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Are there plenty of fish in the sea? How life history traits affect the eco-evolutionary consequences of population oscillations
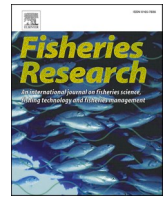
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A B S T R A C T

Understanding fish population oscillations is important for both fundamental population biology and for fisheries science. Much research has focused on the causes of population oscillations, but the eco-evolutionary consequences of population oscillations are unclear. Here, we used an empirically parametrised individual-based simulation model to explore the consequences of oscillations with different amplitudes and wavelengths. We show that oscillations with a wavelength shorter than the maximum lifespan of the fish produce marked differences in the evolutionary trajectories of asymptotic length. Wavelengths longer than the maximum lifespan of the fish, in turn, mainly manifest as ecological effects seen as the population biomass oscillation. The evolutionary and ecological differences increase with increasing amplitude, however, the two-year wavelength causes opposing results from all the other scenarios. This is likely facilitated by the relatively stable number of fish in the population as a poor year is always counteracted by the previous good year and vice versa. Our results highlight the evolutionary signatures and following ecological consequences that natural population oscillations can cause.

1. Introduction

Population oscillations are widespread in nature. They are observed in the avian, terrestrial, and aquatic realms. Understanding the mechanisms behind population oscillations has been a central theme in ecological research over the past century (Beddington and May, 1977; MacArthur, 1955; Sawyer and Slatkin, 1981; Shelton and Mangel, 2011). In the aquatic realm, these yearly variations in recruitment can be several orders of magnitude (Houde, 2016; Schwartzlose et al., 1999; Sette, 1961). A lot of research has focussed on the causes and mechanisms behind population oscillations (Hamrin and Persson, 1986; Houde, 2016; Kawasaki, 1992; Kristiansen et al., 2011; Marjomäki et al., 2014; Pepin and Myers, 1991; Sawyer and Slatkin, 1981; Sissenwine, 1984), while the eco-evolutionary consequences of such oscillations remain unclear and largely understudied.

Understanding fish population oscillations, whether natural or human induced, is important for both fisheries science and fundamental ecological and evolutionary theory. On the one hand, it sets the margins within which fisheries must operate to maintain sustainable harvesting. On the other hand, population oscillations introduce changes in population density, which in turn have wide reaching effects on food availability, competition, and mate choice and can therefore leave an

ecological and evolutionary signature in the population. Density dependence is known to affect many life history traits and aspects in an individual fish's life, such as survival (Minto et al., 2008) and growth (Lorenzen and Enberg, 2002). Density mediated selection can be complex, as various evolutionary agents act simultaneously. For instance, harvest-induced selection often exerts direct selection pressure against large phenotypes (Matsumura et al., 2011), but also reduces population density and thereby increases the available resources per capita, resulting in higher rates of somatic growth (Hilborn & Walters, 1992). Further, recent research has shown complex, intertwined patterns between ecological change in the environment and evolutionary change in the population (Bouffet-Halle et al., 2021; Gobin et al., 2018), further highlighting the need to disentangle the role of different evolutionary pressures influencing population eco-evolutionary dynamics.

Previous literature has documented links between life histories and environmental variability, and some of these links may be delayed in the sense that variable environment in the past can give rise to life history effects in the future through, for instance, parental effects or feeding interactions (Beckerman et al., 2002). These life history effects in turn can affect population dynamics, and changes in the population dynamics, particularly in the population density, can then feed back to life history evolution (Heino et al., 1998). However, little research exists on

the feed-back link of how population dynamics can affect the evolution of individual life histories (De Roos et al., 2003). Understanding how population oscillations may affect the evolution of life history traits could help us better manage and conserve our natural ecosystems (Eikeset et al., 2016; Ranta et al., 1995). While the mechanisms behind population oscillations are important, we approach this topic from the opposite direction and ask instead: What are the consequences of population oscillations? Here, we do not focus on the causes of environmental oscillation but instead on the consequences of environmental oscillation for eco-evolutionary dynamics in the population. Particularly: how does the wavelength and the amplitude implemented in the survival probability of juveniles affect the evolution of life history traits with implications for population dynamics? The model used here is an individual based model and as such does not include an environment per se, therefore the cause of the oscillation is of no interest, but the survival probability of the juveniles is forced to oscillate to mimic a response (Karjalainen et al., 2000; Marjomäki and Huolila, 2001) to an oscillating environment. We use vendace (*Coregonus albula*), a small, schooling freshwater fish known for its natural population oscillations (Marjomäki and Huolila, 2001), as a model species. Using an empirically parametrised, individual-based eco-evolutionary simulation model, we simulate population oscillations with different degrees of oscillation in terms of wavelength and amplitude, derived from empirical estimates (Kolari and Hirvonen, 2018). We explore how those oscillations affect the life history evolution and population dynamics in pristine, fished and recovering populations. Given the importance of body size as a driver of many ecological and evolutionary processes (Ahti et al., 2020), we focus on the evolution of asymptotic length as a key life history character, and additionally investigate the effects on population biomass. Specifically, we ask the following questions: What are the (1) evolutionary and (2) ecological consequences of population oscillation?

2. Material and methods

To explore the eco-evolutionary consequences of population oscillations, we used an individual-based simulation model (Kuparinen et al., 2011). The model is based on empirical data of vendace populations in Lake Puulavesi in Central Finland and incorporates life-history data and quantitative genetics with population demographic processes. The model is thoroughly described elsewhere (Kuparinen et al., 2011 details

the initial model, parametrised for *Gadus morhua*; Ahti et al., 2021 parametrises the model for *C. albula* and adds reproductive and actuarial senescence), so we will here provide a general description of the modelling approach and modifications relevant to present work.

2.1. The model description

The model incorporates five main components to describe individual life histories and population dynamics: growth, fecundity, senescence, population demographics, and oscillating survival probability (Fig. 1).

The growth component (Fig. 1a) utilises back calculated length-at-age data from fish scales. These data were used to fit the von Bertalanffy growth curve (von Bertalanffy, 1938, 1949) (although see criticism: Pardo et al., 2013; Roff, 1980) and estimate the asymptotic length (L_∞) and intrinsic growth rate k (the rate at which an individual approaches L_∞) of each individual fish. The parametres L_∞ and k were assigned at birth. There is a strong negative correlation between the two parameters, so the inheritance was coded so that based on an individual's genotype, the individual was assigned an L_∞ value. Then using a statistical fit of the regression $\log(k) \sim L_\infty + \varepsilon$ to the above mentioned empirically estimated set of L_∞ and k, the growth rate k was predicted based on the value of L_∞ and a normally distributed random noise term whose standard deviation matched with that of the residuals in the regression fit. The L_∞ genotypic value was described by 10 diploid loci with two alleles in each, one from the mother, one from the father. This was done because life history traits such as L_∞ are known to be coded by several loci (Mousseau and Roff, 1987), and previous quantitative estimates have revealed that 10 is a sufficient number of loci with small additive effects, adding more loci does not affect the simulations (Kuparinen et al., 2011). The alleles were coded as 0 or 1, and the sum of these alleles described the genotype of L_∞. To add phenotypic plasticity around the genotype, a random, normally distributed number (x̄ = 0, s. d. = 4) was added to the genotype of L_∞, and this sum was linearly translated to the phenotypic L_∞ value. The standard deviation of the random number was chosen to produce a realistic heritability of 0.2 – 0.3 (Mousseau and Roff, 1987). From here on, when L_∞ is discussed, we refer to the phenotypic L_∞ which consist of the genotypic L_∞ plus added phenotypic plasticity.

The fecundity component (Fig. 1b) is based on a length-weight relationship specifically calculated for vendace in Lake Puulavesi.
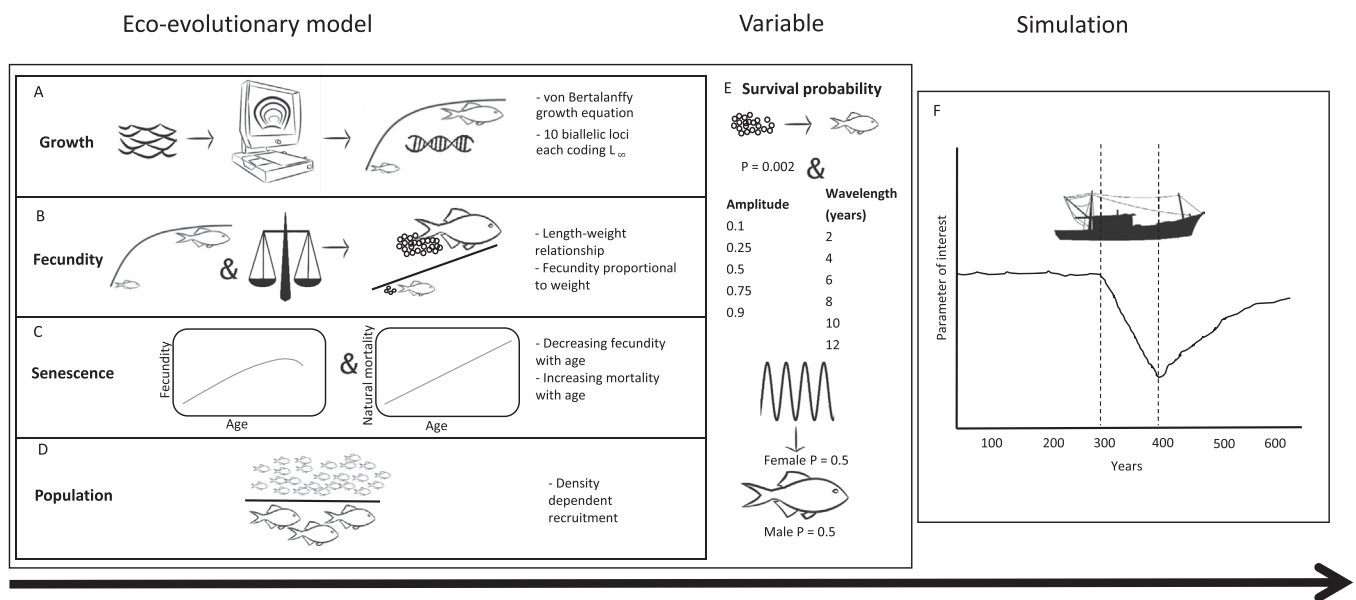

Eco-evolutionary model   Variable   Simulation

Fig. 1. A schematic diagram showing the modelling approach. The model had five main empirically parametrised components: A) growth which was inherited B) fecundity based on the body size of the fish C) reproductive and actuarial senescence D) the effect of density on population growth E) oscillating survival probability and F) the final simulation that allowed the different oscillation scenarios to "live" for 600 years. Fishing took place between years 310 – 400.

Vendace is known to mature during its second autumn (Karjalainen et al., 2016), so the maturation threshold was set to be 67% of their L_∞, i. e. the mean size at two years of age (see also Jensen, 1998). The maturation age was allowed to evolve freely but was restricted so that it could not drop below two years. A linear model for fecundity was then fitted based on the length-weight relationship (details at "Model parametrisation") and on previously published empirical data on egg numbers (Karjalainen et al., 2016).

The senescence component (Fig. 1c) is modelled (Ahti et al., 2021) based on empirical data on actuarial (Marjomäki, 2005) and reproductive senescence (Karjalainen et al., 2016). Actuarial senescence included an instantaneous mortality rate of M = 0.2 for 2 year olds, and the increase in natural mortality for each year class was based on data from Marjomäki (2005). We used the data of Karjalainen et al. (2016) to calculate gonadosomatic index (GSI) for vendace and this was used as a proxy for reproductive senescence, so that the linear model from the above fecundity component (Fig. 1b) was multiplied by a fecundity factor derived from the GSI.

Density dependence was described through two components: the growth of an individual and the number of eggs (Fig. 1d). As the population density increases, the growth rate of an individual continuously decreases, so that, for instance, at 85% of the population carrying capacity the individual's growth rate was reduced to 50% of that predicted by its von Bertalanffy growth curve. However, this reduction in growth does not affect the initial L_∞ value assigned to each individual fish. Similarly, egg production declined so that the closer the spawning population was to the population carrying capacity, the fewer eggs were produced, and in contrast, the sparser the population the more eggs were produced. Both the individual growth and the egg production were described through the following equation: growth time available for the individual or the egg production $\propto \frac{e^{\left(a+b*\frac{BM}{CC}\right)}}{\left(1+e^{\left(a+b*\frac{BM}{CC}\right)}\right)}$, where BM = biomass in units, CC = carrying capacity in units, and $a = 15$ and b = -a/0.85 describe the slope. Due to lack of data, the density-dependency is not based on species specific values, but was implemented to mimic the natural consequences of density dependency in nature, ie. slowing down of growth and reproduction, and also to help keep the population in equilibrium. It is kept constant in all the scenarios, and therefore does not affect the end results.

To simulate population oscillations (Fig. 1e), we assumed that the oscillation itself was independent of spawning stock biomass, and thereby driven by external factors. This is because vendace population oscillations are known to be somewhat synchronous across lakes, suggesting population oscillations are affected at least in part by external drivers, and not purely by density dependence (Kolari and Hirvonen, 2018; Marjomäki, 2003). The average survival probability of an individual from an egg to a 2-year-old was set to 0.002, according to empirical data (Karjalainen et al., 2016; Marjomäki et al., 2014). Every year, the survival probability of 0.002 was then multiplied by a cosine function with five different amplitudes and six different wavelengths, totalling 30 different oscillation scenarios. The five different amplitudes were: 0.1, 0.25, 0.5, 0.75, and 0.9. An amplitude of 0.1 means that the crest and the trough of the cosine wave were 10% above and below the average, an amplitude of 0.25 was 25% above and below the average, and so forth. The wavelengths were chosen to be 2, 4, 6, 8, 10, and 12 years. These numbers were chosen as they allowed the wavelengths to coincide with the cosine wave crest and trough. This way, each cosine wave crest and trough occurred at exactly 2, 4, 6, 8, 10, or 12 years, and never between those years. This method allowed for a careful mechanistic investigation of the effect of different degrees of oscillation on the eco-evolutionary dynamics of the population. To reduce the likelihood of results being purely plastic phenotypic responses to different population densities, the average biomass was the same in all oscillations, only the amplitude and wavelength varied. From here on, the above-described oscillation pattern will be referred to as oscillation, and not recruitment variability which is more often seen in the literature.

This is to enhance the idea that we are investigating the consequences of oscillations in populations, regardless of the ultimate cause of them. It is important to notice, that despite the oscillation patterns this model should be considered as a deterministic model, as no noise was added in the simulation, apart from the indirect variation that comes from the plasticity in growth (k) and body size which translates to variation in reproductive capacity, as well as density dependent variation in growth and reproduction.

2.2. The simulation setting

The initial starting population was set to 2000 individuals, and it plays no role in the final results of the study but was chosen purely for model optimisation. We allowed the initial populations for each scenario to find ecological and evolutionary stability by running a 1000-year long burn-in simulation. During this burn-in simulation it was also ensured that no genetic fixation took place and therefore the population would maintain its genetic variation. The populations reached stability in approximately 600 years. Fifty replicates were saved to be used as starting populations in further simulations. Further simulations drew their starting populations randomly from these 50 populations. No fixation occurred during the burn-in periods.

The simulations were run for 600 years, of which years 1 – 300 were in pristine conditions, years 301 – 400 were fished, and years 401 – 600 were a recovery period. The traditional fishing methods for vendace are trawling and seining (Salmi, 1998). To mimic trawling and seining selection, we implemented a logistic curve $r(l) = \left(\frac{\exp{(c+dl)}}{1+\exp{(c+dl)}}\right)$, where $r(l)$ = the catching probability of a fish of length l, and $c = -9$ and $d = 0.85$ are shape parameters so that 50% retention probability is achieved at $-c/d$ (Kuparinen et al., 2009). The fishing mortality M for a fully selected size class was set to 0.7 according to local estimations (Viljanen, 1986). Fifty independent replicates were created for each oscillation scenario. Each simulation recorded population and individual data at annual time steps. The data of interest in this study were asymptotic length L_∞, biomass, number of juveniles, and number of recruits. All simulations and analyses were run using R version 1.1.456 (R Core Team, 2018).

2.3. Empirical data and model parametrisation

The data were collected from Lake Puulavesi in Central Finland between 1977 and 2017. The lake is an oligotrophic lake with an average depth of approximately 9 m (max. 62 m) and an aerial coverage of 330 km². The lake represents an average Finnish lake in terms of fishing activity (Marjomäki and Huolila, 2001). A total of 93 specimens were collected (female N = 62, male N = 31). While the number of specimens is relatively low, each individual provides data for all the years it has been alive, i.e. a 4-year-old fish provides growth data from 4 years, and therefore the sample size was adequate for the parametrisation of the model. Scales below pelvic fins were collected and stored, and the age (3-year-olds N = 34, 4-year-olds N = 20, 5-year-olds N = 37, 6-year-olds N = 2) was determined from these scales. To determine the length-at-age, the scale radius (S) and the radius from the scale focus to the annulus i (S_i) were measured from the anterior part of the scale. To magnify the scale to a readable size (20–40 x), we used a microfiche reader. The Monastyrky's equation (Monastyrsky, 1930) was used to back-calculate the length at age as follows: $L_t = L \times \left(\frac{s_t}{s}\right)^b$, where L = the total length measured when the fish was caught, S_t = the annulus width at age t, S = the radius of the scale, and b = 0.641, which is an estimate from several vendace stocks across Finland (Marjomäki and Huolila, 2001). While using scales for age determination may underestimate the age of the fish and thus overestimate the growth of the fish (Aass, 1972), this estimation bias would be systematic and therefore not an issue in a modelling study focussed on ecological and evolutionary mechanisms. The length-weight relationship was specifically calculated for vendace from Lake Puulavesi using von Bertalanffy growth

trajectories and empirical weight data from 27 of the above individuals. For this, we used the Ricker's method $W = a \times L^b$ (Ricker, 1975), where W = fresh weight in grams, L = length in centimetres. The scaling coefficient for the weight at length of the fish was calculated to be $a = 7 \times 10^{-6}$, and the shape parameter for the body form of the species was calculated to be $b = 2.943$. In the dataset the lengths varied between 120 and 170 mm (mean 146 mm, s.d. = 8.63), and the weights varied between 12 and 27 g, (mean 18.7 g, s.d. = 3.7).

The growth trajectories based on the back-calculations were summarised using the von Bertalanffy growth curve (von Bertalanffy, 1938, 1949) as follows: $L(t) = L_\infty - (L_\infty - L_0)e^{-kt}$, where L_t = fish length at age t, L_∞ = asymptotic length, L_0 = length at time $t = 0$, and k = the intrinsic individual growth rate, i.e. how fast an individual approaches L_∞. The von Bertalanffy parameters k and L_∞ are known to have a strong negative correlation. To estimate this association, a linear regression model $\ln(k) = 1.27 - 0.13 \times L_\infty$ with a residual s.d. = 0.30 was fitted.

An age-dependent decrease in gonadosomatic index (GSI = (gonad weight/ total tissue weight) $\times$ 100) has been used as a proxy for reproductive senescence in previous studies (Benoît et al., 2020; Hendry et al., 2003). Based on the data of Karjalainen et al. (2016), we calculated GSI that was used as a proxy for reproductive senescence (Ahti et al., 2021). Since the empirical GSI only extended to 4-year-old fish, it was linearly extrapolated to 5- and 6-year-olds. Reproductive senescence was modelled by taking the linear function for individual fecundity per gram body weight: $39.06 + 118.47 \times$ wet mass in grams (Karjalainen et al., 2016) and multiplying it by a fecundity factor for each age group. The fecundity factor was standardised so that the age group 1 had a fecundity factor of 1, and age groups 2–6 had a fecundity factor proportional to that of age group 1, based on the empirical or extrapolated GSI. The fecundity factor was calculated by dividing the GSI of age group 1 by the GSI of the age group of interest. In a similar manner, actuarial senescence (increase in natural mortality with age) was added to a baseline natural mortality of $M = 0.2$ for 2-year-old fish (Ahti et al., 2021). The increasing natural mortality was adjusted to proportion from Marjomäki (2005). The reproduction data was used to calculate the average lifetime reproductive output (LRO, i.e. the cumulative number of offspring during an individual's lifetime). LRO was used to estimate evolutionary fitness in terms of reproduction for the L_∞ values in different oscillation scenarios.

Another important life history trade-off is the increase in natural mortality following maturation (Bell, 1984; Kuparinen et al., 2012). The magnitude of this was calculated from the increase of natural mortality in age group 1 to natural mortality in age group 2 as in Marjomäki (2005), therefore contributing towards the annual natural mortality rate for all mature fish (Kuparinen et al., 2012).

3. Results

The main consequence of oscillations was the difference in the population evolutionary trajectory in terms of L_∞ and ecological response in terms of biomass oscillation. Whether the response was primarily evolutionary or ecological, depended on whether the oscillation wavelength was shorter (evolutionary) or longer (ecological) than the maximum lifespan of the fish. Fishing always led to evolution towards lower L_∞, and the rate and magnitude of this change was nearly identical in all scenarios regardless of wavelength or amplitude of the imposed oscillation. No trends in the variation of asymptotic length between different scenarios were found.

3.1. Evolutionary effects

The differences in L_∞ between different scenarios were used to explore the evolutionary effects of varying oscillation wavelengths and amplitudes. All populations were evolutionarily stable prior to fishing, and L_∞ had settled between approximately 14 and 16 cm with only

minor variation in L_∞ with time (Figs. 2, 3). When fishing started in year 301, the L_∞ dropped in every scenario. When fishing was ceased in year 400, the L_∞ in all scenarios started to recover. However, the recovery was slow and in 200 years of recovery the L_∞ had not recovered to the initial level in any of the scenarios.

When the wavelength of the oscillation was 2, 4 or 6 years, it caused clear evolutionary differences in L_∞ (Fig. 2a, b, c). When the wavelength was 8 years or more (i.e. longer than the maximum lifespan of the fish in the model, 7 years) the evolutionary differences in L_∞ between different amplitudes diminished (Fig. 2d, e, f). The direction of the variation between scenarios with different amplitudes differed, depending on the wavelength. When the wavelength was 4 or 6 years, the L_∞ increased with increasing amplitude (Fig. 2b, c). However, when the oscillation wavelength was 2 years, the effect of amplitudes was reversed, so that the higher the amplitude, the lower the L_∞ (Fig. 2a). When the L_∞ values were grouped by the amplitude of the wave (Fig. 3), it could be seen that the evolutionary differences in L_∞ increased with increasing amplitude. However, reflecting Fig. 2, simulations with a wavelength of 8, 10, or 12 years showed less differences between them, while the simulations with a 4- and 6-year wavelength evolved towards increasing L_∞ with increasing amplitude, and the simulations with a 2-year oscillation evolved towards decreasing L_∞ with increasing amplitude.

To estimate the evolutionary fitness in terms of reproduction for the L_∞ values in different oscillation scenarios, an LRO was estimated for the pristine population. The wavelength does not translate to marked differences in the LRO between scenarios, but as the amplitude increases, the differences between wavelengths become more visible (Fig. 4). Similar to Fig. 3, which showed an increasing variation in the evolutionary response of L_∞ between scenarios with increasing amplitude, the variation of LRO between scenarios also increased with increasing amplitude (Fig. 4). In Fig. 4c – e with the high amplitudes (0.5, 0.75, 0.9), the scenarios with wavelength 4, 6 and 12 show the lowest fitness in terms of LRO. These correspond to the highest L_∞ in Fig. 2 and Fig. 3., indicating that large body size does not equal the highest fitness, but instead, as a result of trade-offs, body size is optimised to maximise fitness. This is true when comparing fitness between scenarios. Regardless of the wavelength or the amplitude of the scenario, the highest fitness is always in the L_∞ range of approximately 14 – 16 cm (the peak in the curves in Fig. 4), indeed as this is the range within which the L_∞ found an evolutionary balance in all scenarios (Figs. 2 & 3).

3.2. Ecological effects

The ecological consequences of population oscillation are seen in the variation of biomass over time. Increase in both the wavelength and the amplitude increased variation in biomass (Figs. 5, 6). When the oscillation wavelength was set to be 2, 4, or 6 years, the variability in biomass increased respectively (Fig. 5a – c). For wavelengths higher than six, the variability in biomass increased with increasing wavelength, but not as strongly as when the wavelength was 6 or under (Fig. 5d – f). When the oscillation wavelength was two (Fig. 5a), the effect of the amplitude on the biomass was a reverse of that seen in any of the other scenarios with longer wavelengths, reflecting the inverse relationship between L_∞ and amplitude seen in Fig. 2, and the lower LRO of higher L_∞ seen in Fig. 4. The 2-year cyclicity also appeared to dampen the effect of amplitude (Fig. 6), so that while in every other scenario the increasing amplitude led to increasing variation in biomass, when the wavelength was 2, the amplitude did not markedly increase variation in biomass. However, in other scenarios, similar to the variation in L_∞, the variation in biomass increased with increasing amplitude (Fig. 6). The changes in biomass reflect those of L_∞ and LRO.

The changes in juvenile (< 1-year-old fish) and recruit (1–2-year-old fish) numbers are shown in the phase diagrams in Fig. 7. When the oscillation was 2 years (Fig. 7a), the number of young (juveniles and recruits) was relatively constant over time, as whenever the population had around 3000 – 4500 juveniles, it had around 1000 recruits, and
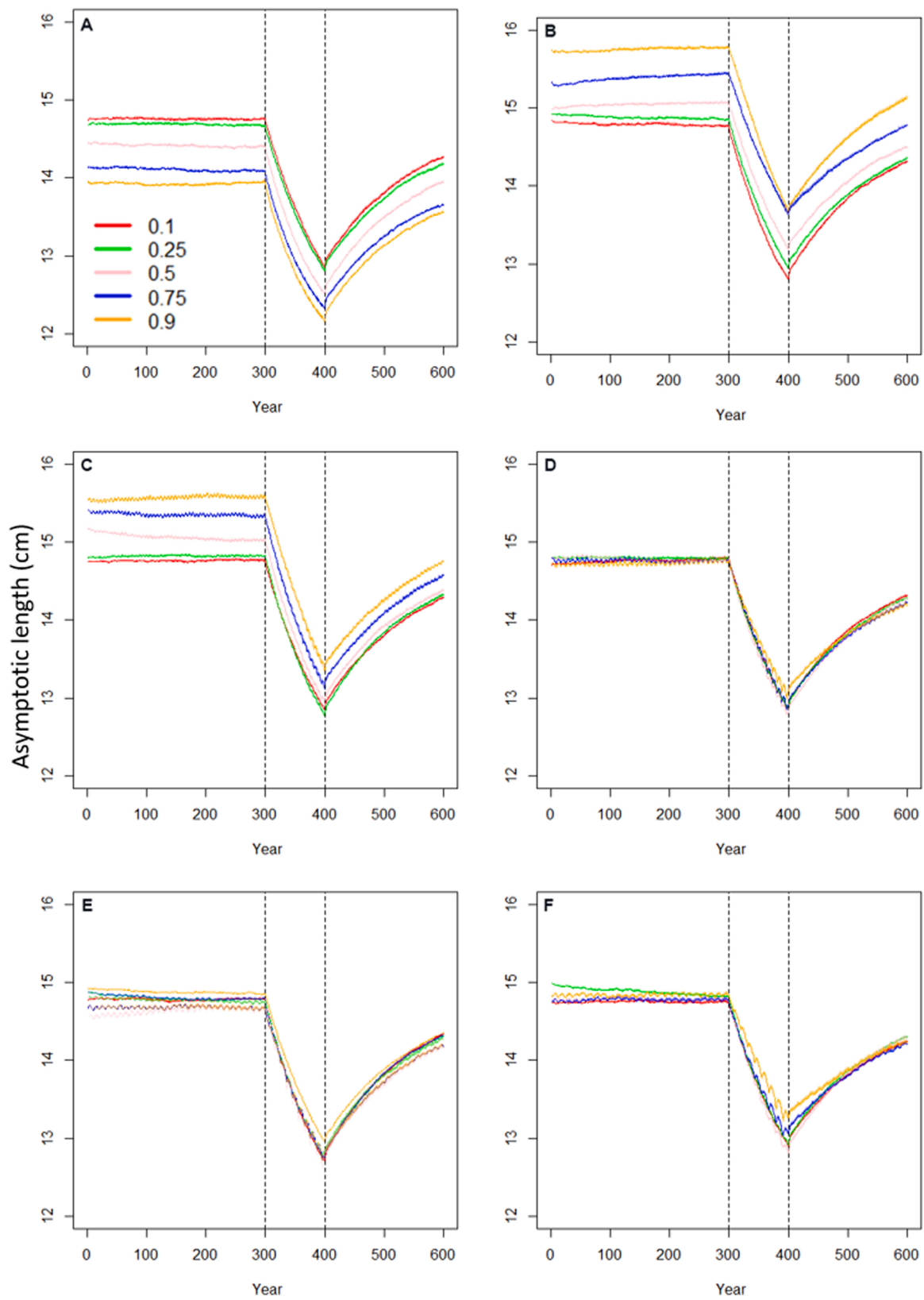
Fig. 2. The mean asymptotic length (cm) of the fish in each scenario. The dashes lines denote the beginning and end of fishing. The panels a, b, c, d, e, and f show the wavelengths of 2, 4, 6, 8, 10, and 12, respectively. Each line in the panel is the mean of 50 independent replicates for varying oscillation amplitudes explained by the colour coding in the figure legend.
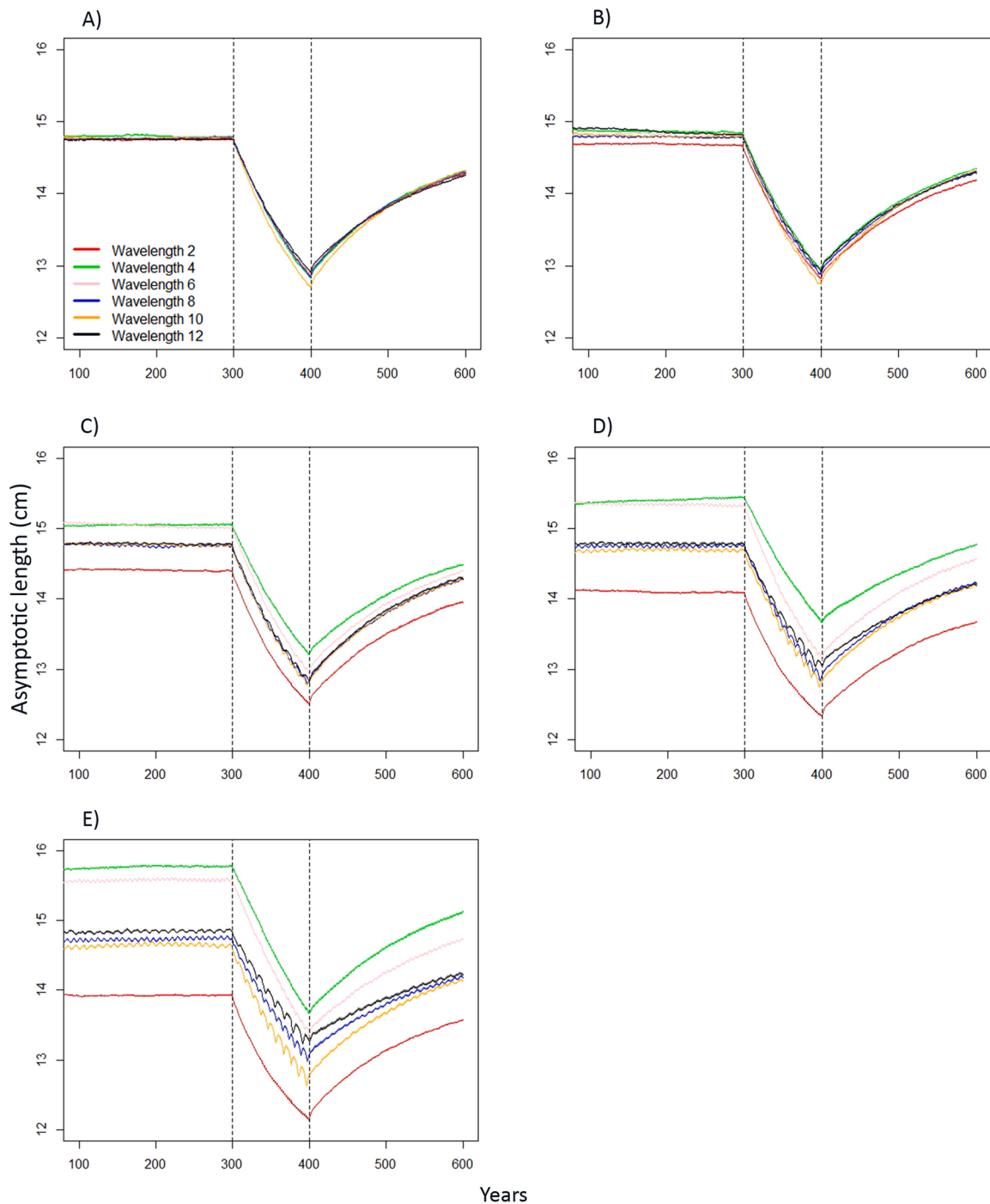
Fig. 3. The mean asymptotic length (cm) of the fish in each scenario. The dashes lines denote the beginning and end of fishing. The panels a, b, c, d, and e show the amplitudes of 0.1, 0.25, 0.5, 0.75, and 0.9, respectively. Each line in the panel is the mean of 50 independent replicates for varying oscillation wavelengths explained by the colour coding in the figure legend.

whenever the population had around 3000 – 4500 recruits, it had around 1000 juveniles. Therefore, the number of young remained relatively constant at 4000 – 5500. This reflects the little variation in biomass for the 2-year oscillation seen in Fig. 6, as well as the inverse relationship between L_∞ and amplitude because there are no years with very low population density. The longer the wavelength, the more variation there was in the number of young between years (Fig. 7b - f). Longer wavelengths resulted in longer periods of low juvenile and recruit numbers and therefore periods of lower population density, while due to carrying capacity, the number of juveniles and recruits could not increase in the same manner.

4. Discussion

Our investigation on the consequences of population oscillation revealed different evolutionary and ecological responses depending on the length and amplitude of the oscillation wave. The maximum lifespan of the fish was critical in determining the direction and strength of the response. The maximum lifespan of the fish was 7 years, and wavelengths shorter than this resulted in clear evolutionary differences between oscillation scenarios, manifesting in the asymptotic length of the fish. The higher the amplitude, the clearer the differences were (Fig. 3). However, once the wavelength exceeded the maximum lifespan of the
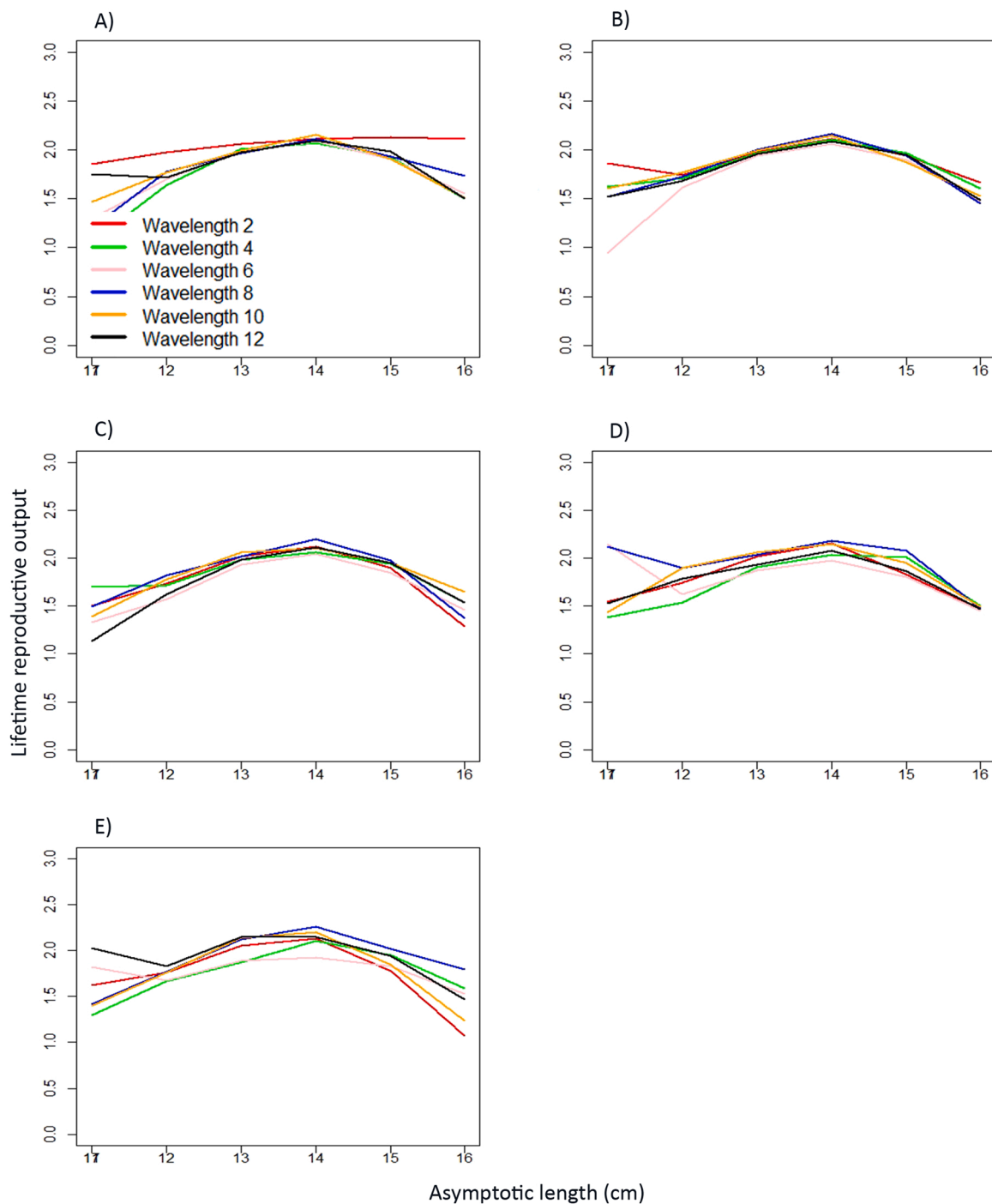
Fig. 4. The lifetime reproductive output (LRO) for all the scenarios during the pristine phase, grouped by the amplitude. Each line shows a different wavelength, as explained by the colour coding in the figure legend.

fish the evolutionary differences largely diminished, regardless of the amplitude of the wave (Fig. 2). Instead, wavelengths exceeding the maximum lifespan of the fish yielded ecological consequences in the form of biomass oscillation (Fig. 5). Generally, the higher the amplitude, the stronger the biomass oscillation, regardless of the wavelength. However, the mean biomass for the two-year oscillation scenario during fishing was a reverse of that seen in the other scenarios. While fishing caused a steady decline in the asymptotic length in all the scenarios, fishing did not significantly change the evolutionary trajectory caused by different oscillation patterns, suggesting the effect of fishing is additive.

Understanding the evolution of fishes under different stressors is a topic of intense research (Griffen et al., 2016). The selection pressure exerted by size-selective fisheries is likely the most studied stressor, and known to affect the life history traits and dynamics of harvested populations (Sbragaglia et al., 2019; Uusi-Heikkilä et al., 2015), and amplify oscillations in natural populations (Anderson et al., 2008). However, many wild populations undergo strong oscillations in population size naturally (Houde, 2016) which can, as suggested by the present study, itself cause selection in the population, which is then topped off with the additive effects of fishing.
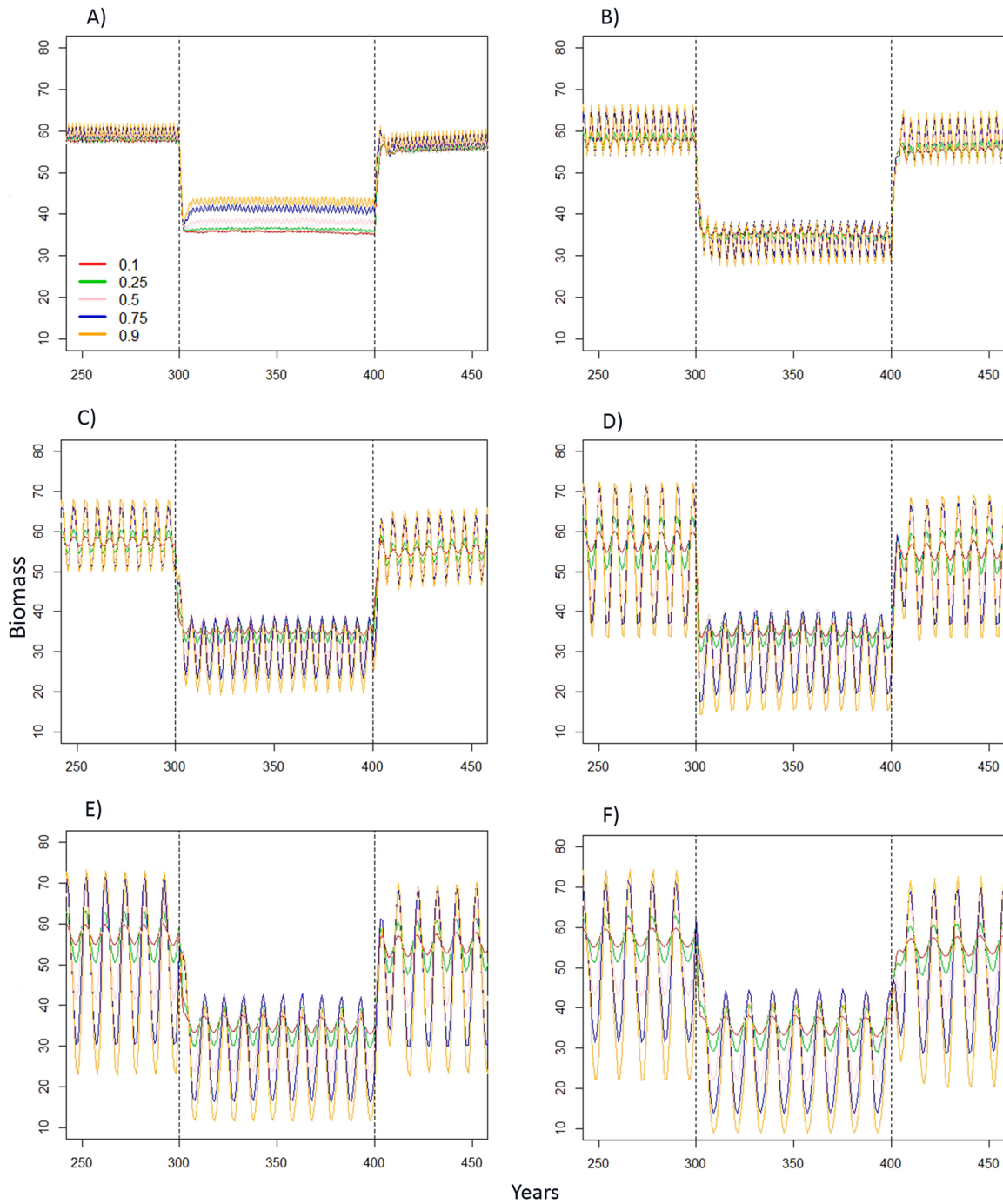
Fig. 5. The mean biomass (in units) of the population in each scenario. The dashes lines denote the beginning and end of fishing. The panels a, b, c, d, e, and f show the wavelengths of 2, 4, 6, 8, 10, and 12, respectively. Each line in the panel is the mean of 50 independent replicates for varying oscillation amplitudes explained by the colour coding in the figure legend.

4.1. Evolutionary consequences of population oscillations

What kind of evolutionary trajectory is imposed by population oscillations, depends on the combination of wavelength, amplitude, and life history traits. Oscillation wavelengths shorter than the maximum lifespan of the fish exposed evolutionary differences between scenarios with different amplitudes. Wavelengths of 4 and 6 years revealed selection toward higher asymptotic length with increasing amplitude (Fig. 2). This is likely because in the 4- and 6-year oscillations the number of juveniles and recruits decreased for a few consecutive years, decreasing the population density (Fig. 7). Changes in population density can drive life history evolution (Kuparinen et al., 2014), and

population density and fish body size are often reported to be inversely related, primarily due to food availability (Cyr et al., 1997; Hazlerigg et al., 2012; Lorenzen and Enberg, 2002). Indeed, also in Lake Puulavesi, where the data for the parametrisation of the present model were collected, the vendace growth rate is known be negatively density dependent (Marjomäki and Huolila, 2001). Given that life history traits such as body size are known to have both plastic and inherited components (for a review, see Ahti et al., 2020), the higher asymptotic body size acquired during low population densities was at least in part genetic, and was thus inherited by the next generation and evolution towards higher asymptotic length took place. Importantly, this evolutionary trajectory was facilitated by a wavelength shorter than the
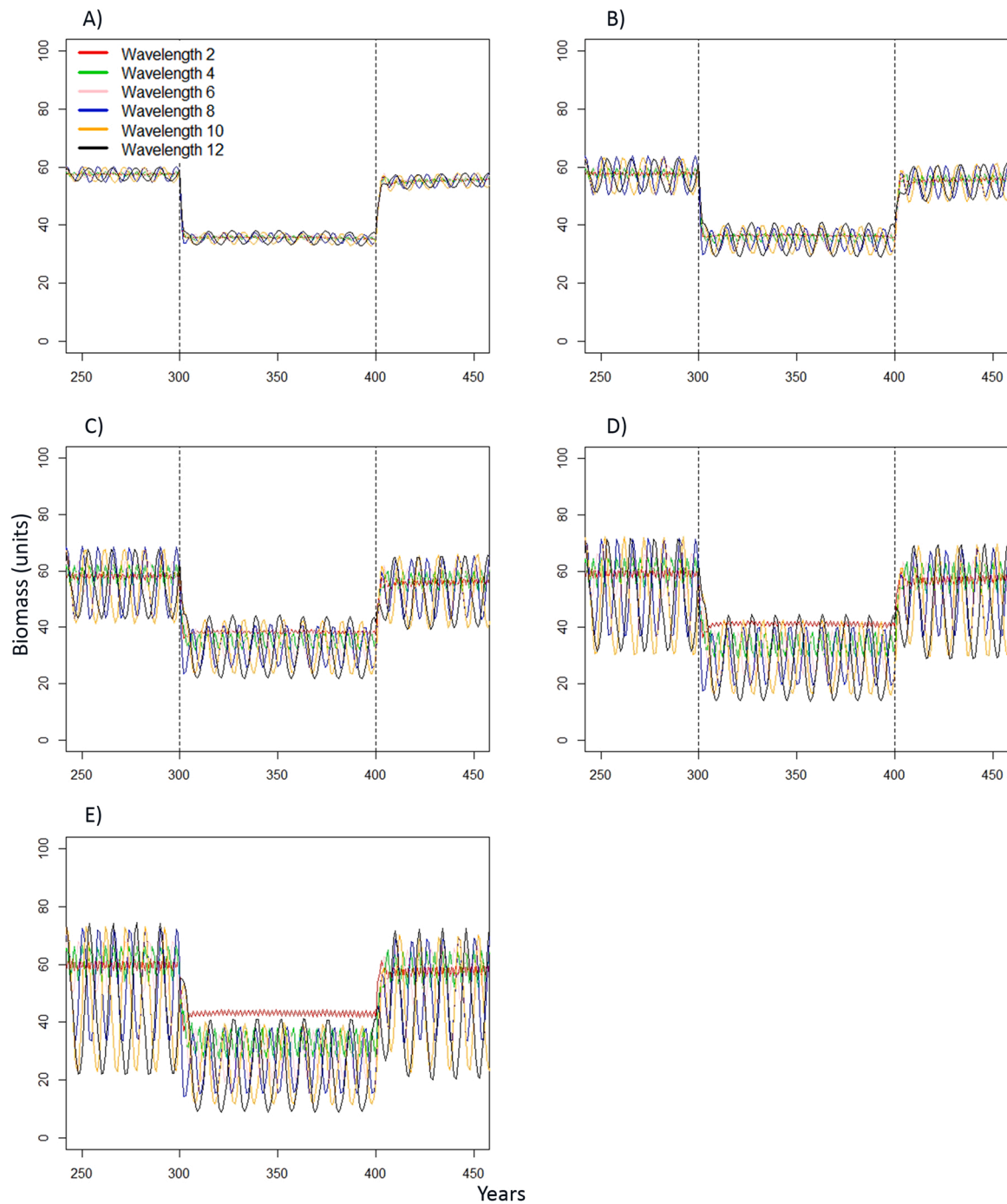
Fig. 6. The mean biomass (in units) of the population in each scenario. The dashes lines denote the beginning and end of fishing. The panels a, b, c, d, and e show the amplitudes of 0.1, 0.25, 0.5, 0.75, and 0.9, respectively. Each line in the panel is the mean of 50 independent replicates for varying oscillation wavelengths explained by the colour coding in the figure legend.

maximum lifespan of the fish, which enabled strong selection over consecutive generations. Indeed, the main message relating to the effect of oscillation on the evolution of asymptotic length is that the combination of high amplitude and wavelength shorter than the maximum lifespan of the fish subjected the asymptotic length to the strongest selection.

In contrast, the evolutionary trajectories caused by a two-year oscillation were a reverse of those seen in 4- and 6-year oscillations. The two-year oscillation resulted in a relatively little variation in the density of juveniles and recruits, because a year with few juveniles was always counterbalanced by the high number of juveniles from the

previous year – and vice versa. This way, the population always maintained a relatively stable number of young fish, which also resulted in the dampening effect seen on the whole population biomass oscillation: increasing amplitude did not increase the biomass oscillation when the oscillation wavelength was two years (Fig. 6). While our model made no distinction between the density of the young fish and the density of the mature fish in terms of evolution of asymptotic length, the density dependent processes in the model are primarily driven by the density of the young because of the substantially higher number of them compared to older fish. In a similar way, in a cannibalistically driven population, the juvenile population density (controlled by cannibals) is crucial in
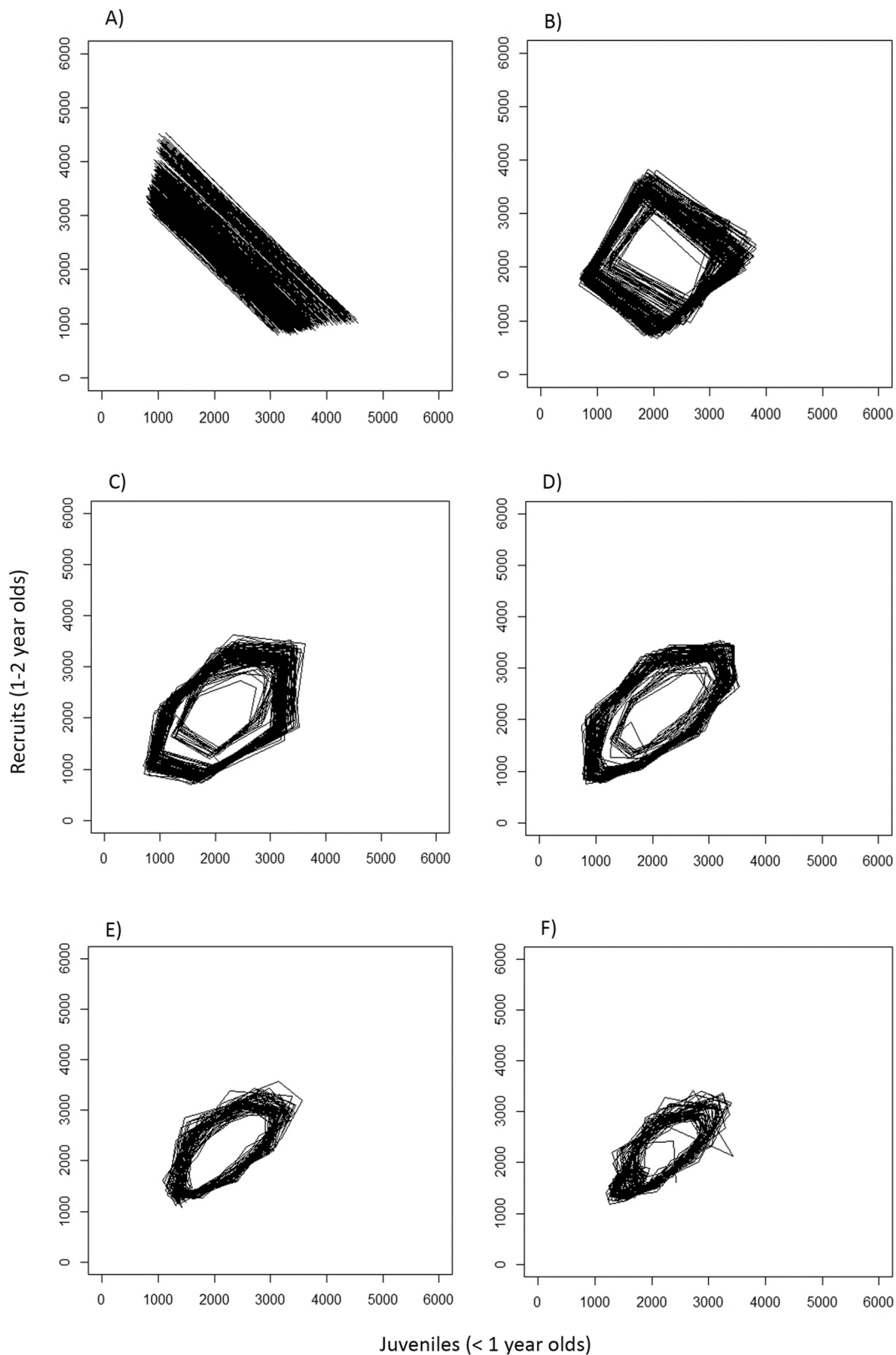
Fig. 7. Changes in juvenile (< 1-year-old fish) and recruit (1–2-year-old fish) numbers over time. Each corner in the diagram shows simultaneously the number of juveniles (X-axis) and the number of recruits (Y-axis) on any given year. The panels a-f show 2, 4, 6, 8, 10, and 12 year cyclicity, respectively, and for these example figures we picked the 0.5 amplitude (for comparison, smaller amplitude would only make the diagram smaller, while retaining the same shape, and higher amplitude would make it larger while retaining the same shape). Each corner describes one year in the wavelength number, and after the wavelength 6 (Fig. 7c), the corners become harder to separate as stochasticity increases.

determining the population dynamics and the consecutive effects on life history traits (De Roos et al., 2003). As a result, during two-year oscillation, the population did not experience periods of relaxed population density, that would have allowed for evolution towards higher asymptotic length. Instead, the relatively stable, and relatively high biomass push the asymptotic length towards declining evolutionary trajectory. Therefore, the higher amplitude and the following constantly high population density (as opposed to the scenarios with longer wavelength that had periods of low population density in between) led to a lower asymptotic length (and vice versa), in line with long-term records on the effect of density on fish growth in nature (Lorenzen and Enberg, 2002), and a pattern similar to that seen for vendace body size in nature (Marjomäki and Huolila, 2001). The capacity for continuous high population density during two-year oscillation is the opposite of what occurred when the wavelength was 4 and 6 and the population had sparser years in between, thereby allowing evolution towards higher asymptotic length.

Like many freshwater fish (Claessen et al., 2002) vendace, too (Urpanen et al., 2012), is known to be cannibalistic. Cannibalism is a source of population oscillations in populations where cannibals consume the smallest of the young of the year, a phenomenon known as cannibalism-driven dynamics (Claessen et al., 2002; Persson and De Roos, 2006). In populations like these, the cannibalism-driven changes in the density of the young of the year is an important driver causing population oscillations, and consequently leading to changes in body size distribution in the population (Claessen et al., 2002). While our model did not consider cannibalism, it showed that oscillations in the population density (irrespective of the cause), even without the presence of cannibalism, can induce changes in body size, and that those changes can leave an evolutionary signature in the population. Density dependent processes induce both plastic and genetic changes in life history traits. Low population density is associated with large body size mainly due to the indirect link of more energy being available per capita (Arranz et al., 2016; Cyr et al., 1997) and has been reported in many fish populations (Lorenzen and Enberg, 2002). Additionally, high population density itself can cause stress-related effects on growth. In Windermere pike, for instance, density-related social stress in a population has been reported to cause reduction in body size (Edeline et al., 2010). However, works on various taxa, including fish, show that density dependent natural selection favours larger body size at high population densities (Bouffet-Halle et al., 2021; Calsbeek and Cox, 2010). Studies on other model organisms such as the anole lizard (*Anolis sagrei*) have reported that high population density selects for large body size, likely because of increased interference competition (Calsbeek and Cox, 2010). However, in nature, many phenomena are optimised rather than maximised (Enberg et al., 2012), and the tug-of-war between different selection pressures is not well understood. Our simulations explored the role of population oscillations, meaning the density of the population changes constantly, and can therefore improve our understanding of density dependent process and how they may affect evolution.

4.2. Ecological consequences of population oscillations

Selection in nature is complex, and many different agents may simultaneously be acting on the same trait, selecting either toward the same or opposing directions, directly or indirectly. A recent study showed that ecological conditions such as invasive species causing density-dependent changes in somatic growth can alter the evolutionary response to harvest (Gobin et al., 2018). Our results showed that such density-dependent changes in a population were strongly affected by a life history trait of the fish, i.e. the maximum lifespan, so that the maximum lifespan directed whether the effect of oscillations was primarily seen as evolutionary (ie. change in asymptotic length) or ecological (changes in biomass). When the oscillation wavelength was shorter than the lifespan, the effect was mainly evolutionary. When the oscillation wavelength was longer than the maximum lifespan, the effect was ecological. With increasing amplitude and wavelength, the oscillations in population biomass became larger, regardless of whether the population was in pristine, harvest, or recovery phase.

The wavelength standing out from the regular pattern was again the two-year oscillation. While the relationship between amplitude and biomass was inverse in all other scenarios, the two-year oscillation resulted in a positive correlation between amplitude and biomass so that the smaller the amplitude the lower the biomass and the higher the amplitude the higher the biomass (Fig. 5). This reflects the evolutionary changes in asymptotic length (Fig. 2). The scenario that produced the lowest asymptotic length (amplitude of 0.9 and wavelength of 2) maintained the highest biomass. This is mediated by the associated changes in age and size at maturity (Ahti et al., 2021; these results are not shown as they are a consequence of the model where the size at maturity is determined to be 67% of the asymptotic length, see model parametrisation). Fish with smaller asymptotic length started reproducing earlier and could therefore maintain higher biomass. This is supported by the result that the highest LRO was not associated with the largest fish, but the with the medium sized fish. LRO is often used as a measure of individual fitness (van Daalen and Caswell, 2017). In our model, the highest overall fitness in terms of LRO was found in the phenotype associated with the 8-year oscillation. This phenotype had an intermediate asymptotic length, so it could be speculated that even between scenarios, optimisation resulted in the highest fitness. Similarly, within scenario investigation of LRO tends to coincide the most evolutionarily stable asymptotic length with the highest LRO.

Fish population oscillations have been described as "nightmare-ish" to fishery biologists, not least because of the economic catastrophes they may cause (Sette, 1961). It is important to note that our model is a simplification of the complex dynamics taking place in nature. The model, for instance, makes no distinction between the ecology of young and mature fish in terms of habitat choice, behaviour, cannibalism, or competition, but rather considers all fish as equal contributors to the population and biomass, body size depending. Similarly, the model does not include any specific noise in the oscillations in order to be able to carefully investigate the interplay between different wavelengths, amplitudes and life history traits. This highlights the need to use multiple research methods in science, and not rely only on modelling or for instance experimental work. Rather, these various methods should complement each other and illuminate different angles of the same problem. The advantage of modelling in this case is that it allows for a fine-tuned investigation of how different oscillation wavelengths and amplitudes affect the eco-evolutionary mechanisms of a fish population, all else being identical. This kind of fine-tuned, controlled evolutionary study would be challenging to produce experimentally. Understanding the underlying selection processes caused by either natural or human-induced oscillations in the population serves as a baseline that enables us to make more accurate predictions of how any added selection may act on a population. And, importantly, it can improve the management of our common natural resources.

CRediT authorship contribution statement

Pauliina A. Ahti: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Silva Uusi-Heikkilä:** Conceptualization, Writing – review & editing, Supervision, Funding acquicition, Formal analysis. **Anna Kuparinen:** Conceptualization, Writing – review & editing, Supervision, Funding acquicition, Project administration, Resources, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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