

Evolutionary pressures under the current fishing practices in European hake (*Merluccius merluccius*)

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Abstract

There is a rising concern involving the impact of modern fisheries on the dynamics and viability of the exploited fish populations. The increasing fishing pressure has been recorded to cause declines in age and size at maturation in variety of marine fish species. In this study I have aimed to detect heritable phenotypic changes of the European hake (*Merluccius merluccius*) under the currently prevailing fishing intensity. Using dataset of 64 individual-based growth parameters of the studied species and an individual-based simulation, which incorporates quantitative genetics, ecological processes and biological characteristics, I have simulated ecological and evolutionary dynamics of hake. Species` phenotypic traits were observed through three different scenarios which showed significant ecological consequences for hake population under the current fishing strategies but detected no evolutionary changes in life-history traits, e.g. growth and age and size at maturation. Even though, the current fishing intensity does not appear to select for a specific life-history type, the ecological impact observed under the current fishing practices can pose a severe risk through direct population declines.

Introduction

Various anthropogenic disturbances have been recognized as potential drivers for phenotypic trait evolution in different ecosystems and their representative species (Palkovacs et al. 2011). One of such is the fisheries-induced evolution (FIE) hypothesized in many fish species owing to observed changes in size and age at maturation in populations exposed to intensive fishing (Jørgensen et al. 2007, Kuparinen and Merilä, 2007). The theoretical background of FIE lies in the effect of fishing mortality, which operates as a strong selective force removing larger and older individuals from the population (Law, 2000). In addition to direct selective removal of such large-growing late-maturing life-history types, the remaining smaller and younger individuals can exhibit faster growth rate as a result of reduced competition for space and resources; consequently causing maturation at a smaller size and earlier age (Law, 2000, Sharpe and Hendry, 2009, Kuparinen and Merilä, 2007).

Since potential fecundity is positively correlated with the age and size of the individual, declines in average age and size are then reflected in the reduced potential fecundity and egg quality (Mehault et al. 2010). As an example, the meta-analysis by Venturelli et al. (2009) provided an overview of 25 species (or 35 marine populations) and showed an overall positive response of recruitment levels to the increasing

reproductive lifespan across both species and families. The study by Wright and Trippel (2009) provided further insight into the impact of fisheries on reproductive success in harvested stocks through investigating how the timing of spawning and changes in day of birth can have major consequences for the survival of the individual in later life-stages. Individuals maturing at smaller size and younger age undeniably affect the demography and dynamics of the whole population causing, e.g. higher variations in fish abundance in comparison to non-fished populations (Hsieh et al. 2006, Anderson et al. 2008). Moreover, as fish species often play an important trophic role in the ecosystem, such phenotypic changes could cause significant top-down and bottom-up shifts through the trophic web (Shackell et al. 2010, Audzijonyte et al. 2013, Palkovacs et al. 2011).

Nevertheless, much is argued whether FIE is truly the cause underlying the observed phenotypic changes. In wild fish populations, the same trends in size and age at maturation can be seen, for example, under declining population density or increasing sea surface temperature, as a result of plastic phenotypic responses (Heino and Dieckmann, 2008, Sharpe and Hendry, 2009, Kuparinen et al. 2009b, Dominguez-Petit et al. 2007). Therefore, attempts have been made to address the challenges of detecting and quantifying genotypic changes and to provide arguments that support the theory behind FIE.

One such particular study, conducted by Kendall et al. (2009), investigated selection differentials of gillnet commercial fishery of the sockeye salmon (*Oncorhynchus nerka*) using a long-term series of catch and escapement data collected between 1946 and 2005. Their quantitative analysis of the magnitude and nature of the selective pressure revealed a dominant exploitation of larger and older individuals during the majority of the studied time period. The level of susceptibility to the fisheries was especially significant for female sockeye salmon which in 52 out of 57 years (or 91% of the studied time period), had a negative selection differential. This essentially showed that larger and older females were more vulnerable to fishing than other demographic groups, which had a significant negative effect on their abundance and length distribution. Furthermore, statistical analyses showed that the most important causes of the negative impact on sockeye salmon population was explained by a model including gillnet mesh size regulations, stock abundance and deviation of the body length from the long-term average value.

Since the current methodology in FIE is limited by the lack of adequate knowledge in genes responsible for expressing evolutionary responses concerning, e.g. growth (Kuparinen and Merilä, 2007) methods used in these studies are traditionally based on the observations of phenotypic traits such as the size-age relationship (Kuparinen and Merilä, 2007, Enberg et al. 2009). However, despite the difficulties in disentangling the evolutionary effects of fishing pressure and phenotypic plasticity, current studies have shown that the fishing mortality increases with the age of fish, it “exceeds the natural mortality by several hundred percent” (Heino and Dieckmann, 2008) and has the potency to remove up to 50% of the population at a time (Sharpe and Hendry, 2009). In the study by Sharpe and Hendry (2009), the authors elaborate on the mechanisms behind FIE and its concomitant responses, providing pros and cons for the

FIE with the quantitative analysis on stock- and species-level. Their conclusions corroborate the notion of stock exploitation as a selective force capable of inducing evolutionary changes.

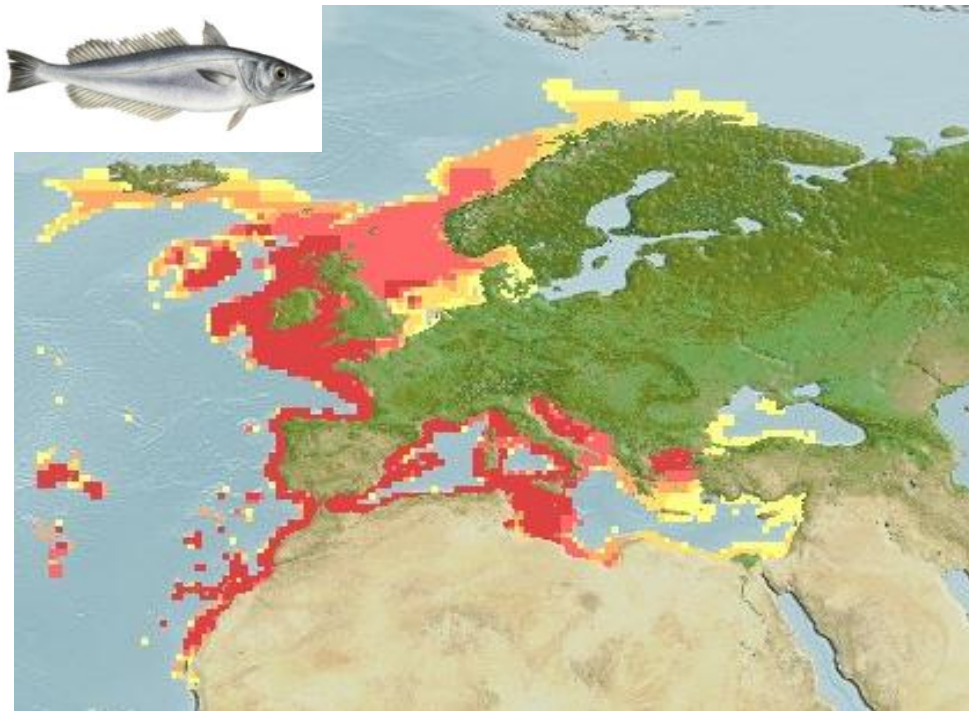


Figure 1. The distribution of the European hake (www.fishbase.se, www.ec.europa.eu).

Following the increase in growth in interest of potential FIE in numerous highly exploited fish species, the aim of my Master thesis is to investigate the impact of currently prevailing fishing intensity on the stocks of the European hake (*Merluccius merluccius* L., 1758; Fig 1). As a commercially highly exploited fish species, hake represents an important demersal stock for the countries of the northeast Atlantic shelf, the Mediterranean Sea and the Black Sea (ICES, 2012, Ragonese, 2009). Moreover, as a predatory species, the dynamics of hake can have a significant top-down effect for the species it preys upon which, depending on the availability, can be various clupeids, mackerel, horse mackerel, blue whiting, silver smelts and silvery pout (Casey and Pereiro, 1995). So far, there is a body of studies exploring the fishing impact on hake populations focussed on aspects such as the growth rates and different growth performance indexes (de Pontual et al. 2006, Ragonese, 2009, Ragonese et al. 2012), the retention of fish by fishing gear of different mesh sizes (Campos and Fonseca, 2003, Bianchini et al. 2003, Özbülğün et al. 2003, Lucchetti, 2008) and the link between high fishing intensity on juvenile hake and stable production of adult hake (Abella et al. 1997). The only current study investigating the changes in size at sexual maturity is one by Dominguez-Petit et al. (2008) where, using a long-term data series between the 1980's and 2004, they found significant declines in fish size for the population of the Bay of Biscay decrease of 15cm and for the Galician coast population, an initial decrease in size by 16 cm followed by an increase in size to the level of the initial values. However,

the same authors were not able to explicitly confirm whether the changes were caused by fishing pressure and/or environmental factors. Since little attention has been given to the impact of fishing practices, I have strived to investigate potential evolutionary changes in phenotypic traits of the European hake under currently prevailing fisheries intensity and selectivity.

Materials and Methods

To address the question of evolutionary changes in phenotypic traits of the hake I performed generic modelling of the studied species using an individual-based simulation model that integrated quantitative genetics and ecological processes. Using this model, I was able to simulate evolutionary effects of fishing with a small data-base utilized for model parameterization. The data was combined across different geographical locations to represent generic values and traits typical for the species, rather than those from one specific location. However, in practice most of the data used for model parameterization was acquired from studies of the Southern stock which includes the Atlantic coast of the Iberian Peninsula, the Mediterranean Sea and the Black Sea according to Annex G of the ICES (*International Council for Exploration of Sea*) 2012 WGHMM Report for the Southern stock.

Further details on the applied data, model approach and parameterization with simulation design are given below under their respective sections.

Data collection

The unsexed data on individual-based growth trajectories of hake were obtained from Dr Sergio Ragonese from The Institute for Coastal Marine Environment - National Research Council (IAMC-CNR), Italy. The data was collected from different studies on hake populations of various geographic locations and used in the study by Ragonese et al. (2012) to investigate the behaviour of different growth performance indexes. The dataset of recruitment, spawning stock biomass and parameters for the logistic selectivity curve of the fishing gear were acquired from Dr Santiago Cerviño of the Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Spain. The ICES 2012 WGHMM Report provided data of natural mortality for 0 to 3 year old fish.

Simulation approach

An individual-based simulation model was used to investigate the implications of current fishing regime on the population dynamic, especially, the trends of size and age at maturation. The primary model, previously used and described in the studies of the Atlantic cod (Kuparinen et al. 2011, Kuparinen and Hutchings, 2012), was adjusted to represent the life history of the European hake. The model included principles of quantitative genetics, ecological processes, body size effect on fecundity and integrated empirical data compiled from different geographical areas.

The individual growth trajectories were described by the von Bertalanffy formula (1938) where $L(t)$ is length at age t and is given by $L_{\infty} - (1 - e^{-K(t-t_0)})$, where L_{∞} is the asymptotic length (in practice the maximum length) an individual can reach if the growth was indefinite, K is a species-specific intrinsic growth rate and t_0 the age of fish at zero length (De Graaf and Prein, 2005). This model is based on two important life-history invariants: (1) the negative correlation between K and L_{∞} and (2) ratio (RL) of L_{mst} , the length at full sexual maturity, and L_{∞} . First interaction was used to obtain K , which we calculated through the previous formula using the collected data of L_{∞} (see *Model parameterization* for details). The second interaction, RL , was used to calibrate the fraction of the population at $L(t)$, which was set to mature as it reached the threshold of $0.51 \times L_{\infty}$. Using these interactions, the model is set to create an individual growth trajectory by incorporating empirical data collected for European hake and species-specific biological characteristics. Furthermore, the model includes the genetic information used to express for the phenotypic variation.

Life-histories of individuals ultimately defined by their von Bertalanffy growth trajectories were considered heritable. Under the assumption that a large number of loci has a small effect (Roff, 2002), the genotypes were described through 10 diploid loci what was considered to be a suitable number of genes to account for the genetic variation (Kuparinen et al, 2011). The loci were coded with values of 0 or 1 and randomly assigned to the offspring based on the classical Mendelian inheritance rules. The additive effect of the genetic trait was expressed through the sum of the loci (range 0 – 20) and transferred in the phenotype by adding an appropriate amount of phenotypic variation, set as a standard deviation of 3.5. With the set phenotypic variation around a range of the genetic trait value, the heritability was calibrated within an expected range from 0.2 to 0.3 for the purpose of yielding realistic values (Mousseau and Roff, 1987). Finally, the genetic trait value was then translated into L_{∞} , which gave the value of K based on the negative correlation of K and L_{∞} .

The instantaneous mortality rate consisted of natural mortality (M) and mortality caused by the survival cost of the reproduction (SC). M was equal for both sexes and applied only to individuals older than 3 years, while SC depended whether the individual was mature and was set to 0.1 for both sexes according to Kuparinen et al. (2011). A Bernoulli trial was then used to decide on the fate of the individual at every time step. An individual growth time was introduced to the model to account for the density of the population on growth. The growth time, or the time available for the individual to grow within 1 year, was described as a range between 0 and 1 so that a population at a high density, expressed as the ratio of population biomass and carrying capacity (c), would reduce the growth time following the logistic growth curve of the equation $growth\ time = e^{15 - 17.6 \times c} / (1 + e^{15 - 17.6 \times c}) - 1$.

To every reproduction process, a mature male and a mature female were assigned randomly and the number of offspring depended on the egg production and egg survival. The egg production depended on the weight of the female which was described through the known parameters of the length-weight relationship (see *Model parameterization* below). The survival of juveniles depended on the juvenile mortality

and the density-dependant growth time of the individual where each parameter had an equal contribution (0.5) to the overall survival of the juveniles. The predicted number of juveniles was then rounded and a genetic trait of each individual was added as described before. A Bernoulli trial (with a probability of 0.5) was used to assign the sex.

To address the question of currently prevailing fishing pressure, the fishing selectivity was introduced in the model through a selectivity curve (see *Model parameterization* for more details) that best described the asymptotic trend of removal of larger and older individuals by trawling, according to several empirical studies (Campos and Fonseca, 2003). Parameters used in the selectivity equation were recommended based on the current practices used for hake stock estimation (through personal correspondence with Dr Santiago Cerviño).

Model parameterization

The model was parameterized for a dataset, which consisted of 64 individual-based growth trajectories of the European hake. To attain a normalized dataset, a log transformation of K was modelled through a linear regression to obtain the final model $\log(K) = -0.511 - 0.005 \times L_{\infty}$ with a residual standard deviation of 0.126. Consequently, the simulation linearly calculated the L_{∞} values from the phenotypic trait for the range from 70 to 120 cm and K was predicted through its negative correlation with L_{∞} . Although it is not crucial for the model, L_0 (length at birth) was calculated through von Bertalanffy equation and set for the value of 2.5 cm.

The estimation of egg production was gained using the available data on recruitment, spawning stock biomass and preserving its dependency on the weight of the female producing the eggs. The amount of produced eggs was calculated by multiplying the weight of the female, described through the length-weight equation $weight = 0.00000513 \times length^{3.074}$ (ICES, 2012), and the mean value of the spawner-per-recruit (SPR ; in number per kg of recruit) derived from the collected dataset on recruitment and spawning stock biomass. The juvenile survival was predicted using the average value of data on natural mortality of 0-2 year old fish, obtained from the ICES (2012). In this model, the maximum lifespan of the individual was set to 20 years (www.fao.org, www.fishbase.org).

During fishing periods, only individuals older than 3 years were fished, since they reach their minimum landing size by that age (www.fao.org) in order to restrict the fishing pressure on that demographic group of fish. To mimic the selective pressure by the trawl, a logistic curve was introduced through an equation for selectivity $s = e^{a+b \times L} \times (1 + e^{a+b \times L})^{-1}$ where a and b parameters were -7.6 and 0.38, respectfully, with a 50% retention level at 20 cm of length (L_{50}). The level of fishing mortality was set to 0.15 which coincided with the current level of fishing pressure applied in modern fisheries (through personal correspondence with Dr Santiago Cerviño).

Simulation design

In order to investigate the current fisheries impact on ecological and evolutionary dynamics of the European hake, the above-explained model was run in a full-factorial design with two scenarios of fishing (absent/present) and one scenario for evolutionary processes, each replicated 20 times (Table 1). The scenarios, set as such, will outline the impact of the fishing pressure and the presence/absence of FIE.

Table 1. Table presenting set values of evolution, fishing and fishing mortality (F) for the three simulation scenarios.

| Scenarios | Evolutionary processes | Fishing | Fishing mortality (F) |
|---------------------------|------------------------|---------|---------------------------|
| Non-fishing scenario | Present | Absent | - |
| Non-evolutionary scenario | Absent | Present | 0.15 |
| Evolutionary scenario | Present | Present | 0.15 |

The first scenario (Table 1.) was used as a control population with respect to the last two scenarios. In order to tease apart the differences between present and absent evolutionary processes, in the non-evolutionary scenario the genotypes for the next generation were drawn from the parental gene pool gathered through the records of a fully adapted, non-fished population during a 30 year period of time. As described in the *Simulation approach* above, in the evolutionary scenario, the transfer of genotypes to the juveniles is based on Mendelian heritance rules where the genotypes of the offspring depend on the genotypes of the randomly mated parents. Each simulation was initialized with a population of 2000 individuals, which corresponds to a maximum of 1500 kg. Population carrying capacity was set to 5000 kg. During each simulation run, the population was given 2000 years` time to reach equilibrium and evolutionarily adapt after which the population would undergo a period of 100 years of fishing (non-evolutionary and evolutionary scenario) followed by 400 years of recovery. In order to restrict simulation time (and facilitate adaptation within 2000 years), the initial L_{∞} values and corresponding allele values were drawn between 70 and 120 cm. The appropriateness of this range was changed through preliminary simulation runs. At every simulation time step, ecological parameters and life-history traits were monitored. The monitored traits included population biomass with respect to carrying capacity, recruitment, recruit-per-spawner ratio (RPS or a ratio of recruitment and spawning stock biomass (SSB)), asymptotic length, and the length and age at maturation. Selection differentials on the allele sum (see above) were estimated through the breeder`s equation, $S=R/h^2$, where S is expressed as a ratio between genotypic change (change in the sum of allele values) from one generation to the next (R) and the heritability estimate (h) at the corresponding time step.

All simulation runs and graphical analyses were performed in R 2.15.2 (R Core Team 2012).

Results

The 20 replicated simulation runs of all scenarios are shown in Figure 2. Among the replicates of the non-evolutionary scenario, one replicate experienced a population collapse. Since this event is a product of natural stochasticity, I have taken it into consideration to account for possible outcomes of the scenario.

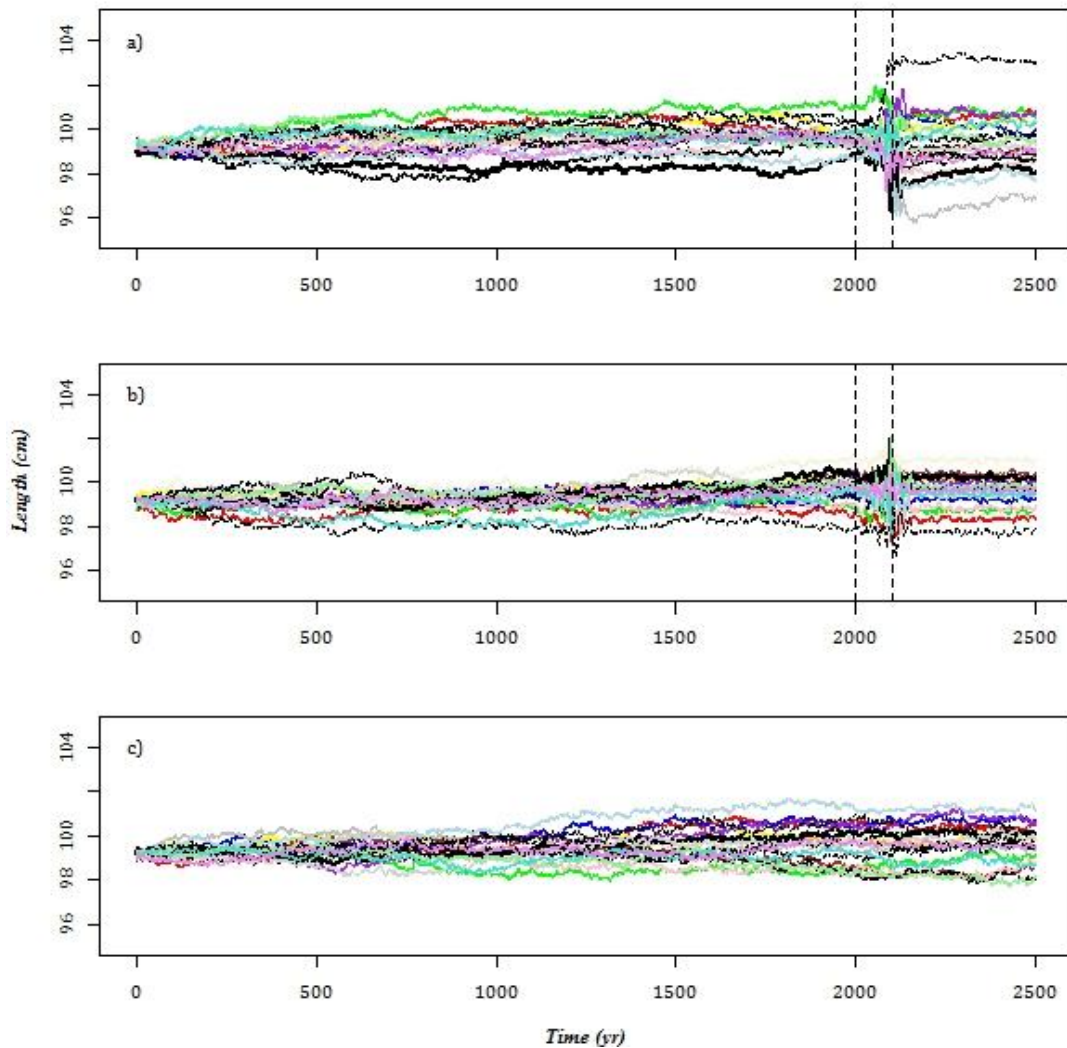


Figure 2. The graphs show average length values in cm plotted against the total duration of the simulation with respect to three different scenarios: (a) evolutionary scenario, (b) non-evolutionary scenario and (c) non-fishing scenario. The lines are presented in different colours to denote the 20 replicates, run for each scenario. Vertical dashed lines in graphs (a) and (b) represent the fishing period between 2000 and 2100 years of the simulation time, and are not present in graph (c) due to the lack of fishing. As expected, the evolutionary and non-evolutionary scenario exhibit changes in length with the introduction of fishing, but the magnitudes of the changes fluctuate depending on the scenario. Logically, the non-fishing scenario shows no change in length. All the scenarios still show a good amount of random fluctuation among the replicates.

For the presentation and interpretation of population demography and the main life-history traits, the last 600 out of the total 2500 years were shown since the first 1900 years represent the adaption period (Fig 3a-d and Fig 4a-d). Therefore, the first 100 years in the results indicate the pre-fishing period in which the population became adapted to the conditions of the set scenario.

With the introduction of fishing at year 100 all presented ecological parameters exhibit immediate response to the fishing pressure. As expected, the population biomass (Fig 3a) decreases with the start of the fishing period exhibiting a drastic fall from 100% to approx. 4% of biomass with respect to the carrying capacity; indicating the ecological impact of fisheries at the given level of fishing intensity. The life-history changes concerning recruitment are shown as a number of recruited individuals, and also, as a number of recruits with respect to the biomass of spawners in Fig (3b) and Fig (3c), respectively. Although the recruitment significantly drops in numbers for both evolutionary and non-evolutionary scenario, the RPS ratio shows an increase of recruits in comparison to the mature biomass with both present and absent evolutionary processes as a result of decreased intraspecific competition.

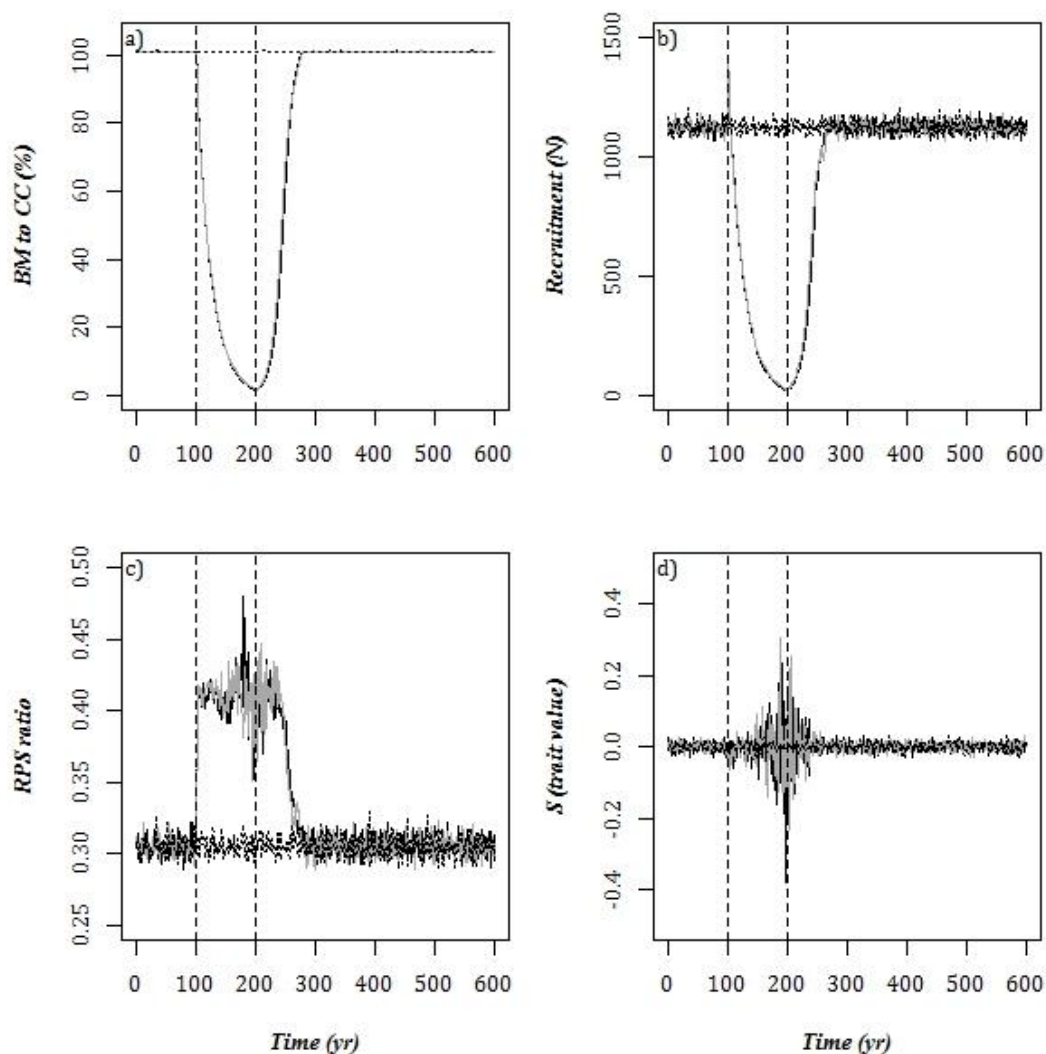


Figure 3. Ecological parameters graphically presented during simulation time. The population biomass with respect to carrying capacity ratio (*BM to CC*) (a), recruitment (b), recruitment-per-spawner ratio (*RPS*) (c) and selective differentials (*S*) are plotted against the last 600 years of simulation time. The simulation time is divided by vertical dashed lines into pre-fishing (first 100 years), fishing (from 100-200 years) and post-fishing period (from 200-600 years). The three different scenarios are shown as averages of the 20 replicated simulation runs and noted as following: the evolutionary scenario (black line), non-evolutionary scenario (dark grey line) and non-fishing scenario (dotted black line). The presented parameters exhibit various responses to the fishing pressure (after 100 years) and to the cessation of the fishing period (after 200 years) depending on the scenario.

As the fishing period ends, recruitment and population biomass reach the pre-fishing level following the removal of the fishing pressure for both evolutionary and non-evolutionary scenario. The *RPS* ratio and the selective differentials gradually stabilize at the pre-fishing level without significant discrepancies between the evolutionary and non-evolutionary scenario. However in comparison to *RPS*, selective differentials (Fig 3d) do not clearly show a direction of the selection, nor do they show any significant differences between the evolutionary and non-evolutionary scenario.

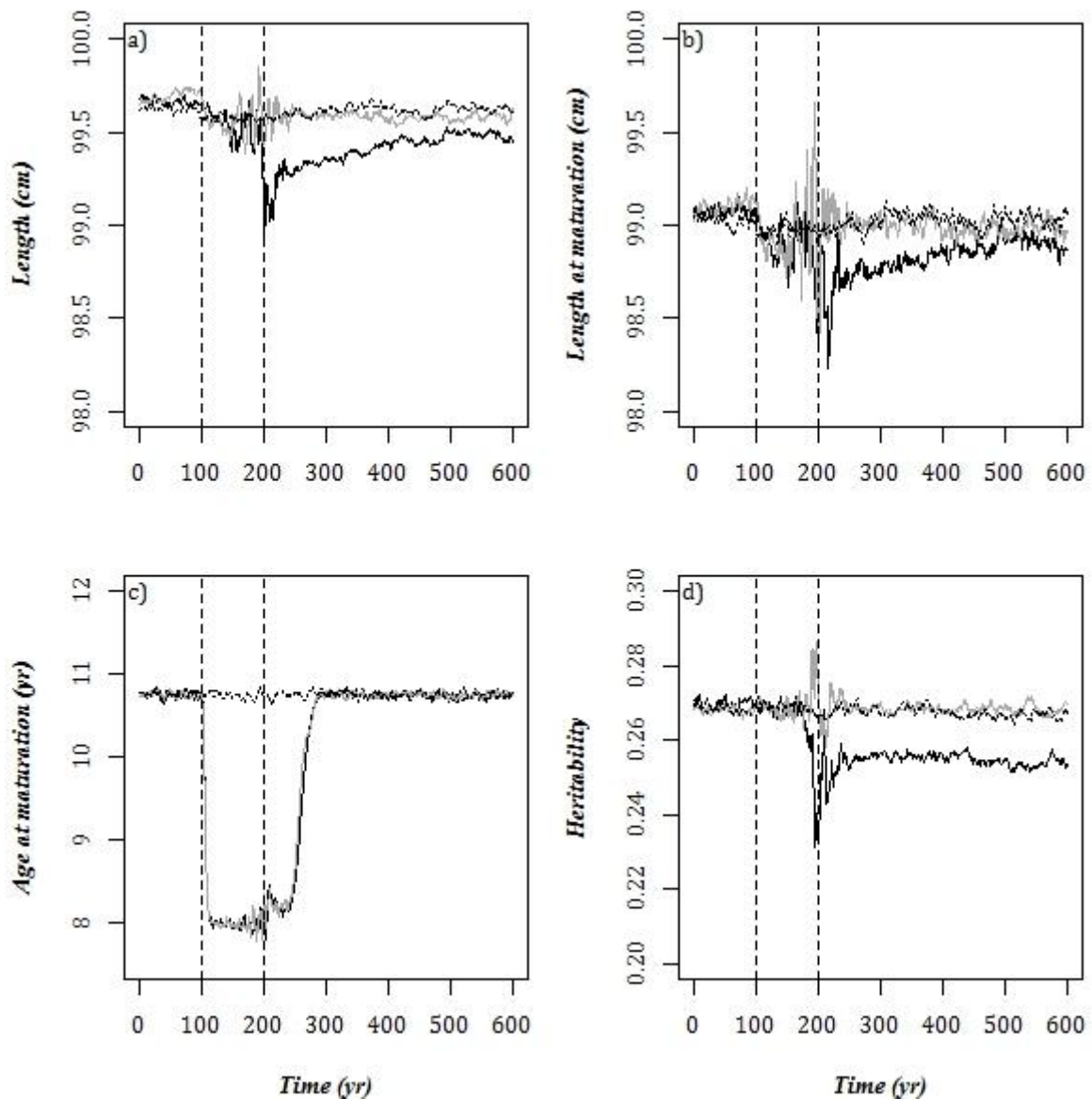


Figure 4. Main life history traits graphically presented for the last 600 years of the simulation. The life history traits including asymptotic length (a), length at maturation (b), age at maturation (c) and heritability (d), are plotted against the first 100 years of pre-fishing period followed by the introduction of fishing for the next 100 years (time period marked by vertical dashed lines) which ceases at 200 years and continues towards the recovery period until 600 years. Each graph contains the averages of the 20 replicated simulation runs for the three scenarios: evolutionary scenario (black line), non-evolutionary scenario (grey line) and non-fishing scenario (dotted black line). There is a noted belated response to the fishing pressure present in most of the graphs of the mentioned traits except for the age at maturation. The three scenarios show different trends during the fishing period with increasing discrepancies between the evolutionary and non-evolutionary scenario in graphs (a), (b) and (d).

Asymptotic length (L_{∞}), heritability and length at maturation (Fig 4a-c) show a clearly belated response to fishing. In Fig (4a), the response to fishing pressure becomes more obvious approaching the end of the fishing period (around 190 years) where the length is reduced by 1 cm in the evolutionary scenario while in the non-evolutionary scenario it exhibits only temporal variation due to demographic stochasticity. Length at maturation shows a high temporal variability in both fishing scenarios during the fishing period (Fig 4b). In comparison to length at maturation, age at maturation (Fig 4c) experiences a distinct decrease by 3 years under the fishing pressure and exhibits no differences between the evolutionary and non-evolutionary scenario. With the cessation of fishing (at 200 years) age at maturation gradually increases and completely recovers to the same level as the pre-fishing period for both fishing scenarios.

It is, however, interesting to notice that in the evolutionary scenario both length and length at maturation do not fully reach the pre-fishing level during the recovery period. With evolutionary processes present, both phenotypic traits maintain the same level reached at the beginning of the recovery period, which gradually increases as the recovery period progresses. The scenario with no evolutionary processes, however, shows no significant difference in comparison to the non-fishing scenario; fluctuates around the level of the non-fishing scenario during the fishing period and then levels out with the cessation of fishing. Lastly, heritability of the observed phenotypic traits shows a rather expected decline under the fishing pressure for both evolutionary and non-evolutionary scenario.

Overall, there seems to be no obvious indications of differences between the fishing scenarios with respect to evolutionary processes. In Figure 5, the cumulative numbers of juveniles are presented with respect to the genotype (the sum of the allele values), simulation scenario and the type of morality to describe the overall fitness of different life-history types. These numbers are presented for the time periods (a) before fishing, (b) during fishing and, (c) after fishing, to compare how fishing and recovery affect the fitness. Although the total range of possible allele combinations (genotypes) range between 0 and 20, none of the tested scenarios exhibit genotypes across the total range. Even though, there is no apparent difference between the time periods with respect to the average number of juveniles per genotype, the results indicate a higher deviation in juvenile numbers during the fishing period, most likely as a result of relaxed competition. The graphs suggest that the fishing pressure does not select for a specific genotype, since the fitness functions are markedly flat across a wide range of possible genotypes and, thus, life-history types.

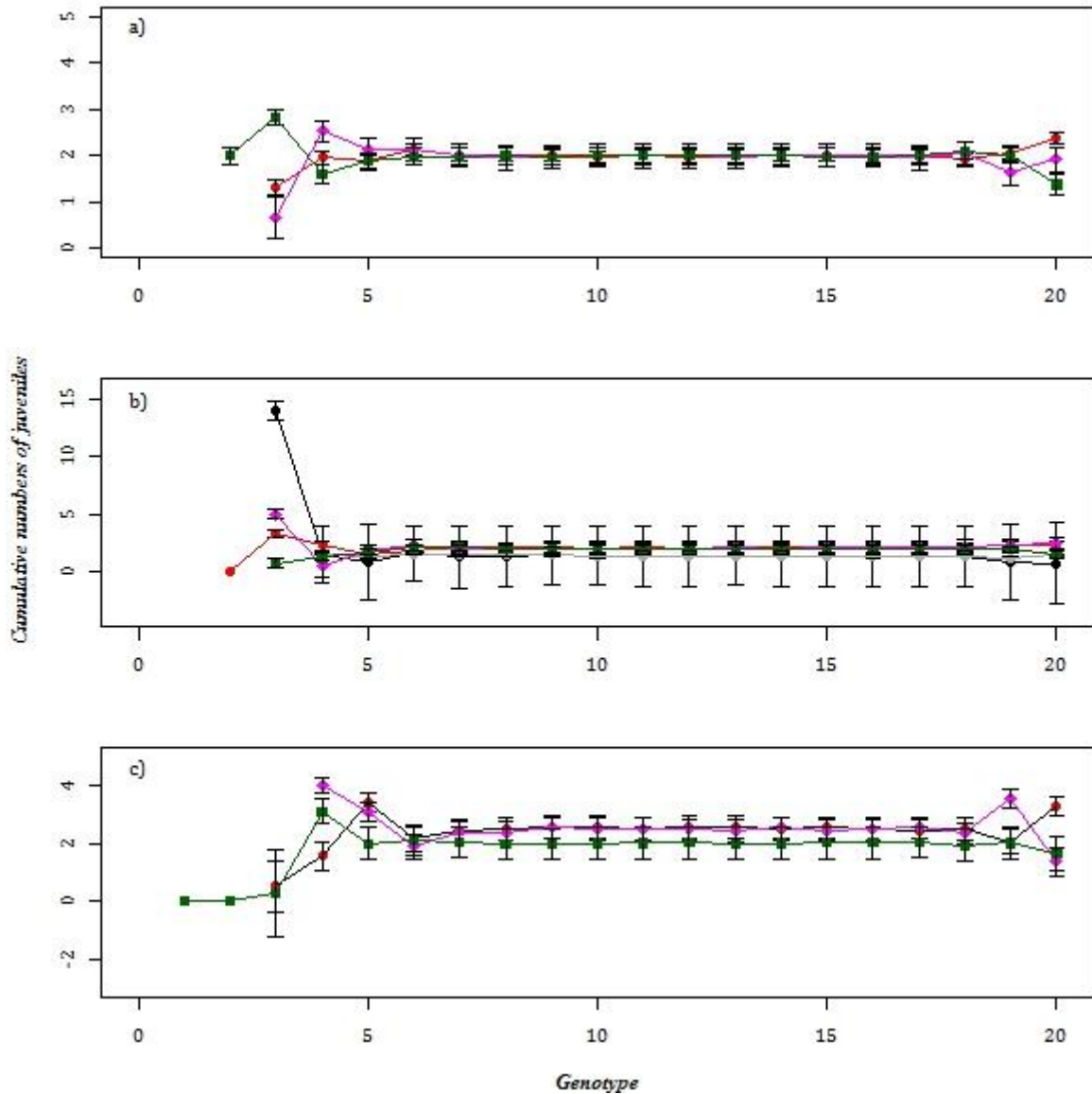


Figure 5. Average cumulative numbers of juveniles calculated from 13 replicates of all scenarios and plotted against the range of genotype with respect to simulation scenario and source of mortality. The graphs average across 50 year time spans for the periods: before (a), during (b) and after (c) fishing period. Data points differ depending on the scenario and source of mortality, connected by lines with a colour corresponding to the colour of the data points and denoted as following: black circular points – evolutionary scenario/died by fishing; dark grey circular points – non-evolutionary scenario/died by fishing; red circular points – evolutionary scenario/natural mortality; blue diamond symbols – non-evolutionary scenario/natural mortality; quadratic green symbols – non-fishing scenario/natural mortality. The error bars of each data point represent their standard errors. According to the scenarios, the individuals who died by fishing appear only during the fishing period in combination with the individuals who died by natural mortality which are also present in panels (a) and (c). Throughout the time periods, all scenarios show a smaller number of genotypes present in comparison of the total range of genotypes (0-20). The fishing pressure does not appear to select for a specific genotype although there is more deviation in numbers of individuals during the fishing period.

Discussion

Contrary to numerous studies dealing with FIE (Jørgensen et al. 2007, Dieckmann and Heino, 2007), in the present simulations, virtually no evolutionary changes were induced by fishing and the changes projected in phenotypic traits remain so minor that they are likely not biologically significant. Nonetheless, despite the fact that fishing does not appear to have implications at the level of individual fitness and, thus, no clear evolutionary shifts in life-histories, its impacts on the population biomass and recruitment are substantial: 100 years of fishing with 0.15 annual mortality leads to steep declines in population biomass and recruitment. The lack of evolutionary changes in hake phenotypes can be explained by the lack of phenotypic selectivity associated the simulated fishing strategy. As seen in Figure (3d), current fishing selectivity does not seem to favour individuals of specific phenotypic characteristics, such that selection differentials on life-history types scatter around zero. This is because the fishing selectivity with L_{50} of 20 cm selects fairly evenly over individuals of different body sizes. This poses a potential explanation to the lack of evolution since the change in the asymptotic length was only by 1 cm (Fig 4a), which is very minor from a biological perspective. It can be concluded that the prevailing fishing pressure on the European hake does not select for certain hake phenotypes (Fig 5a-c) and, therefore, does not drive fisheries-induced evolutionary changes in the observed phenotypic traits.

Recent studies on FIE warn about the difficulties in obtaining a straight-forward answer when testing for evolutionary changes, especially in model-based approaches (Kuparinen and Hutchings, 2012). The usage of evolutionary models or models in general has proven useful since it allows us to observe an evolutionary change in a “fast-forward” time (Heino and Dieckmann, 2008, Dunlop et al. 2009). However, it also constrains the interpretation of results through the set assumptions. For the purpose of this study, I have disregarded any environmental, seasonal or behavioural implications in the growth and fishing practices of hake. The assumptions set by the simulation approach in this project involved: (a) no difference in growth rate and retention by fishing gear between sexes, (b) the phenotypes among sexes were assumed equal for the sake of simplicity and to keep the focus of the genetic structure on a species level rather than sex, (c) reproductive success was based solely on the female’s size but not its previous spawning experience or age and (d) natural mortality of post-larval and adult individuals depended only on sexual maturity but not growth speed or body size. Despite the potential uncertainties introduced through these assumptions, they are set in order to simplify the simulations of individual growth trajectories and to address the aim of the project. Similar assumptions are also used in stock assessment models for fisheries management.

With all the assumptions stated above, one crucial limitation of this model-based project should be addressed separately. The dataset used for the growth trajectory simulation did not only stem from different locations, but was also acquired from hake populations that have been exposed to different fishing intensities for a long period of time. The issue in using such a dataset is that it can mask the real values of the studied

phenotypic trait, meaning that it is hard to identify whether the current state of the population is a consequence of phenotypic plasticity, or that it has already reached a stable state after the long exposure to the fishing pressure.

Other FIE studies using simulation models that integrate ecological and evolutionary processes (so called eco-gen models), have demonstrated significant negative effects of FIE on the population biomass and life-history traits, e.g. the Atlantic cod (*Gadus morhua*; Dunlop et al. 2009, Enberg et al. 2009). This gadoid species notably differs in biological characteristics in comparison to the European hake concerning their reproduction or, more precisely, the type of spawner and spawning frequency. Additionally, the fishing intensity applied in the studies on Atlantic cod ranged from 0.1 up to 0.6, while the fishing intensity in this study was set to 0.15. Therefore, the discrepancies in life-history characteristics and fishing pressures between this project and the afore mentioned studies suggest a possible explanation to the lack of FIE in the current exploitation pattern of the European hake. It should also be noted that the present results agree closely to a few previous studies: in the study by Andersen and Brander (2009) and Hilborn and Minte-Vera (2008), an estimation of the expected rate of the evolutionary changes was calculated under current fishing practices (e.g., trawl fishing). The expected FIE rate was shown to be generally slower than previously expected, which corroborates the conclusions on the lack of FIE in hake fisheries in the present study. Nonetheless, a comparative study by Kuparinen et al. (2009a) investigated the changes caused by trawl and gillnet on the population of Baltic cod, which demonstrated how trawl and gillnet methods retain different ranges of body length. According to this study, fishing performed by gillnets shifted the size at maturation towards larger body lengths while the trawl fishing had the opposite effect. Coinciding with the results of the previous study, the trawl was less selective capturing a wider range of body length and therefore, had a lesser effect on the size at maturation than gillnet fishing. Apart from the trawling, hake is also targeted by gillnets as well as gillnets and longlines combined (ICES 2012 Report), which could separately have a stronger selective effect on the hake in comparison to the fishing parameters used in this study.

Nevertheless, the presented results provide an important insight into the life-history of European hake under the current fishing strategies. Even though fishing mortality and selectivity applied in this study did not cause evolutionary changes in phenotypic traits, the effect of fishing can have major ecological and conservational implications such as direct population declines and loss of local or behavioural adaptations. Comparative studies investigating geographical and seasonal variations of reproductive potential in hake (Mehault et al. 2010, Murua et al. 2006) have indicated that hake populations are subject to local adaptations which can cause discrepancies in phenotypic traits and pose a significant threat to the natural populations if these traits are lost through harvesting. Studies on fish behaviour indicate that adult individuals tend to evade the fishing gear better than juvenile fish (especially relevant when using passive fishing gear) or simply reside in the refugias such as spawning areas which are less targeted by the fisheries (Uusi-Heikkilä et al. 2008, Abella et al. 1997). According to

Abella et al. (1997), such adaptations can explain, for example, the observed increase in recruitment, despite the high fishing mortality of adults. In the study by Anderson et al. (2008), the authors investigated why fished populations experience higher temporal variability in abundance than unexploited stocks. Furthermore, the same authors stress that the implications of such exploitation can increase the instability in the dynamics of the harvested population and, subsequently, lead to a local extinction. In comparison to this study, where the present results do not show obvious variability in abundance through time, fluctuations in population dynamics can still indicate the unsustainability of the current fisheries management despite the lack of FIE. For that reason, it might be prudent to conduct further investigations for the sake of precaution.

In conclusion, significant population declines demonstrated in the present results show that the lack of FIE is not an indicator of sustainable fishing practices. In wild populations, there are factors other than just ecological and evolutionary effects of fishing pressure that can affect population viability such as: ecosystem changes, changes in predation and prey availability, population resilience against environmental changes and potential loss of local adaptations (Audzijonyte et al. 2013, Palkovacs et al. 2011, Naish and Hard 2008). These factors should be accounted for when assessing sustainability of fisheries management. However, due to the absence of knowledge in the processes underlying or interacting with these factors and their roles in population dynamics of the species, the simplest precautionary approach is to reduce the fishing mortality, leading to relaxation of both ecological and evolutionary pressures. This will, in return, most likely decrease ecosystem impacts as well as keep the population at a level where it is more tolerant to environmental variations.

Conclusion

Here, a model-based approach has been used to investigate the effect of the current fishing practices on the European hake and to detect potential evolutionary phenotypic changes. The results of the study show significant ecological impacts of the currently prevailing fishing pressure on the biomass and recruitment of the population. Such practices indicate unsustainable level of exploitation, results that can be strengthened by the continuously recorded decline of the hake stocks (especially the Southern stock) recognized both by ICES and European Commission. No evolutionary changes in observed phenotypic traits of age and size at maturation and asymptotic length were found in the present study. The current fishing pressure does not select for a specific life-history type and, therefore, does not appear to cause heritable changes in phenotypes. The lack of FIE can likely be explained through the prevailing fishing selectivity: fishing practices target across a wide range of body sizes such that the probability of being caught does not differ between small and large growing individuals.

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