-material

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