A blue and white fishing boat is on the water. Two dolphins are visible in the foreground, swimming. The background shows a coastline with hills.

Fisheries Sustainability in the Presence of Predation by Marine Megafauna

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FISHERIES SUSTAINABILITY IN THE PRESENCE OF PREDATION BY MARINE MEGAFAUNA

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ACADEMIC DISSERTATION

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LIST OF ORIGINAL PUBLICATIONS

This thesis consists of a summary and three research articles. All published articles have been reproduced with the permission of the journals concerned. The following publications have been included:

- I Jusufovski, D. and Kuparinen A. (2014) Contrasting evolutionary and ecological management objectives in the context of sustainable harvesting. *Evolutionary Ecology Research* 16: 133-142

- II Jusufovski, D., Saavedra, K. and Kuparinen, A. (2019) Competition between marine mammals and fisheries in contemporary harvested marine ecosystems. *Marine Ecology Progress Series* 627: 207-232

- III Jusufovski, D. and Kuparinen, A. (accepted) Exploring individual and population eco-evolutionary feedbacks under the coupled effects of fishing and predation. *Fisheries Research*

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THE INDIVIDUAL CONTRIBUTIONS OF THE AUTHORS OF ARTICLES I – III

- I D. Jusufovski was responsible for the data collection, model parameterisation, simulations, analyses and the interpretation of results. A. Kuparinen provided the initial model used in the research. Both authors wrote the article jointly.
- II D. Jusufovski was responsible for the literature search, definition of selection criteria and literature selection as well as writing. C.Saavedra assisted in literature selection and writing the article. A.Kuparinen contributed with writing.
- III D. Jusufovski was responsible for the collection of data regarding the predation and the study species' sexual dimorphism which were subsequently introduced to the model. With the introduction, D. Jusufovski has also conducted the model parameterisation, simulations, result extraction, analyses and interpretation along with the writing of the article. A. Kuparinen provided the initial model and guidance for the model parameterisation as well as contributed to the article writing.

ABSTRACT

Overexploitation is still a leading problem of many commercially targeted fish species. In addition to the high harvest rates and increasing biomass removals, harvested marine ecosystems have become a stage for the dynamic interplay of evolutionary and ecological processes. Removal through size selective fishing gear can cause negative pervasive effects on individual as well as population level. Observations of the individual phenotypic traits show a general trend of decreasing size and age at maturity that can have further negative effects on fecundity and population productivity. As these phenotypic changes become heritable (i.e., fisheries-induced evolution or FIE), this can further diminish the fish available to fisheries and render future fishing yields unsustainable.

Current management requires additional measures to include avoidance and detection of evolutionary changes. In order to understand which fishing objectives precede evolutionary change in individual traits, in my thesis I explored how different fishing strategies of the European hake (*Merluccius merluccius*) fishery reflect on ecological and evolutionary processes. While management focusing on the protection of juvenile fish can minimise the negative ecological impact of fishing, it increases the potential for evolutionary change in fish phenotypic traits. In contrary to this, fishing mortality targeting a wider range of age–size classes avoids evolutionary shifts in individual traits, however such fishing strategy demonstrates higher biomass removals.

In the wild, fisheries continuously interact with other predators, such as marine mammals, which can prey upon the same fish species or stock. The impact of these direct and indirect biological interactions between the marine mammals and fisheries is harder to detect and quantify, especially in synergy with other natural or anthropogenic stressors. In the context of fisheries-induced evolution, changes observed on an individual and population level caused by fisheries will also affect the prey size selectivity and prey availability to natural predators. My synthesis of recent research and findings on marine mammal–fisheries biological interactions demonstrates the need for improvement on data regarding marine mammal dietary and energetic requirements as well as their representation in model-based approaches. Moreover, combining different sources of knowledge about marine mammal–fisheries competition can aid to better quantify fish mortality caused by predation. Subsequently, this information would improve the fish stock assessments and provide insight on a sustainable window of opportunity to catch fish for fisheries and natural predators.

Thus far, attempts to quantify predation and fish availability for fisheries and natural predators exist through studies using mainly ecosystem and fisheries models. To explore how predation and fisheries shape and direct individual as well as population parameters, I have used an individual-based model to simulate hake

growth trajectories with regards to its own biological characteristics. As an individual grows, its life history is formed by ecological and evolutionary processes which also take into account the reproductive cost of survival and sexual size dimorphism (SSD). With co-evolved interactions between hake and the bottlenose dolphin (*Tursiops truncatus*) as the predator, fishing is introduced through a limited time period in order to observe prey recovery and resilience on an individual and population level. Although different types of predation give insight to discrepancies in the intensity of predation mortality, mere presence or absence of predation determines the projected values reached by prey individual and population parameters. Moreover, the joint effect of predation and fishing reveal contra-intuitive trends in hake individual traits and population parameters. The combination of duration and intensity of both size-selective removals, predation type and SSD determine the potential for persistent phenotypic and demographic changes after a period of overexploitation. Additionally, not all individual traits are equally susceptible to fisheries-induced evolution where the accountability of SSD and predation type can play a critical role. While fisheries remain the most detrimental source of mortality and size-selective removal for the harvested species, the indirect effects of fishing intensity diminish predator survival, thus having direct implications for top predator conservation. In conclusion, increasing the biological realism of the targeted species and incorporating different predation types with respect to evolutionary processes provide a more holistic approach to fisheries management: as it helps to avoid potential FIE and an overestimation of fish available to fisheries that can prevent top predator collapse. This will, ultimately, lead to a more ecosystem-based management with sustainable harvest rates and optimised fishing effort as well as the minimal cascading effects of size-selective removals.

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1 INTRODUCTION

1.1 HARVESTING AND MANAGING CONTEMPORARY MARINE ECOSYSTEMS

Contemporary marine ecosystems experience various anthropogenic pressures, yet among these various threats (e.g., Gordon et al. 2018), natural scientists have identified overfishing as the one of four major threats of concern (Boonstra et al. 2015). The historic exploitation of marine resources have led to deep structural changes and regime shifts in various marine ecosystems. While earliest records of commercial and recreational fishing date back from 90,000 to 4,000 BP, aquaculture has also been practised for several thousands of years (Lackey 2005). With technological and technical advancements, fishing grounds expanded from coastal to off-shore and oceanic fishing and with it, the shifts brought upon intensive and mainly, size-selective fishing. Nonetheless, fisheries still remain most intensive in coastal areas where its direct and indirect effects adversely impact species richness, trophic interactions and habitat heterogeneity (Lackey 2005; Jackson et al. 2007).

Ecological and trophic interactions are, in particular, sensitive to selective removals as certain trophic links formed through size-dependent processes are pivotal for the success of, for instance, juvenile fish survival and reproduction (Ohlberger et al. 2014; Fung et al. 2018). Furthermore, fishing from upper to lower trophic levels (i.e., “fishing down the food web”) directly contributed to the removal of top predators and the desynchronization between trophic levels, i.e. trophic cascades (Daskalov et al. 2007; Estes et al. 2011). As the ecosystem destabilizes further, this opens new trophic pathways facilitating bioinvasions as well as weakening ecosystem resilience to other threats, with a higher impact on local scale (Estes et al. 2011).

In response to the size-spectrum degradation by selective fishing, specific managerial approaches and fishing regimes have emerged. Most recent of those are ecosystem approach to fisheries management (EAFM) and balanced harvesting that strive to preserve community structure and trophic interactions (Pikitch et al. 2004; Garcia et al. 2012; Kolding et al. 2015). EAFM aims to ensure maximum sustainable yields with consideration to ecosystem health and functioning, preserving trophic structure and ensuring optimal yields in the long run (Pikitch et al. 2004; Garcia et al. 2012). Balanced fishing proposes a different harvesting strategy where harvest rates are determined in proportion to stock’s productivity with respect to species and size classes (Garcia et al. 2012; Burgess et al. 2016). Thus, balanced fishing can lead to optimal yields with low impact on the ecosystem, including reduced fishing selectivity on upper trophic levels as well as larger fish species (Gemert and Andersen 2018). Main criticism towards EAFM and balanced harvesting are logistical limitations (e.g., fishing gear, vessels), lack of data or

methods for measuring productivity, targeting of economically invaluable species as well as manipulation of other non-target species' abundance (e.g., marine mammal culls, disregarding uncertainties in multispecies modelling) for the purpose of maximising economically valuable yields (Corkeron 2006; Burgess et al. 2016).

Most fisheries are still predator-focused and, while transition to prey-focused fisheries would enable top predator conservation, truly sustainable ecosystem-based fisheries requires balancing between predator and prey as it improves species coexistence and ecosystem resilience (Tromeur and Loeuille 2017). Currently overexploited commercial stocks require revised management strategies, since recovered stocks have primarily density-dependent growth and recovery of large-bodied fish species will undoubtedly have a strong impact on lower trophic levels (Gemert and Andersen 2018). While EAFM and other similar multispecies approaches are focussed on ecological (trophic) processes and fisheries impact on ecosystem, the following subsection addresses the increasing need to include evolutionary aspects of selective removal by fisheries in fish stock assessments.

1.2 FISHERIES-INDUCED EVOLUTION (FIE)

Reductions in size and age at maturity have been observed for the past few decades in many commercially exploited fish stocks (Law 2000; Hilborn and Minter-Vera 2008). As fisheries target and remove mostly older and larger individuals, this releases the intraspecific competition for space and resources which increases the *per capita* intake (but see Enberg et al. 2012 that distinguishes resource acquisition and allocation). This enables earlier maturity at a smaller body size for the remaining individuals, as the energy once allocated to somatic growth is now allocated to the development and growth of reproductive organs, reducing the intrinsic growth rate as well (Eikeset et al. 2016). While reductions in size and age at maturity have been the general trend, delayed maturity is also possible specifically in case of fishing using passive gear (i.e., gillnets; Boukal et al. 2008). Additionally, delayed maturity has also been recorded, for instance when fishing occurs in species' spawning grounds, as is observed in cases of the Atlantic salmon (*Salmo salar*, L.; Jørgensen et al. 2007; Heino et al. 2015).

Changes in phenotypic traits can arise as a temporary response (i.e., phenotypic plasticity) to any force that selects for specific phenotypes, such as predation or increased temperature (Crozier and Hutchings 2014; Audzijonyte et al. 2014). Predation, in particular, has been documented to induce changes in size and age at maturity which ultimately alters the prey's maturation schedule and reproductive output (Abrams and Rowe 1996). For these reasons, phenotypic plasticity can mask potential evolutionary changes caused by fisheries (Hendry 2016). Furthermore, the potential of evolutionary change differs among late-maturing, slow-growing fish species and early-maturing, fast-growing species where the latter show a lower chance of heritable change in individual traits (Heino

and Gødo 2002; Devine et al. 2012). In addition, it is suspected whether current exploitation rates could incur evolutionary changes or whether the rates of evolutionary change are indeed significant (Andersen and Brander 2009; Hilborn and Mente-Vera 2008).

While fisheries are primarily size selective, there are other traits that can be targeted directly or indirectly through fishing activities and gear. Passive fishing gear, for instance gillnets and traps, may select for individuals of bold, even aggressive behaviour as those may be more vulnerable to being captured (Hilborn and Mente-Vera 2008; Uusi-Heikkilä et al. 2008). Contrary to passive, active fishing gear select more for shyer individuals whereas bolder ones have a higher success rate of escaping the nets (Diaz Pauli et al. 2015). Furthermore, boldness in behaviour is positively associated with fast-growing individuals in certain species where such individuals are also higher risk-takers (see Biro and Post 2008). This is especially pronounced in crustaceans where voraciousness is observed in fast-growing males (less in females), whose size also increases the chances of successful mating (Biro and Sampson 2015). In addition to behavioural traits, other individual characteristics that would lead to increased susceptibility to capture have been less explored, such as different physiological traits (see Hollins et al. 2018) or timing of breeding (Tillotson and Quinn 2018). This can offer additional insights into the impact of fisheries-induced alterations.

Discerning FIE from phenotypic plasticity is quite a methodological challenge. Detecting evolutionary changes is mainly restricted to experimental and model-based approaches due to the time needed to detect evolutionary change as well as the lack of information on species-specific genes responsible for the fisheries-induced response in size and age (Heino and Dieckmann 2008; Heino et al. 2015). However, empirical studies are also possible with the existence of long, historic data-series which allow for the comparison of genetic material before and after a certain period of size-selective removal (e.g., Czorlich et al. [2018] conducted an empirical genomic study on Atlantic salmon, *Salmo salar*). Experimental methods have gained valuable knowledge on the rates and mechanisms of trait change, but have disadvantages when transferring these findings on larger scales and complex systems (Conover and Baumann 2009). Among the most recent experimental studies, the study by Therkildsen et al. (2019) have attempted to elucidate the genomic aspects of FIE in the Atlantic silverside (*Menidia menidia*) and detected more than one simultaneous phenotypic shifts, revealing the complexity of trait correlation under size-selective fishing.

Model-based approaches can address a variety of species and systems as well as explore various traits that are directly and indirectly targeted by fisheries (reviewed in Govaert et al. 2019). Models are mainly focused on a specific trait or ecological process selected or affected by fishing in order to explore the trait heritability as well as process sensitivity through various scenarios differing in study species, fisheries or environmental conditions. Alternatively, the Probabilistic Maturation

Reaction Norms (PMRNs) are an example of a reaction norm method used to project the probabilities of an individual becoming mature in dependence of its size and age within specific time interval (Heino and Dieckmann 2008). While individual energy allocations can be challenging to incorporate in models, PMRNs have proven useful in overcoming biases associated with growth-driven responses to fishing in individual traits, contributing thus to an easier distinction of the phenotypic from an evolutionary response (Dieckmann and Heino 2007). Therefore, PMRNs are applied in model-based approaches as well as used to describe individual maturation trends.

Reduced population productivity and lower recovery rates can originate from fisheries-induced changes in individual traits (Audzijonyte et al. 2006; Enberg et al. 2009; Kuparinen and Hutchings 2012). The potentially irreversible negative impact of evolutionary changes can cause shifts in maturation schedule and trophic level, affecting not just the viability of the targeted fish species and its concomitant trophic links, but also sustainable fishing yields (Conover and Munch 2002; De Roos et al. 2006; Enberg et al. 2009; Heino et al. 2015; Kindsvater and Palkovacs 2017). Furthermore, as fish populations' biological limits shift, this will inevitably render the currently applied stock reference points (e.g., recruitment, spawning stock biomass) inexact leading to inadequate fisheries management (Heino et al. 2013). Thus, it has become an imperative to integrate an evolutionary impact assessment (EIA) into standard fish stock assessments which will aid to timely detect and prevent changes accompanied by harmful pervasive effects of FIE (Fraser 2013; Laugen et al. 2014; see Mollet et al. 2016 for an example of EIA for North Sea plaice).

1.3 MARINE MAMMALS: PREDATORS AND COMPETITORS

'Predation, put simply, is consumption of one organism (the prey) by another organism (the predator), in which the prey is alive when the predator first attacks it.'

*Begon, Harper and Townsend (2005)
Ecology: from individuals to ecosystems
297 pp*

Predation is a source of natural mortality, an uptake of fish defined by predator's prey selectivity. Predator's selectivity is determined by multiple factors such as prey's individual traits (e.g., size, age, fitness, physiological status), nutritional quality, prey availability in relation to other prey species and other competitors as well as habitat complexity or season (Pettorelli et al. 2015; Spitz et al. 2018). Through biomass removal, predators exert a top-down control directly on the prey population and indirectly onto secondary consumers affecting even the primary producers (Baum and Worm, 2009). Indirect bottom-up control is also possible where upper trophic levels provide organic enrichment to primary producers

through excretion (i.e., faeces), but also through decomposition of dead organic material (i.e., carcasses; Roman and McCarthy, 2010). Among marine top predators, marine mammals are known ecosystem engineers, contributing to the nutrient cycle, mixing of water layers and controlling the abundances of lower trophic levels (Lavery et al. 2014; Roman et al. 2014). Driven by trophic interactions, the life-history traits of both prey and predator have co-evolved increasing their chances of survival along the borderline between co-dependence and co-existence. Yet, trait-mediated interactions between prey and predator go beyond consumption and are not necessarily lethal in effect (Pettorelli et al. 2011). Prey-predator population dynamics are shaped through various behavioural, morphological and physiological traits formed from and by their two-way interaction (e.g., Schmitz 2017). Ultimately, modifications made through trait-mediated prey-predator interactions can induce plastic or evolutionary changes in their phenotype (McCoy and Bolker 2008; reviewed in Kishida et al. 2010).

Marine mammals usually occupy upper trophic levels where fisheries also tend to operate (Trites et al. 2006). This common pursuit for fish has led to a long history of human and marine mammal encounters. Ultimately, such competitive interactions have resulted in negative attitude towards marine mammal species, observed to interfere with fishing activities, and a notable number of marine mammal culling events (Goldsworthy et al. 2003; Bowen and Lidgard 2013). Although retaliations towards marine mammals are mostly a ‘thing of the past’ and widely considered illegal, some countries have continued to control for the marine mammal populations in their territorial waters through whaling and pinniped hunting (e.g., Norway, Iceland, Canada, USA; Reeves and Smith, 2006). Maintaining a healthy status of these predators has become one of EAFM objectives (Constable 2001; Link 2002), since unregulated removals of marine mammals erode trophic structure and decrease ecosystem resilience (Yodzis 2001; Gerber et al. 2009; Morissette et al. 2012).

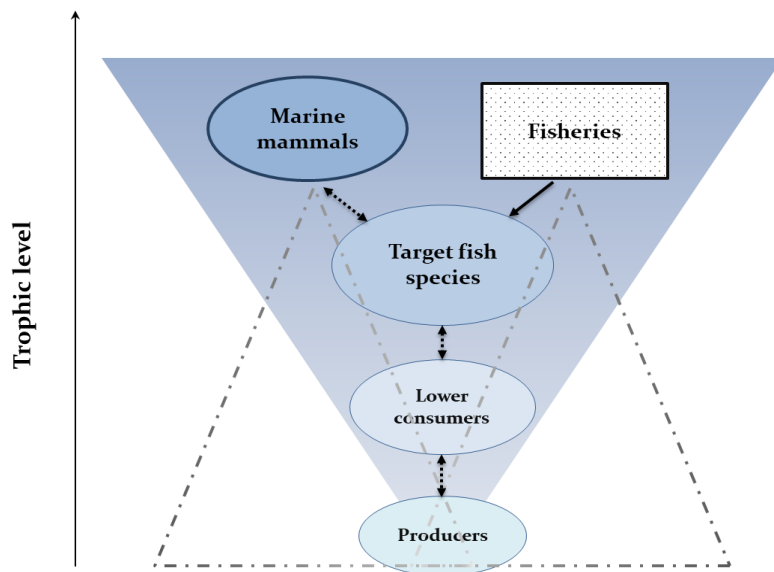


Figure 1. Graph presenting the interactions between marine mammals and fisheries with regards to the marine food web and its actors (reproduced from Article II). The blue gradient triangle depicts the range of direct operational and biological interactions between marine mammals and fisheries as well as how it radiates through the food web.

Grey dot-dashed triangles denote the indirect competition between marine mammals and fisheries for the primary production that supports them, also known as ‘food-web competition’.

At least, 90% of marine mammal species (or 105 out of 113 total) interact with fishing gear and vessels in one way or the other (marinemammal.org). The most obvious type of interaction between marine mammals and fisheries are the *operational interactions* which include depredation (i.e., removing fish directly from the fishing nets and traps) and any other form of physical interference with fishing operations (Fig. 1.; Matthiopoulos et al. 2008). Interactions that are harder to detect and observe are biological (or ecological) interactions which can lead to direct competition for fish where there is a clear removal of the same target fish population or stock. Indirect biological interactions refer to a competition between fisheries and marine mammals at the level of primary production (i.e., ‘*food-web competition*’) and thus, limit the primary production necessary to sustain both competitors (Goldsworthy et al. 2003; Trites et al. 2006).

Understanding the impact that marine mammals as predators have on economically valuable species requires quantification of predation. This includes a laborious data acquisition on marine mammal diet composition, foraging strategies and behaviour, dietary requirements as well as other confounding factors relevant for a successful hunt (e.g., predator’s ontogenetic stage and health status). Most of these parameters, especially the data on energetic requirements, are difficult to obtain due to the shyness and elusive behaviour of many marine mammal species (Lockyer 2007). Prey selectivity and preference is a result of the prey and predator co-evolution, which, unlike fisheries and fish dynamics, constitutes a fine balance of survival between prey and predator. Marine mammals as any predator, exhibit prey preference and size selective uptake of fish that, across marine mammal species, seem to target mainly fish below 30 cm of size (Etnier and Fowler 2010). Yet, in marine mammals other factors exist which can shift the prey preference due to easier catchability, higher nutritional quality and/or availability (Spitz et al. 2018). With the trend of reduced size-at-age in overexploited fish populations, individuals of such morphological traits are exposed to higher predation and more likely to get caught (Abrams and Rowe 1996). Size selective removals by predation, fisheries or otherwise are bound to alter the demographic structure of fish populations as they affect their individual traits. This ultimately demands a fish stock assessment that better integrates predation effects for future fishing yields, but also account for the effect fisheries have for predator conservation (Constable 2001; Froese et al. 2016).

1.4 STUDY SYSTEM

The European hake (*Merluccius merluccius* Linnaeus, 1758) is a demersal gadiform species with a native distribution ranging from North and Barents Seas, Irish and UK waters to the southern Mauritanian waters, and further to the Mediterranean and Black Seas, with the highest occurrence along the Atlantic coast, Macaronesian islands and in the Western Mediterranean basin (Fig. 2.; Murua, 2010; Sion et al., 2019). Hake is a predatory fish and, with their ontogenetic development, their diet shifts from mainly crustacean to piscivorous diet at which

point they can also be prone to cannibalism (Casey and Pereiro, 1995; Carpentieri et al., 2005; Rueda et al., 2019). Hake reproduces in batches and exhibits a protracted spawning period (Murua, 2010). According to Cerviño (2014), hake displays a sexual size dimorphism (SSD) where females are larger than males at any given age, and tend to mature later and reach older ages than males. The maximum recorded age for hake is 20 years (Muus and Nielsen, 1999), however, for the NE Atlantic populations most individuals reach a maximum of 12 years of age (Murua, 2010; GFCM, 2016).

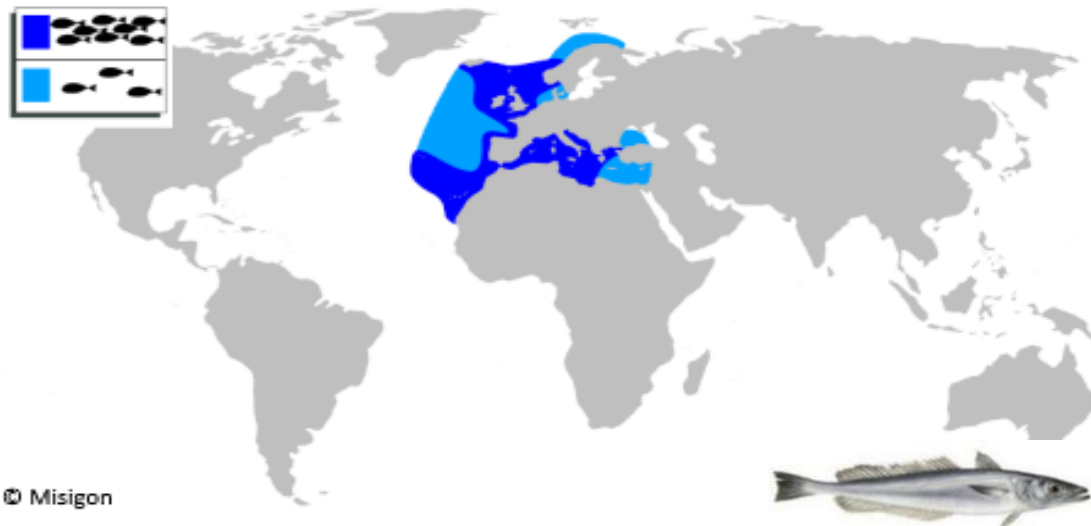


Figure 2. European hake and its distribution range in the Atlantic, Mediterranean and Black Seas (reproduced from Wikipedia Commons, Misigon and ec.europe.eu).

Hake represents a highly valuable commercial species, particularly for the countries of NE Atlantic and the Western Mediterranean. Hake is mainly fished by trawling nets, but also longlines, gillnets and various artisanal tools (Murua, 2010; GFCM, 2016; ICES, 2019). Among different hake populations and their concomitant fisheries, the Bay of Biscay and the Galician hake populations exhibited notable fluctuations in size at maturity during 1980s (Domínguez-Petit et al. 2008). Later studies determined discrepancies in the strength of the phenotypic plasticity between these populations to the fisheries size selectivity (Hidalgo et al. 2014). While there was no clear indication of a possible FIE, these populations have been and continue to be heavily exploited (ICES, 2019).

One of hake's natural predators is the bottlenose dolphin (*Tursiops truncatus* Montagu, 1821) a globally distributed marine mammal species. Although most dietary studies of the bottlenose dolphin confirm its diverse diet and opportunistic feeding (Bearzi et al. 2008), prey preference among bottlenose dolphins has been noted in experimental conditions (Corkeron et al. 1990). Hake is among the bottlenose dolphin's most frequent prey in the areas of their geographic overlap. Hake is reported in the diet composition of Irish, Ibero-Atlantic and the West Mediterranean bottlenose dolphin subpopulations (Blanco et al. 2001; Fernández

et al. 2011; Hernandez-Milian et al. 2015; Santos et al. 2007, 2014). However, the lack of hake in the dolphin's diet has been noted in the Scottish waters, the Eastern Mediterranean basin and the Black Sea which can indicate the lower availability or absence of hake in those regions (Santos et al. 2001; Gladilina and Gol'din 2014; Scheinin et al. 2014).

The bottlenose dolphins are known to interact with fisheries and have been observed to follow trawlers and depredate coastal nets (e.g., López 2006; Bearzi et al. 2010; Goetz et al. 2015). In addition to operational interactions, there are historical records as well as current events demonstrating the fishermen's negative attitude towards bottlenose dolphins based on the biological interactions between fisheries and bottlenose dolphins (i.e., direct or indirect competition for the same resource or fish; Bearzi et al. 2002, 2008). Nevertheless, studies that attempted to quantify the fish uptake by bottlenose dolphins suggest a notably lesser impact than the fisheries biomass removal (e.g., Bearzi et al. 2010). As with other marine mammal species, difficulties still arise when addressing predation as a source of natural mortality due to low data on energetic requirements of the bottlenose dolphins. Santos et al. (2014) used available data on bottlenose dolphins' abundance, diet, energetic composition and requirements to quantify their predation on hake in Spanish provinces of Galicia and Asturias. In this study, the bottlenose dolphin makes up of 82% of predation on relevant hake stock, exceeding the value of the usual natural mortality applied in fisheries assessment and underestimating the true mortality caused by predation.

1.5 AIM AND SCOPE OF THE DOCTORAL THESIS

The underestimation of the ecological and potential evolutionary effects induced by fisheries and predation poses an additional risk of overestimating the fish availability to all its consumers. Moreover, the unknown independent effects of predation as well as the joint effects of fishing and predation could lead to detrimental impacts on fish phenotypic diversity. On the ecosystem level, it can become an even greater total loss affecting directly various stakeholders that rely on marine resources. In this project, I strive to address the sustainability of fisheries and the stability of trophic interactions with respect to different fishing practices, predation and underlying eco-evolutionary dynamics. Additionally, I explore how species' life-history influences the availability of fish to natural predators and fisheries, respectively.

The current research encompasses the following working hypotheses:

- 1) The long-term sustainability of fisheries, viability and phenotypic diversity of hake changes in dependence of fisheries strategies and objectives.
- 2) The coupled effects of predation and fishing will:
 - a) have a detrimental impact on size and age at maturity with regards to the species' ecological characteristics, increasing the potential for FIE;
 - b) reduce the population resilience and recovery after fishing cessation.

- 3) The discrepancy in body size among hake sexes will cause discrepancies in their vulnerabilities to predation and fisheries.
- 4) Prey-predator interaction and predator density will be negatively affected by the fishing intensity.

In Article [I], I address the first hypothesis by exploring two different fishing strategies — one that aims to preserve the juveniles and allows for at least one spawning event, and the other that distributes the fishing mortality across a wide range of age-size classes — with respect to the ecological and evolutionary effects on fish phenotypic diversity and abundance. These opposing fishing regimes, with their own short- and long-term benefits and caveats, provide an opportunity to optimise the fishing efforts whilst minimising the impact on fish individual traits and population productivity. Depending on the priorities implemented within the fisheries management, applying appropriate operational measures can lead to sustainable harvesting levels and a stable fish population structure. Furthermore, Article [II] provides a synthesis of knowledge on how trophic structure or rather, prey-predator dynamics play a role in supporting the fisheries in the long run, especially when predators are regarded as boosters of fish population productivity rather than mere competitors. As marine mammals and fisheries exhibit, among others, size selective uptake of fish, it is plausible that jointly they could complement or even annul their, otherwise, independent effects on fish. This synthesis also provides a preliminary insight into the dynamics between the target fish, predators and fisheries necessary for expanding the model-based approach and forming the scenarios to address the hypotheses 2.-4. in Article [III].

To describe the predator's size selectivity and removal in Article [III], I use functional responses and explore potential eco-evolutionary feedbacks to fish abundance, growth and reproduction whilst respecting the species' ecological characteristics. While investigating the direct effect of predation based on individual's size, the indirect effect is reflected on the individual's age and sexual maturity due to trait correlation. Fishing is introduced in a limited time frame to the co-evolved prey-predator dynamics where fish parameters indicate how joint impacts of fishing and predation shape their responses to the size-selective removals. At the population level, the amount of fishing pressure endured by hake demonstrates the capacity of the population to resist to fishing-induced changes, whilst undergoing predation. Furthermore, the return of individual and population parameters to their pre-fishing values indicates the population recovery potential. Additionally, feedbacks of fishing intensity and fish life-history traits aid to determine the fishing strategies that are sustainable from fisheries perspective with respect to top predators (see Fig. 3. for graphical description).

2 METHODOLOGY

2.1 MODEL – BASED APPROACH

Individual-based model: basic features

Individual-based models (IBMs) predict and project population trends based on individual's life cycle with the assumption that individual variability has a considerable effect on the population level (Plagányi 2007). IBMs are used interchangeably with agent-based models (ABMs) as their dynamics are described and calculated at the same level. Yet, IBMs usually imply modelling based on the 'true' individual organisms while ABMs mainly refer to associations based on, e.g. developmental/ontogenetic stage (e.g., juvenile and adults), behavioural type (e.g., shy vs. bold types) or perhaps used to describe different fisheries (Plagányi 2007). There is a wide application of IBMs/ABMs in natural sciences (DeAngelis and Mooij 2005) and they extend from single- to multi-species as well as to complex, ecosystem models used to test various managerial decisions and strategies such as InVitro and OSMOSE.

In the current IBM, the individual is characterised by its own growth trajectory which is described by the von Bertalanffy (VB; 1938) equation (presented in detail in the following subsection). This approach has been used in numerous studies addressing different types of growth in various organisms exploring the patterns of life-history traits (e.g., size or age at maturity) under a variety of conditions (Lester et al. 2004). The VB equation assumes an asymptotically diminishing growth rate with age with no explicit growth cost for the reproductive investment starting at maturation. One of the critics to the usage of this equation for the description of growth trajectories in fish is its weak representation of the transition from determinate (before maturation) to indeterminate (after maturation) growth (Day and Taylor, 1997). Furthermore, VB equation is more appropriate for describing the adult or post-maturity growth than the juvenile growth trajectories (Lester et al. 2004). Yet, while the energy allocation or the growth type are not currently in focus, this does not notably affect the interpretation of crucial individual and population parameters addressed in the context of current research questions. The application of VB here allows for the exploration of growth determined by the cost of reproduction which affects mature individuals as well as the phenotypic shifts in all parameters associated with the maturity status. Despite that the introduced fishing and predation also targets immature individuals, the current research does not focus on juvenile growth *per se*. While the transitional growth between pre- and post-maturity stage can increase fish vulnerability to fisheries or predation and it is therefore underrepresented when using VB equation: this is still accounted for through the additional source of natural mortality caused by the reproductive cost.

Addressing the eco-evolutionary dynamics on an individual level requires an introduction of the principles of evolving traits through sexual reproduction. Thus, in this research I apply an eco-genetic, life-history model which was initially developed and parameterised for the Baltic cod (*Gadus morhua*; Kuparinen et al. 2012). Other applications of the current model include the research of the population recovery and the potential of an Allee effect in the Atlantic cod stock (Kuparinen and Hutchings 2012; Kuparinen et al. 2014). The model incorporates quantitative genetics which allows for detection and testing of an evolutionary change in individual traits, overcoming the lack of knowledge about the genetic basis of FIE in fish. Each gene of a genotype is located within a specific locus of the chromosome concerned and in a diploid organism such as fish, each gene consists of 2 loci. Following the quantitative genetics principle, we add a value to each loci with the assumption that the sum of all loci has a very little effect for the trait in question (Roff 2002). Through its life cycle, each individual undergoes main ecological processes with included information about the species' biological characteristics (Fig. 3.). Predation and fishing are separate sources of mortality, whose effects are observed through a set of individual and population parameters. In the following subsections, I will describe how growth and other main ecological processes along with evolution, predation and fishing are described and integrated into the model.

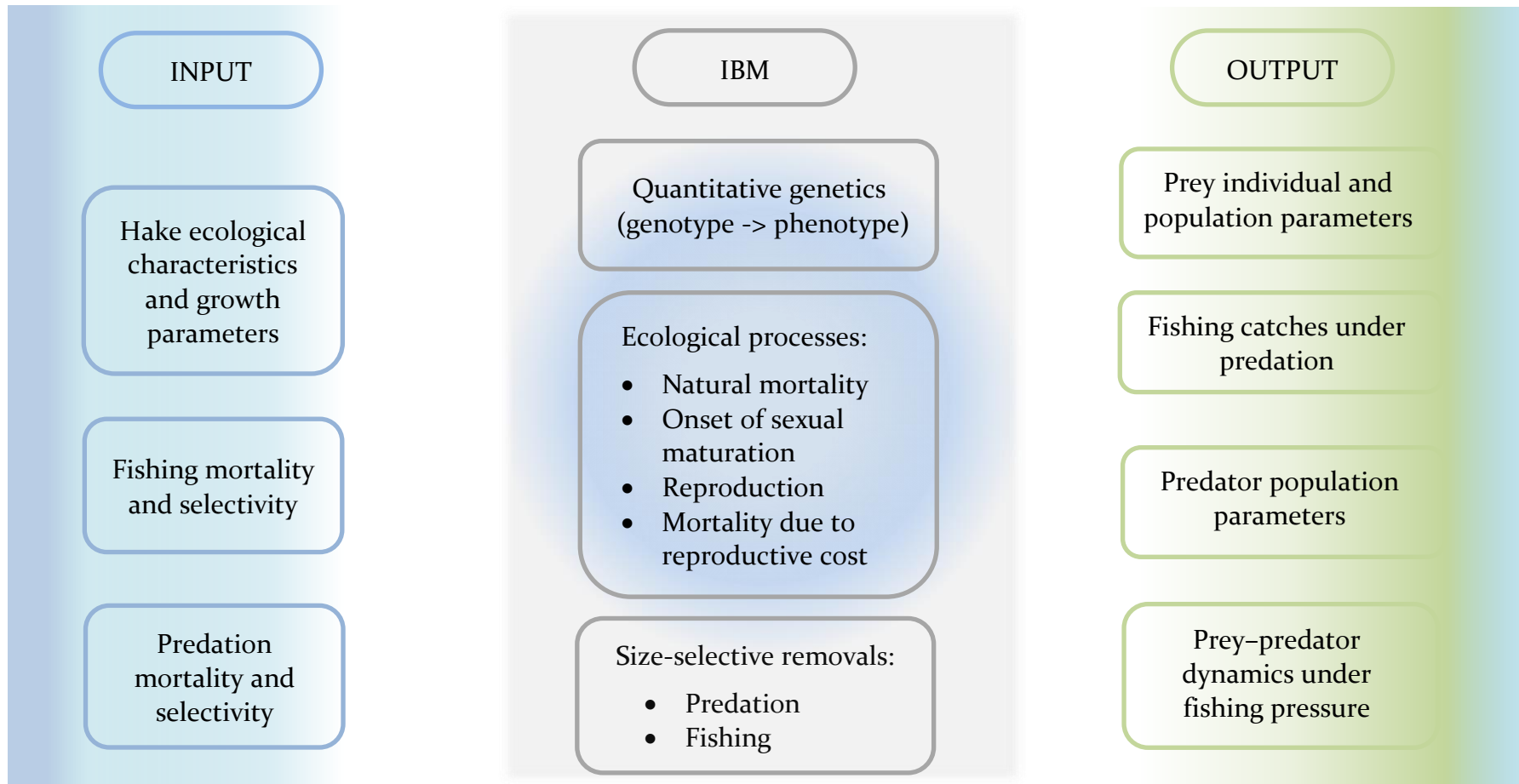


Figure 3. Graphical representation of the three main parts in the model-based approach showing from left to right: 1) the input variables; 2) main features of the individual-based model (IBM) and 3) crucial output parameters. The input refers to the relevant information on hake and bottlenose dolphin characteristics as well as the hake fisheries. The IBM applies quantitative genetics approach, which allows the translation of the genotype to phenotype via the asymptotic length. Each individual experiences the listed ecological processes under specific conditions and at a specific point in its life cycle. While predation is constantly present during the individual's life, fishing is applied during a set time period (see *Simulation design and scenario* for details). The output variables provide different aspects of the fish, fisheries and prey-predator dynamics experiencing overexploitation, with respect to eco-evolutionary feedbacks.

Growth

Individual growth trajectories are described by the von Bertalanffy equation where hake length L at age t is calculated as:

$$L_t = L_\infty - (1 - e^{-K(t-t_0)}) \quad (1)$$

The length is predicted based on the theoretically maximum length (L_∞) the length of fish under unlimited resources and the species-specific intrinsic growth rate (K). The age of hake at zero length (t_0) is currently irrelevant for the description of growth trajectories and thus, it is the same for all individuals. Based on the VB growth trajectory, fast-growing (i.e., higher values of K) individuals have lower values of L_∞ as well as achieve lower size and age at maturity (Kuparinen et al. 2012). As females of many fish species mainly exhibit higher values of L_∞ in comparison to males, the sex-specific L_∞ (i.e., SSD) is calculated at this point for each sex separately (see further details in *Model parameterisation*). Depending on the known variable, growth described as such allows us to calculate K or L_∞ owing to their negatively correlated relationship. Furthermore, by using the RL ratio of the length at maturity (L_{mat}) and L_∞ , we can define the proportion of individual's length at which it reaches sexual maturity.

Population growth is also defined through density dependent processes, introduced through the individual's growth time. The growth time is defined by the time available for an individual to grow within one year (i.e., $L_t - L_{t+1}$) and described by a range from 0 to 1. Population density is calculated as a ratio of population biomass (BM) and carrying capacity (CC), so that at a high population density, growth time (Δt) is reduced by 50% (Fig. 4.) following the logistic growth curve:

$$\Delta t = e^{a-b \times BM/CC} (1 + e^{a-b \times BM/CC})^{-1} \quad (2)$$

Where a and b parameters were estimated through model parameterisation (see *Model parameterisation* for further details).

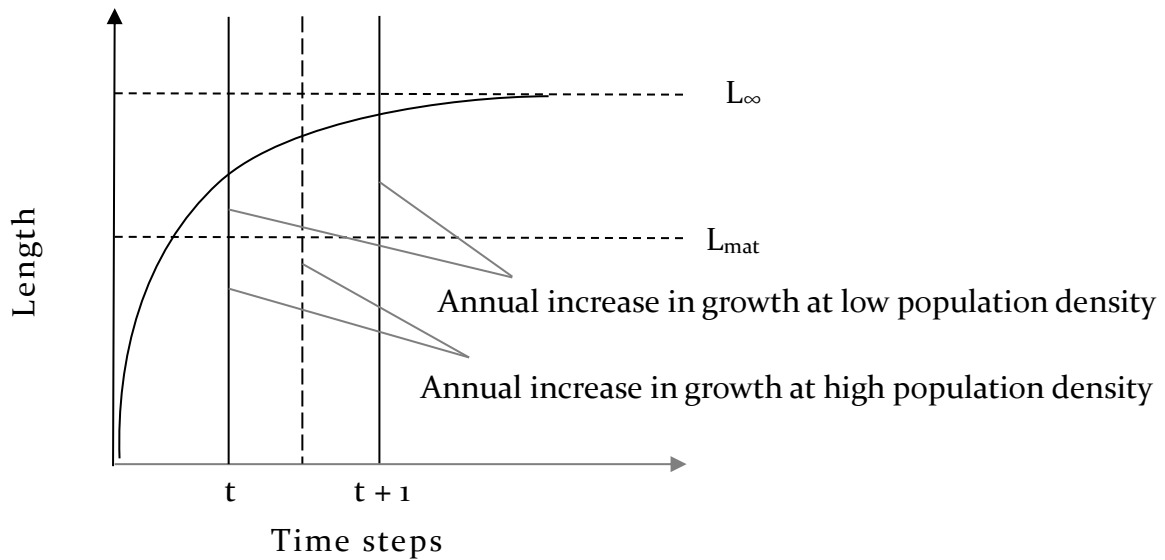


Figure 4. Graph showing growth of each individual in dependence of population density. The individual's trajectory (asymptotic, curved line) is described by its asymptotic length (L_{∞}) and the length at maturity (L_{mat}) reached at the 51% of L_{∞} . Growth time is observed between two time steps shown on x-axis where the individual's growth is reduced by 50% in case of high population density.

Evolution

Every individual is genetically described by 10 diploid loci where each loci is additive and of equal impact. The total number of diploid loci is derived through previous parameterizations of the model and considered sufficient to capture the genetic variation (see Kuparinen et al. 2012 for details). Each allele has a randomly assigned code of either 1 or 0 where the additive effect of a genetic trait is expressed as the sum of alleles, ranging from 0 to 20 (Fig. 5.). During sexual reproduction, the genotypes are passed down to the next generation of offspring following the classic laws of Mendelian inheritance. Once assigned, the genotype is then transferred to the phenotype by adding a standard deviation of 3.5 (i.e., phenotypic variation) which gives out heritability values within an expected range for a fish species (0.2 – 0.3; Mousseau and Roff, 1987). The genetic trait value is then incorporated into L_{∞} , at which point K can be predicted owing to their negative correlation.

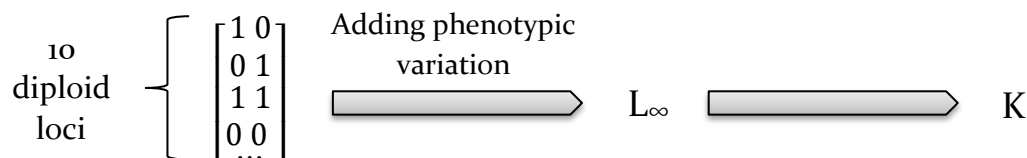


Figure 5. Stepwise presentation incorporating the genotype with a range of sum values from 0 to 20 through the phenotype into the individual's asymptotic length (L_{∞}), which allows for the calculation of the intrinsic growth rate (K).

The description of growth and the evolution of traits applied in the current model encompass different life-history strategies. The evolution of all genotypes is directly linked to L_{∞} where individuals within the higher range of L_{∞} values are derived from higher phenotype values. Moreover, evolutionary changes that occur in L_{∞} affect other life-history traits owing to the associated trade-offs. For instance, greater L_{∞} and lower K values are associated with longer life span albeit low reproductive output. Reductions in L_{∞} (caused by either harvesting or predation) and consequently, lower size/age at maturity also diminish the maximum age, but increase the reproductive effort (Shuter et al. 2004). Although the correlations among life-history traits are phenotypic rather than genetic in the current model (Kuparinen et al. 2012), such inclusion of evolutionary processes on the level of L_{∞} is an advantageous approach due to the low demand of data (i.e., L_{∞} and K) which are widely available for many fish species.

Reproduction and the instantaneous mortality rate

During every reproduction event, a mature male and a mature female are randomly assigned. The number of offspring is based on the egg production and survival. The egg production is predicted based on the recruit-per-spawner value (RPS) and the female weight. RPS is obtained through the available information on recruitment and spawning stock biomass (ICES, 2012), while the female weight (W) was calculated using the length-weight relationship as:

$$W = a \times size^b \quad (3)$$

Where the a and b parameters are species-specific. Juvenile survival is calculated in dependence of the juvenile mortality as well as the density-dependent growth time where both parameters equally (0.5, each) contribute to the overall juvenile survival. Once the estimated number of juveniles is rounded, the genetic trait is then added to each individual as described above. Sex is assigned through a Bernoulli trial with a 50% probability.

In addition to the juvenile mortality, the individual also experiences three other sources of mortality: (1) instantaneous mortality rate consisted of natural mortality (M) and the mortality caused by the survival cost of the reproduction (SC), and (2) size selective predation (see the following subsection for explanation). M is applied only to individuals older than 2 years while SC is dependent on the sexual maturity of the individual. Both M and SC are equally applied for both sexes. At every time step, the fate of the individual is decided using a Bernoulli trial.

Predation

Predation is described through functional responses proposed by Holling (1973). There are three main types of Holling's functional responses that describe a predator's kill rate. The functional responses differ depending on the level of

complexity used to describe the predator's rate of prey consumption. While Type I Holling's functional response linearly increases the number of eaten prey with prey density where the predator never satiates, Type II and III describe a predator that reaches a point of satiation with time. However, these two types of functional responses differ in the consumption trend of prey at low population density (Fig. 6.). Type II is better at consuming prey at low population density, whereas Type III is described as a slower consumer of prey at the same level of prey density. In this study, I have applied Type II and III functional responses (hence fort FRII and FRIII, respectively) assuming that the predator will eventually reach a point of satiation and cannot consume prey continuously due to costs and risks related to foraging and feeding (i.e, energy expenditure, exposure to other predators etc.).

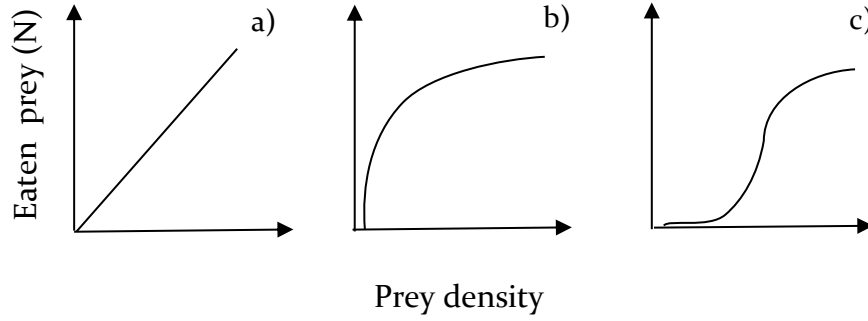


Figure 6. Three types of Holling's functional responses: (a) Type I; (b) Type II and (c) Type III. Type I is characterised by a linear trend of prey consumption, while Type II and III show an asymptotic and sigmoidal trend, respectively.

Firstly, the predator is introduced through a predator population equation adopted from the Rosenzweig & MacArthur's prey-predator model (Rosenzweig and MacArthur, 1963) which represents a generalization of the Lotka-Volterra (LV) predator-prey model providing a more realistic numerical response than the LV model. With regards to the applied Holling' functional response, the predator population density (p) is then calculated at each time step t . Thus, with FRII, p_t is given by:

$$p_t = p_{t-1} e^{(e_p a_p n_t / (1 + h_p a_p n_t) - d_p)} \quad (4)$$

While for FRIII, p_t is calculated as:

$$p_t = p_{t-1} e^{((e_p a_p n_t)^2 / (1 + (h_p a_p n_t)^2) - d_p)} \quad (5)$$

Where predator density depends on the initial predator density or precisely, the density calculated in the previous time step (p_{t-1}), and prey density (n_t) calculated as a ratio of BM and CC at each time step. The predator population dynamics is also shaped by predator death rate (d_p), handling time (h_p), attack rate (a_p) and assimilation efficiency (e_p). d_p is the time needed in order for the predator to find

and capture prey which includes the time it is not handling any other potential prey (Pettorelli et al. 2015). a_p is based on: rate of encounters \times proportion of encounter rate that becomes an attack \times proportion of attacks that are successful, while e_p is a proportion of assimilated energy gained from ingested prey.

The predator densities (p_t) given by equations (4) and (5) at each time step allow for the calculation of the probability of a prey being eaten (p_{eat}), expressed through a predator rate:

$$p_{eat} = \frac{a_p p_t}{(1 + h_p a_p n_t)} \quad (6)$$

In case of FRII. For FRIII, p_{eat} is given as:

$$p_{eat} = \frac{a_p p_t^{(2-1)}}{(1 + (h_p a_p n_t)^2)} \quad (7)$$

While the predation (meaning, p_{eat}) is applied on an individual level, the predator output (i.e., predator density) is calculated on a population level to observe its dynamics in dependence of the available prey.

Fishing

Fishing is described through a logistic selectivity equation (see Fig. 5.) as:

$$s = e^{a + b \times L} (1 + e^{a + b \times L})^{-1} \quad (8)$$

Where the selective pressure (s) is defined by a and b parameters estimated to reflect the hake length at 50% of retention by the fishing gear (L_{50}). Fishing is applied for individuals older than 3 years of age, since hake has already reached its minimum landing size at that age. Fishing selectivity along with fishing intensity determines the probability of the fish being caught.

2.2 MODEL PARAMETERISATION

Data acquisition

Individual growth parameters of hake were attained through unsexed data obtained from Ragonese et al. (2012). This dataset is compiled of 64 data points gathered across mainly Mediterranean hake population providing a general sample of individual-based growth parameters (L_∞ , K , RL and t_o) for this species. Other biological characteristics (see Table 1. for details) as well as the prevailing fishing regimes reflect the biology and fisheries of the NE Atlantic (Spanish) hake population (see the following subsection below for details). In the current study, I aim to address the study species in general and do not focus on the species

characteristics formed by the particular geographical area or its genetic origin. The bottlenose dolphin population data and dietary information were collected from published reports and studies presented in the following subsection.

The parameterisation of the current model was performed in two separate stages (see Table 1.): (1) model parameterisation to hake biological parameters and fisheries (Article I) and (2) introduction of SSD and predation with the updated biological data on hake (Article III).

Parameterisation of hake growth trajectories and biological features

Once the sum of alleles with the phenotypic variation was transferred to the L_{∞} (as explained in the *Evolution* subsection), the following step to parameterisation of growth trajectories is the linear regression of $\log K$ and L_{∞} data points. Through this I obtained the final model as: $\log(K) = 0.511 - 0.005 \times L_{\infty}$ with a standard deviation of 0.126. Using the same equation, L_0 was attained and the same value set for both sexes. Furthermore, the RL ratio was set to 0.51 obtained as an average value pulled across RL values using the mentioned hake dataset. Specific biological characteristics introduced at this point refer to the applied range of L_{∞} , max age set and length–weight relationship (see Table 1. for exact values).

Introducing SSD, predation and the update of hake ecological characteristics

During the second stage of the parameterisation, SSD is accounted at the level of L_{∞} calculus. The SSD is expressed as a proportion of 0.41 by which the female L_{∞} is larger than male (i.e., L_{∞} (female) = L_{∞} (male) \times 0.41). This proportion is estimated through the calculation of L_{∞} for each sex as $RL \times L_{mat}$. Here, I used the already known RL ratio (0.51) and, male and female L_{mat} values (female = 45 cm; male = 32 cm) obtained from Cerviño (2014). Predation is introduced for individuals ranging between 21 and 51 cm of size with a mean of 36 cm hake size corresponding to the reported mean hake size found in diet composition of NE Atlantic bottlenose dolphins (Saavedra, 2017). Predator population density and other parameters (i.e., a_p , h_p and d_p) were estimated with consideration to the published research on species-specific dietary requirements, diet composition and feeding pattern as well as generation time (Kastelein et al., 2003; Lockyer, 2007; Santos et al. 2007, 2014; Saavedra, 2017; Spitz et al. 2018). Furthermore, an assimilation efficiency (e_p) value was set according to the observed range of values for toothed whales (0.90 – 0.95; Lockyer, 2007).

Owing to the publication of new literature regarding hake ecological characteristics crucial for the increase of the biological realism in the model, length-weight relationship parameters as well as maximum life span were updated (Table 1.).

Table 1. Set initial and fixed values of individual and population parameters, and their sources categorized with regards to the ecological processes and size-selective pressures. (LW = length-weight parameters; L_0 = length at birth; RL = ratio of L_{mat} and L_{∞} ; M = natural mortality; SC = natural mortality due to cost of reproduction; N_i = prey initial population size; CC = prey carrying capacity; DD = density dependent growth a and b parameters; p_i = predator initial population size; K = predator carrying capacity; a = predator attack rate; e = assimilation efficiency; d = predator death rate; h = predator handling time; F = fishing intensity; a and b = fishing selectivity parameters; L_{50} = length at 50% retention).

	<i>Parameters</i>	<i>Parameterisation</i>	<i>Source</i>	<i>Parameterisation</i>	<i>Source</i>
		<i>stage 1</i>		<i>stage 2</i>	
<i>Prey parameters</i>	Max age	20 yrs	Muus and Nielsen, 1999	12 yrs	Murua, 2010
	LW	a = 0.00000513; b = 3.074	ICES, 2012	a = 0.00000659; b = 3.001721	ICES, 2019
	L_0	2.5 cm	Estimated	3.9 cm	Estimated
	RL	0.51		0.51	
	L_{∞} range	70 – 120 cm		70 – 120 cm	
	M	0.15		0.1	
	SC	0.1		0.1	
	N_i	2000		4000	
CC	5000	6000			
DD	a = 15; b = -a/0.85	a = 10; b = -a/0.90			
<i>Predation</i>	p_i	NA	0.3	Estimated	
	a	NA	0.5		
	h	NA	0.5		
	d	NA	0.06		
	e	NA	0.90		Lockyer, 2007
<i>Fishing</i>	F	0.15	0.15	Estimated	
	a	-7.6 -20.025	-10.85		
	b	0.38 0.267	0.411		
	L_{50}	20 cm 75 cm	26,4		ICES, 2019

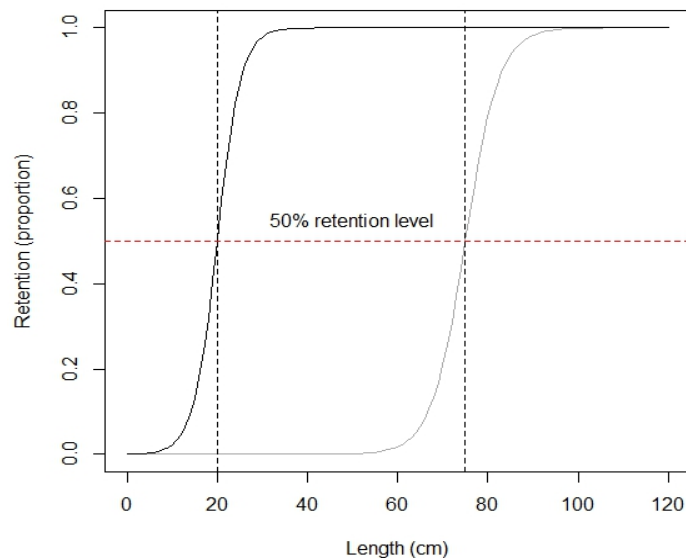
2.3 SIMULATION DESIGN AND SCENARIOS

All simulations in Article [I] and [III] were performed in R Programming Environment, versions 2.15.2 and 3.6.1, respectively (R Core Team, 2012; 2019). Full code is available in the *Appendix* of the current summary.

Evolutionary vs ecological fisheries objectives

In Article [I] the simulation design consisted of two scenarios with opposing fishing objectives where I compared the effects of the scenarios with regards to evolutionary processes. First scenario addresses the prevailing fishing regime based on the best estimate of L_{50} set across the main fishing tools applied with a at -7.6 and b at 0.38 (Santiago Cerviño, person. communication; Fig. 7.). Second scenario addresses the ‘spawn-at least-once’ fishing regime, where the set fishing selectivity allows for at least one reproduction event for an individual before being harvested (Fig. 7.).

Figure 7. Selectivity retention curves presenting the two tested fishing regimes (reproduced from Article II). First scenario with the prevailing fishing regime is depicted by black colour, while the spawn-at least-once fishing policy is depicted by light grey colour. L_{50} of each scenario is denoted by vertical dashed lines that corresponds to each scenario and marked by the red horizontal line marking the 50% retention level.



Each scenario was run for a total of 2500 time steps (i.e., years) where the first 2000 time steps were needed in order for the hake population to stabilise and adapt. Fishing was introduced between 2000 and 2100 time steps, followed by the recovery period of 400 time steps. For this part of the study, I ran 10 simulations of each scenario in order to get the most representative outcomes of all relevant parameters. All parameters are presented as average values pulled across all simulations for each scenario.

Investigating predation and fishing impacts

In Article [III] I addressed the coupled effects of predation and fisheries on hake individual and population parameters. In order to detect the changes caused by

the selective removals of predation and fishing with regards to present or absent evolution, I have tested 8 different scenarios in total presented in Figure 8. There are two scenarios without predation (NP), FRII and FRIII scenarios with respect to evolutionary processes. In addition, to demonstrate the contribution of SSD to the hake individual and population responses to the size-selective removals, I have also simulated two scenarios without the sex-specific difference in length and without predation (SL/NP). Fishing is applied in all scenarios.

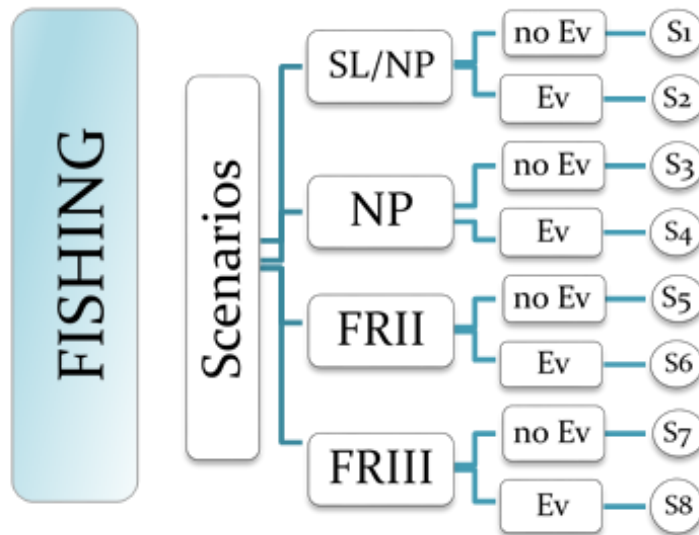


Figure 8. Diagram of simulated scenarios to investigate the joint impact of predation and fishing with regards to evolutionary processes and hake’s sexual dimorphism (adapted from the Article III). Each scenario is simulated with and without evolution denoted as Ev and no Ev, respectively, while fishing is introduced in all scenarios. The scenarios are denoted as follows: (S1–S2) without predation and sex-

specific difference in L_{∞} (reference scenarios); (S3–S4) no-predation scenarios; (S5–S6) scenarios with FRII predation and (S7–S8) scenarios with FRIII predation.

To reduce the computation time, I ran simulations of 3000 time steps to record the adapted hake populations beforehand (last 150 time steps of the simulation) for all scenarios separately. The simulation time for all scenarios of the presented outputs is 600 time steps. To allow for the prey and predator to co-evolve, predation is applied during the entire simulation time. During the initial fishing introduction at the simulation testing stage, scenarios exhibited differences in the fishing duration that can be applied without causing a demographic collapse, which is presented below as part of the results. This demonstrates the capacity of the population or rather, its resilience to sustain and absorb fishing pressure as the disturbance that induces various changes on both individual and population level. In all graphs with the applied fishing period, the cessation of fishing marks the time period during which the recovery is observed as a trend showing the return of the parameter value to its pre-fishing level. While fishing is introduced at the 400th time step in all simulations, fishing duration introduced in further simulations performed to test the impacts of size-selective removals on hake parameters was 30 time steps (based on all FRIII scenarios which exhibited the lowest resilience to fishing pressure as presented below). All graphically presented outputs are average values of each parameter pulled across 30 simulations for each scenario.

3 RESULTS

3.1 IMPACT OF MANAGEMENT OBJECTIVES

The overall results of the two fishing regime characterized by ecological vs. evolutionary objectives (Article I) demonstrate different types of long-term unsustainability. While spawn-at-least-once fishing strategy has a low ecological impact on hake biomass, in the long-term it has a strong negative impact on the L_{∞} that exhibits no recovery after cessation of fishing (Fig. 9.a).

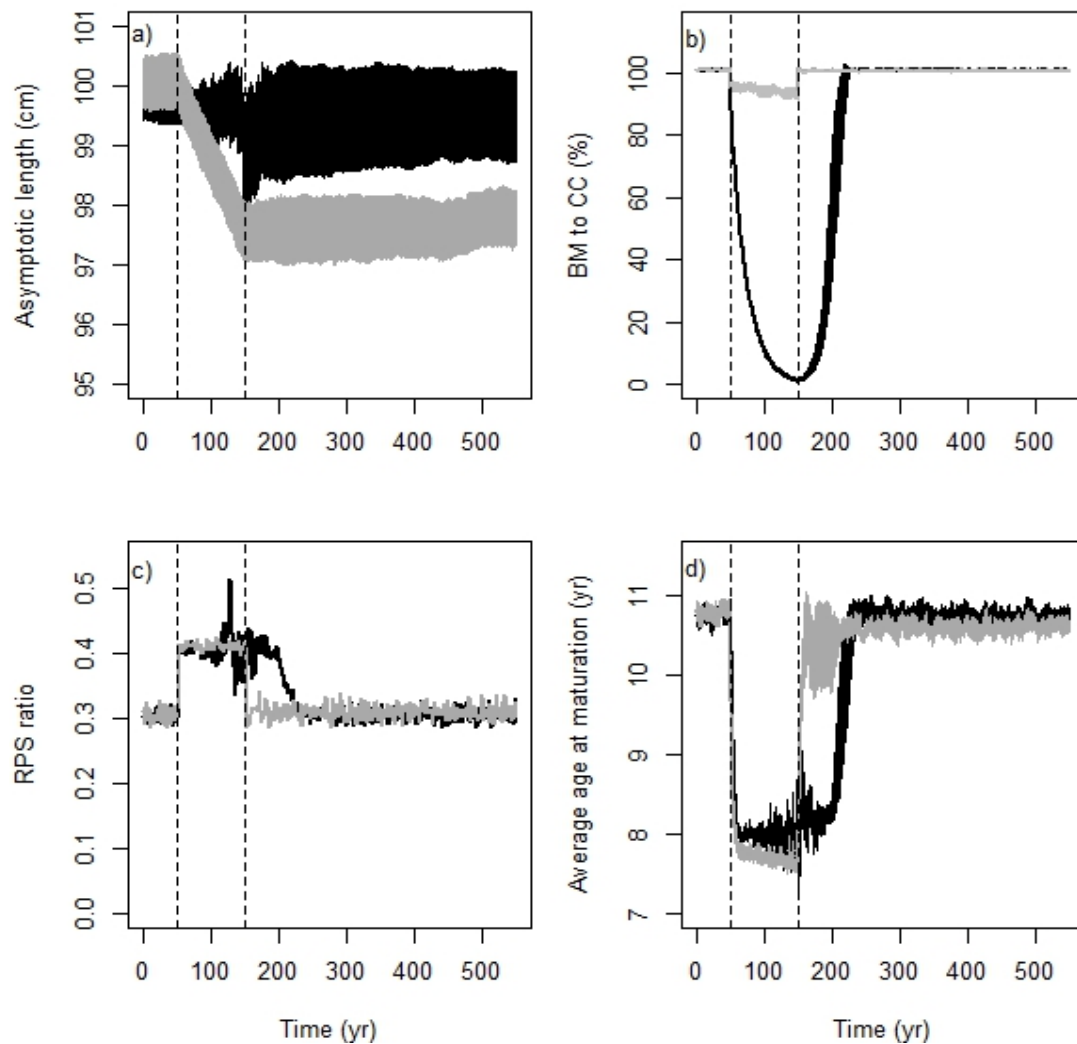


Figure 9. Comparison of two distinct fishing regimes with respect to individual and population parameters of the European hake under fishing pressure (reproduced from Article [I]). The results show the mean value of presented parameters with 95% confidence interval depicted by vertical lines. The spawn-at-least-once scenario is denoted with grey line, while the prevailing fishing regime is denoted in black colour. Vertical dashed lines indicate the fishing period (50-150) where the recovery period starts after fishing cessation (150-500). Plots present the following parameters: a) asymptotic length (L_{∞}); b) biomass with respect to carrying capacity (BM to CC); c) recruit-per-spawner (RPS) ratio and d) average age at maturation.

The prevailing fishing regime, however, shows very unsustainable level of exploitation on the population level (Fig. 9.b), but causes no reduction in L_{∞} (Fig. 9.a). While the recovery of L_{∞} to its pre-fishing values occurs shortly after fishing cessation for the prevailing regime, the biomass demonstrates slower recovery under the same conditions. For both scenarios, the RPS ratio increases due to the relaxation in intraspecific competition (Fig. 9.c). However, the RPS remains higher for a certain period of time after fishing cessation showing somewhat slower recovery in case of the prevailing fishing regime. Same trend is observed on an individual level in age at maturation (Fig. 9.d), which decreases during the fishing period, but recovers faster under the conditions of the spawn-at-least-once scenario.

3.2 IMPACT OF PREDATION

Predation effect on resilience under fishing pressure

Initial introduction of fishing period revealed different population resilience capacities depending on the conditions of the scenario. The introduction began with 100 time steps of fishing period where only the scenarios without predation demonstrated resilience towards this fishing duration (Fig. 10.). The scenarios without predation and sex-specific difference in L_{∞} endured only 75 time steps of fishing period, followed by FRII scenarios with 35 and FRIII scenarios with only 30 time steps of fishing. While all scenarios with predation demonstrate lower hake abundance, hake numbers and age at maturity persistently change during longer periods of fishing in reference scenarios: suggesting stronger negative phenotypic and population responses with longer fishing period, absent predation and unaccounted SSD. FRII predation type is in more intensive competition with fisheries for fish as observed in the strong overcompensation of prey–predator ratio after the relaxation of fishing pressure (Fig. 10.c).

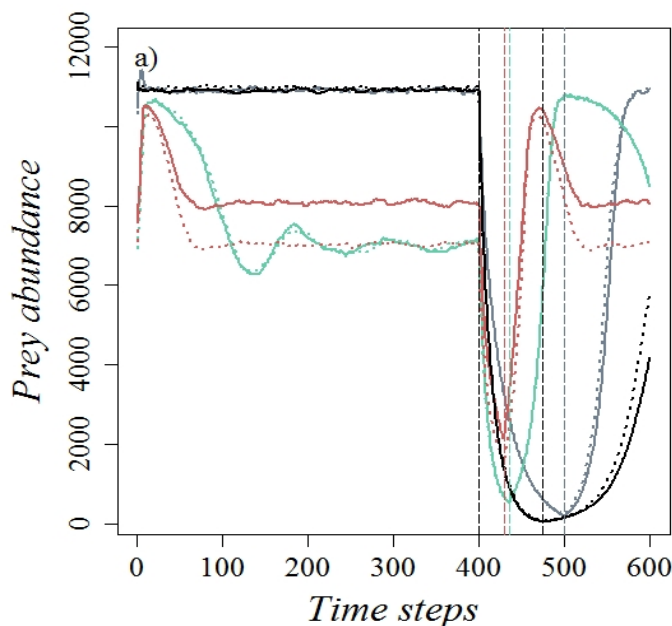
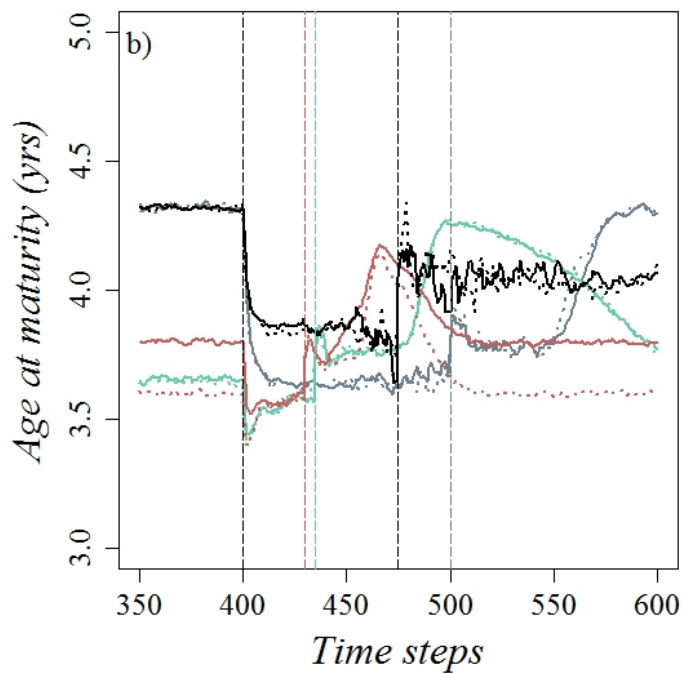
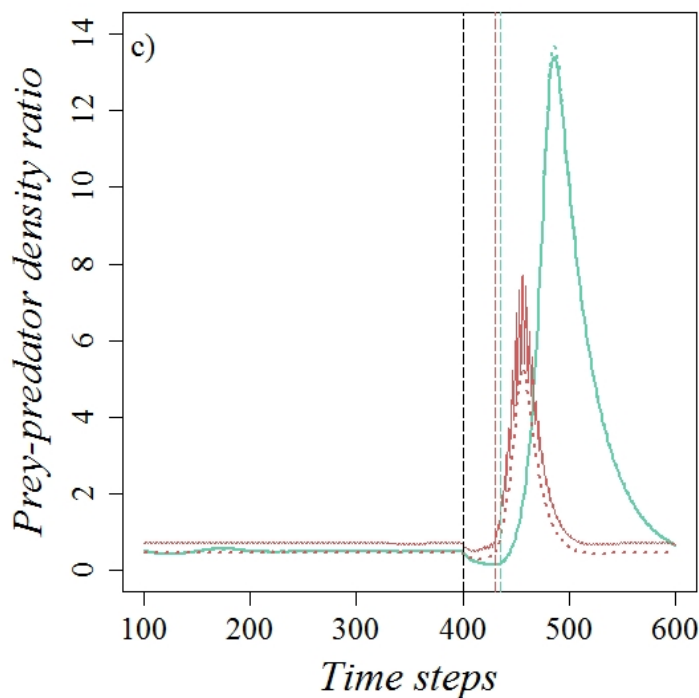


Figure 10. Resilience of hake population and individual parameters during the fishing parameterisation stage. Prey abundance (a), hake age at maturity (b) and hake–bottlenose dolphin density ratio are presented with respect to tested scenarios, although plot c) includes only two predation scenarios. The vertical dashed line at 400th time step marks the beginning of fishing, while the following vertical lines down the x-axis mark the different durations of



fishing periods per scenario. The vertical dashed lines denoting the fishing cessation are coloured according to the colour of the relevant scenario: 1) reference scenario (black); 2) scenario without predation (grey); 3) FRII predation scenario (green) and 4) FRIII predation scenario (red). Bold lines signify included evolutionary processes, while dotted lines scenarios without evolution.



Predation effect on recovery under fishing pressure

Predation size selectivity and uptake of prey considerably affect individual and population hake parameters (Fig. 11.). Individual level parameters, such as L_{∞} , exhibit higher values in all predation scenarios, but without detectible effect on recovery (Fig. 11.a).

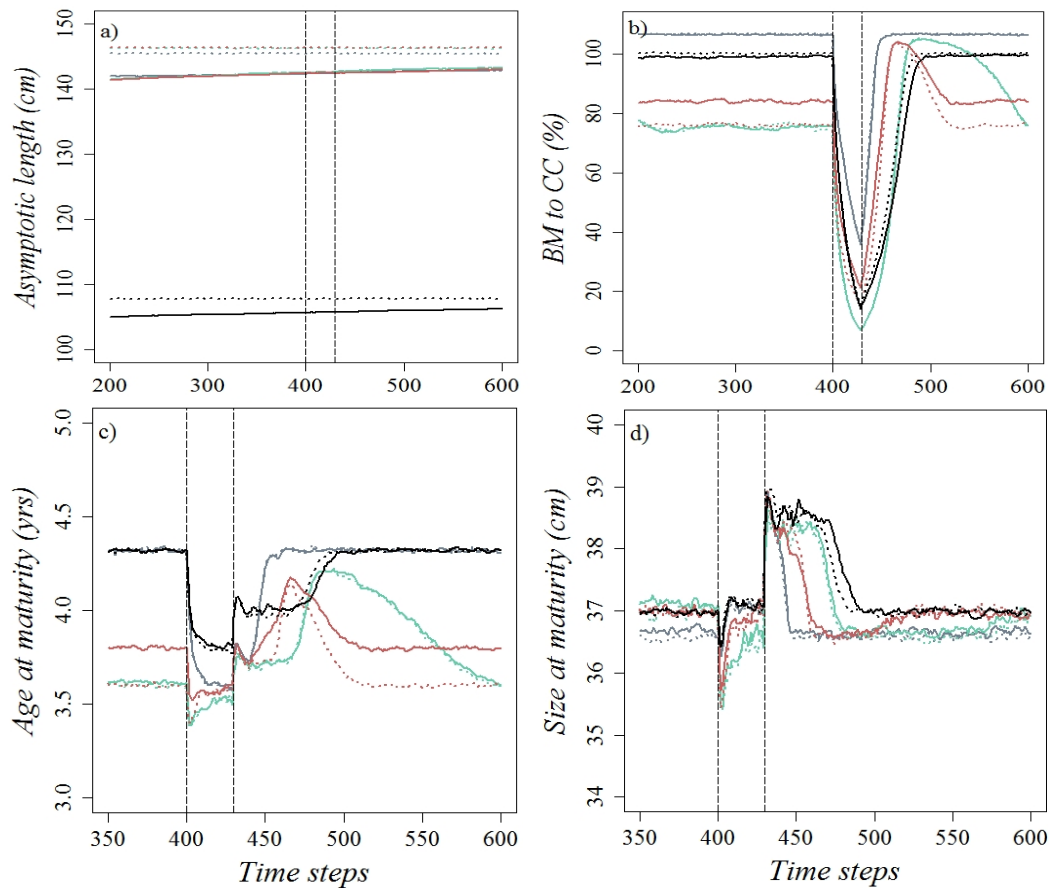


Figure 11. Mean values of individual and population hake parameters under the predation and fishing pressures. Plots show: a) asymptotic length (L_{∞}); b) biomass with respect to carrying capacity (BM to CC); c) age and d) size at maturity. Dotted lines depict non-evolutionary, while bold lines evolutionary scenarios. The reference scenario (without predation and sex-specific difference in L_{∞}) is depicted in black colour, while scenarios without predation, with FRII and with FRIII predation are shown in grey, green and red colours, respectively. Vertical, dashed lines indicate the fishing period (400–430 time steps) which is followed by the recovery period (431–600 time steps).

Furthermore, species characteristics (i.e., SSD and lifespan) as well as density-dependent growth continue to increase L_{∞} in all evolutionary scenarios, suggesting crucial implications of species-specific ecological characteristics for estimation of hake growth parameters. The presence of predation diminishes the age and size at maturity during the pre-fishing period due to mainly trait-mediated effects (Fig. 11.c and d). The no-predation scenarios allow for the fastest recovery after fishing period in both age and size at maturity, which is followed by FRIII scenarios. However, in age at maturity similar recovery speeds are noted in reference and FRII scenarios, while size at maturity recovers faster for the FRII scenarios than the reference scenarios. The difference in predation intensity between FRII and FRIII predator explain for higher hake uptake and slower recovery in age at maturity during FRII than FRIII scenarios. The effect of evolutionary processes and predation is noted only in FRIII predation, which supports higher hake numbers due to evolutionary rescue. Hake biomass is strongly controlled by predation, as

observed in no-predation scenarios where hake ‘outgrows’ its own carrying capacity (Fig. 11.b). Biomass (Fig. 11.b) experiences the largest reductions in the presence of FRII predator (than FRIII), which then leads to the slowest recovery of this population parameter. While FRIII predation is less detrimental than the FRII predation during fishing and recovery periods, the absence of predation clearly leads to smaller reductions in biomass, facilitating thus a quicker recovery.

3.3 IMPLICATIONS OF SSD UNDER JOINT SIZE-SELECTIVE REMOVALS

Hake’s demographic structure exhibits complex responses to predation and fishing pressures with respect to SSD. While during pre-fishing period the female and male hake ratio (Fig. 12.) distinguishes mainly owing to the conditions set in each scenario, the fishing period reveals notable differences between scenarios with and without accounted SSD. In case of unaccounted SSD (reference scenarios) females are more vulnerable to fishing during the first 10 time steps of fishing. However, this trend shifts towards males by the end of fishing suggesting a lower number of females available. With accounted SSD (no-predation scenarios), there is a similar transition (albeit with a slight delay) from female to male hake during the fishing period indicating a lesser impact of SSD to sexes’ vulnerability to fishing.

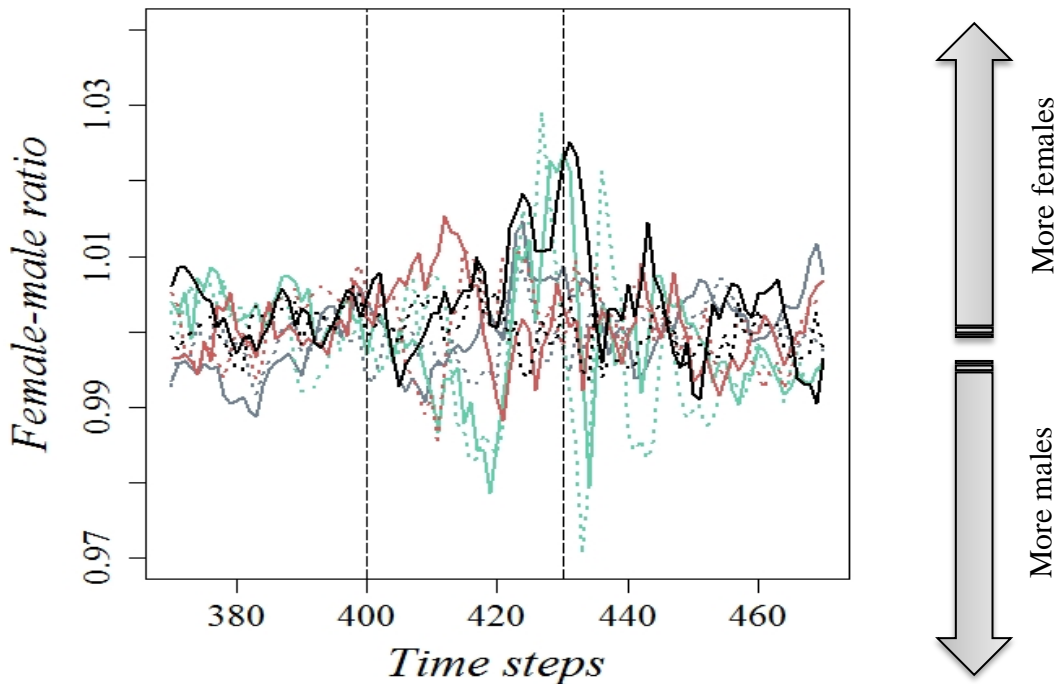
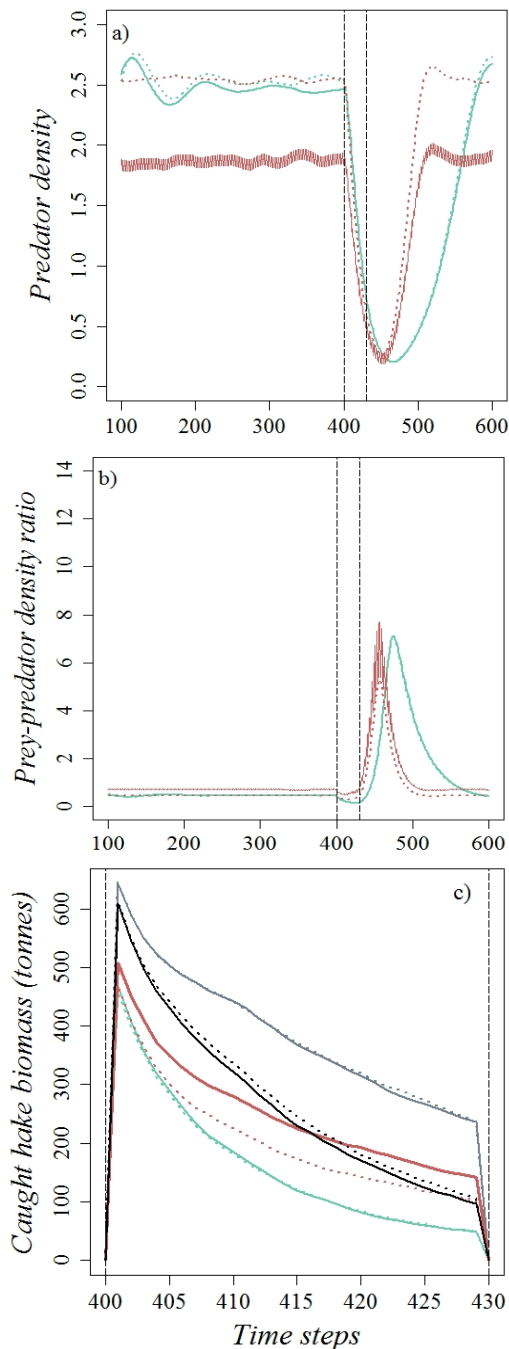


Figure 12. Mean values of the female and male hake ratio presented with respect to all scenarios tested: (1) non-evolutionary (noEv) and evolutionary (Ev) reference scenarios (black, dotted and bold lines, respectively); (2) noEv and Ev scenarios without predation (grey, dotted and bold lines, respectively); (3) noEv and Ev FRII scenarios (green, dotted and bold lines, respectively) and (4) noEv and Ev FRIII scenarios (red, dotted and bold lines, respectively). The fishing period is delineated with vertical, dashed lines (400–430 time steps) after which the recovery period begins.

Once predation is introduced, the FRII scenarios again demonstrate the initial higher removal of female hake by fisheries and predation, which then shifts to higher male catchability towards the end of the fishing period. Opposite to that, in FRIII scenarios hake males are more caught by fisheries during first 20 time steps after which male availability decreases. Although there are no significant differences for the female–male ratio among scenarios for recovery speed, during the fishing period there are no clear overlaps in selected fish size between all scenarios with and without predation. Furthermore, there is no clear indication of any evolutionary shift among the tested scenarios for the hake female–male ratio.

3.4 PREY–PREDATOR DYNAMICS AND FISHERIES



The co-evolved prey–predator dynamics respond differently to fishing depending on the type of predation (Fig. 13.a). Predator population thrives under FRII scenarios and non-evolutionary FRIII scenario, however recovery of predator density after fishing is also slower during the same scenarios. In contrast, both FRIII scenarios exhibit faster recovery after fishing cessation than FRII scenarios. While prey–predator ratio exhibits a weak response to fishing pressure, the relaxation of fishing pressure reveals a distinct fishing effect on hake density through overcompensation (Fig. 13.b).

Highest biomass catch is achieved in conditions without predators, while the steepest decline of hake population is noted in the reference scenarios (Fig. 13.c). Although the biomass level reached under these scenarios (Fig. 12.b) determine the fishing catches, the ardently steep slope of reference scenarios indicate unsustainable fishing practices.

Figure 13. Predator density (a), prey-predator density ratio (b) and caught hake biomass (c) are plotted against the simulation time steps. Vertical dashed lines denote the beginning and the end of the fishing period (400–430). Scenarios with and without evolution are depicted in bold and dotted lines, respectively. While plot a) and b) only present FRII (green colour) and FRIII (red) scenarios, the reference (black) and no-predation (grey) scenarios are also present in plot c).

4 DISCUSSION AND CONCLUSIONS

Exploring the opposing managerial approaches (Article I) provides insight for understanding how different management priorities affect the success of fishing yields and what are the associated trade-offs to such fishing strategies. Although same fishing intensity was applied in both evolutionary and ecological fishing strategy, the difference in the size of individuals targeted by fishing had direct implications for specific life-history traits. While avoiding FIE, population level parameters sustain high removals by the prevailing fishing intensity as opposed to the spawn-at-least-once strategy, which is consistent with the previous study exploring ecological impacts of similar opposing fishing objectives (see Vasilakopoulos et al. 2011). However, the reproductive output in the spawn-at-least-once strategy is preserved with the cost of evolutionary changes in hake individual traits. As size is positively associated with *per capita* fecundity in fish species, long-term effects of spawn-at-least-once strategy will inevitably reduce the reproductive output on individual and consequently, on population level. However, reduction in the reproductive capacity will probably occur on a longer time scale, whereas the pervasive effect of biomass reduction due to the prevailing fishing regime has imminent negative effects for hake abundance and cascading disruptions for close trophic links. This corroborates the importance of highlighting short- and long-term objectives in fisheries management, particularly when avoiding FIE. Similar concerns have been raised in studies promoting the avoidance of FIE through more effective regulation of fishing gear (e.g., Gwinn et al. 2015), introduction of moratoria (see Audzijonyte et al. 2006) and marine reserves (e.g., Baskett et al. 2015).

Choosing an optimal fishing strategy that allows for profitable fishing yields whilst minimizing the potential for FIE as well as preserving a viable RPS ratio, requires a holistic approach to management. According to Fowler et al. (2013), in addition to EAFM there is a need to account for evolution-based effects, relevant for viability of commercial fish stock, but also for the conservation of ecosystem trophic structure that ultimately supports fisheries. This encompasses individual variability that provides more biological realism of the target species as well as other sources of natural mortality, such as predation, which exclusion would lead to an overestimation of fish availability for fisheries. In Article [II], I have presented an overview of models developed for testing the optimality of different managerial approaches. Although the proliferation of models occurred in response to the multifaceted problem of sustainability in fisheries, in practise, there are still numerous challenges for a successful model application and implementation of its results into fisheries management. Marine mammals are still mainly underrepresented in many model-based approaches, mostly due to the difficulties obtaining empirical data on distribution, abundance and diet of many marine mammal species. However, predation is a crucial driver for fish species viability and production not just as a mortality source, but also as an additional size selective pressure. Due to the inevitable competitive interactions between marine

mammals and fisheries, challenges in addressing predation mortality and size selective removal can be potentially minimized through alternative sources of information and interdisciplinary research, such as ethno-ecological and historical data of fishery-based communities.

The competition between marine mammals and fisheries for fish is rarely addressed in cohesion with eco-evolutionary feedbacks, exploring the implications of their dynamics for fish viability and availability to all competitors. Among the existing relevant research, theoretical approach by Gårdmark et al. (2003) reveal rather complex and contra-intuitive trends in evolutionary responses of age-at-first-reproduction to harvesting and predation. Research presented in Article [III] applies Holling's functional responses to describe marine mammal predation within an individual-based model, which is an insufficiently explored approach in addressing the responses of fish life-history traits under a joint effect of fisheries and predation (Pettorelli et al. 2015). Testing 8 different scenarios allowed for a comparative approach into detecting and identifying the potential for FIE, predation impact on prey survival and viability. Furthermore, it allowed for an exploration of the mechanisms determining the role of size-correlated ecological characteristic and predation type for predator survival and sustainable fisheries catches. In addition, the initial introduction of fishing during the simulation testing stage, revealed the variability in hake population resilience depending on the conditions of each scenario (Fig. 10.). The population resilience is the highest in case of all the scenarios without predation (100 time steps of fishing duration) whereas the reference scenarios exhibit lower population resilience (75 time steps), followed by two least resilient scenarios with the FRII and FRIII predation (35 and 30 time steps, respectively). Although evolutionary processes did not affect the population resilience to the joint effect of fishing and predation, the effects of sex-specific difference in hake length and predation pressure induce notable changes in the responses to the joint effect and recovery speed for individual and population parameters. Moreover, the patterns observed in reference scenarios for the prey abundance and the age at maturity (Figs 10.a and c) suggest a higher potential for FIE in these traits in case of unaccounted SSD in hake and predation. Thus, hake life-history characteristics, particularly SSD, exhibit a crucial role in population recovery, which is similar to other studies exploring implications of life-history characteristics for population recovery (Audzijonyte and Kuparinen 2016). Furthermore, considering that prey life-history traits can have implications for the facilitation of fisheries by the predators they compete with (see Huss et al. 2014): it would be prudent to investigate further how differences in life-history strategies impact the direction and the strength of phenotypic and population shifts as well as the potential for FIE.

Complex changes in maturation can occur under size-dependent mortalities as many fish species exhibit indeterminate growth with *per capita* fecundity associated with body size and additional survival costs due to reproduction (see Gårdmark and Dieckmann 2006). The current research shows that a specific

combination of duration, intensity, size selectivity and hake SSD can provide the prerequisites for an evolutionary shift to occur. For instance, in Gårdmark et al. (2003) harvesting of intermediate and old-age fish under Type II predation can shift the evolution towards later age-at-first-reproduction as harvesting diminishes the pressure of age-selective predation on younger classes of age-at-first-reproduction. Here, the potential for FIE is detected in the reference and no-predation scenarios (Fig. 10.) suggesting that longer fishing period in the absence of predation and SSD evolve hake individual and population parameters after a period of intense overexploitation. Fishing duration can increase the impact of fishing intensity and size selectivity through the accumulation of their negative effects on hake individual fecundity and adaptation of individual traits selected by fishing. However, considering that fishing is applied in synergy with two predation types, duration might not be sufficient to exert an evolutionary response. Although both predation types are the same with respect to the selected prey size, their difference consumption patterns indicate a higher intensity of removal in FRII predation than FRIII, which has direct implications for hake maturity schedule as well as abundance and demographic structure. Present evolutionary processes with the included SSD exhibits a slightly increasing trend in the asymptotic length (L_{∞}) mainly due to the continuous adaptation to size discrepancies among sexes, as size-correlated ecological characteristics (i.e., SSD) affect the individual's growth trajectories, age and natural mortality (Cerviño 2014). In addition, the specific life span as well as the set density-dependent growth parameters prolong the adaptation period for L_{∞} and consequently, K parameters. However, the lack of expected evolutionary shifts in individual traits under the joint impact (incl. L_{∞} , K , size and age at maturity) may be partly explained by a strong phenotypic plasticity observed in some hake stocks (Hidalgo et al. 2014).

Values of hake individual and population level parameters are determined by predation through trait-mediated and density-dependent processes (as observed in the pre-fishing period of parameters presented by Fig. 11.). The recovery of hake individual and population parameters is impeded under predation pressure, which is consisted with study cases where overexploited fish species were unable to recover due to increased predation mortality (e.g., Swain and Benoît 2015). However, in order to confirm that one predator species exclusively impedes one prey species recovery, it must be determined that no additional sources of mortality exists as well as no other potential prey species is present. While this is not the case for most marine ecosystems, predator species can specialise for a specific prey species, just as individual predator can show prey species preference over the other. Moreover, fish availability will also impact the choice of prey species in a predator. Due to competitive interactions with fisheries, the bottlenose dolphin will need to adjust in order to increase the probability of successful captures and ingestions of prey. Ratio of female and male hake (Fig. 12.) reveal such adaptations with an opposite trend in sex (i.e., size) caught by fisheries and FRIII predator, which minimizes the intensity of size-selective removal by fisheries similarly to the impact of evolutionary-minded fishing regime addressed in Article

[I]. Therefore, these trends may also be pivotal in understanding the lack or presence of FIE in certain individual and population parameters under joint removals by predation and fisheries. Among predation types, the FRIII predator exhibits lower ecological impact for hake biomass than FRII predation scenarios, suggesting more intense competitive FRII–fisheries interaction with higher negative consequence for hake survival. For the bottlenose dolphin this means that consuming hake as an FRIII predator will increase its adaptability to the varying fish availability shaped by fisheries removals than as an FRII predator.

Different predation types will also affect the fishing catches differently. Firstly, due to the fish abundance controlled by predation mortality before fishing starts and secondly, due to the different predation intensities noted in the two predation types (Fig. 13.c). Fishing catches are the most profitable without predation, although reference scenarios indicate very unsustainable harvest trends, which deplete the hake numbers faster than other scenarios. A predator described by FRII consumption rate will be more harmful for fisheries catches than a predator with an FRIII consumption rate. Higher predator density is followed by a slower recovery as a trade-off observed in the FRII predation scenarios (Figs 13.a and b). Furthermore, while present evolutionary processes in prey suppress the predator density in FRIII predator, absent evolution in prey exhibits a similar predator density trend as in FRII predation scenarios. While different models that include predation mainly use Holling's Type II functional response as it is less data demanding (see Plagányi 2007 for list of models), it is more likely that with the increase in habitat and trophic complexity predation type will resemble more to the Holling's Type III functional response. However, the strength and the direction of the fishing pressure superimposes the question of how much fish is available to predators after fishing cessation. Ultimately, it might be that the irregular windows of opportunity decide on the success of each competitor, such as discrepancies in spatial and temporal overlap between marine mammals and fishing operations.

In the current approach, I have aimed to address some of the most crucial processes and species' characteristics associated with ecological and evolutionary feedbacks on the life-history traits of the European hake under intensive size-dependent predation by the bottlenose dolphin and the prevailing fishing regime. While gradual improvements have been incorporated in the model, it mainly remains a single-species and fish-oriented modelling. Yet, in light of current findings, there are several main considerations that should be taken into account for a holistic approach to fisheries. Firstly, different types of predation imply a difference in the proportion of fish abundance available to fisheries, which could better optimise fishing effort and harvest yields. Secondly, improving the biological realism in model-based approaches, especially descriptions of trait(s) targeted by fishing, can provide a better resolution for estimations of fish stock reference points as well as the impact of planned exploitation rates on predator survival. And lastly, the presence of predation as well as the fish ecological characteristics should be considered in estimations of fish resilience and recovery rate that are pivotal in

successful implementation of fishing moratoria and the envisioning of sustainable fishing strategies.

5 FUTURE RESEARCH

The objectives of this doctoral research have been changing and even evolving with each step as new questions emerged. Although my initial desire was to compare how differences in species-specific life-history strategy determine the direction and strength of the fish response to fisheries and predation, this was unfortunately not possible due to the time needed to complete the model parameterisation and introduction of predation in the model. However, in the light of current findings, one possible future research could lead in the direction of additional prey species characterised by different life-history strategies and experiencing uptakes by fisheries as well as predation. This would allow for further exploration towards multispecies interactions that accounts for predator's shift in prey species, which would also change the predation pattern in terms of attack rate and handling time, ultimately altering the prey's probability of being eaten. Furthermore, different even opposing life-history strategies of prey could provide answers as to how and under which conditions species-specific individual traits determine the probability of an evolutionary change under size-selective removal.

Another complementary sequel to the current research would be to expand the fisheries sustainability agenda towards the bio-economic modelling approaches. As changes in fish size affected by fishing and predation selectivity will affect the fish economic value, it would be of crucial importance for fisheries-based economies and associated stakeholders to address this issue. Moreover, by incorporating a two-way interaction between fish ecological characteristics and how they affect the fish market, it would also be interesting to investigate how the demand for fish (in terms of demand for specific fish body size) affect the size selectivity applied through fishing gear. In this manner, one can observe how or whether consumer choice can alter the fishing size selectivity through the choice of a more sustainable fishing practice that also aims to avoid evolutionary changes in fish phenotypic traits. For this purpose, I would aim to apply a basic bio-economic model advised by the available literature on hake bio-economic modelling, the available data on hake market price, fishing effort and catches as well as types of fisheries.

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Wikipedia Commons:

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(16.12.2019)

APPENDIX

INDIVIDUAL – BASED MODEL : CODE
(R Programming Language)

```
setwd('working directory')
#####

# FUNCTION: From genotypic trait value to phenotypic growth parameters
# Simulation of phenotypic variance around the genotypic trait value
fromGtoP=function(reftrait.G,Pvar,Pmin,Pmax){
  ttt=1
  while(ttt==1){
# randomness of genotype (o-2o loci) - we shift the values by 5 to ensure positive
  values
    refrtrait.P=reftrait.G+5+rnorm(1,o,Pvar)
    if(refrtrait.P>Pmin & refrtrait.P<Pmax){
      ttt=0}
  }

# Phenotypic trait value is deterministically translated into LL and KK
parameters
# LL = asymptotic length

# Introducing sex-based difference in LL or sexual size dimorphism
if(simdata$sex[i]==1){
  LL=(70+refrtrait.P*1.6667)*1.41 # female asymptotic length
}
else{
  LL=(70+refrtrait.P*1.6667) # male asymptotic length
}

if(simdata$sex[i]==1){
  LK=(-0.510871-0.0040556*LL+rnorm(length(LL),o,o.1262129)) * 1.09
}
else{
  LK=-0.510871-0.0040556*LL+rnorm(length(LL),o,o.1262129)
}

KK=10^(LK) #LK= log of K; KK=K; LL=Linf
return(list(refrtrait.P=refrtrait.P,LL=LL,KK=KK))
}
```



```

# FUNCTION: Natural mortality function
# ET=enviro.time - absolute time; M=natural mortality; mat.mort=reproductive
  cost
mort.nat=function(ET,M,maturity,mat.mort){
  if(ET<2){p=0}      # natural mortality not applied to juveniles 0-2 yrs
  else{p=M}

  # Maturity related mortality added to the natural mortality
  if(maturity==T){
    p=min(p+mat.mort,1)  # additive affect of reproductive cost
  }
  # p=probability of dying
  return(1-exp(-p))
}

```

```

# FUNCTION: Fishing mortality
mort.fish=function(ET, size,min.th,F.mort){
  if(size<min.th | ET<3){p=0}      # no fishing mortality before age 3
  else{
    if(dome==T){
      mm=73      # mean
      ssd=110    # deviation from the mean
      selG=exp(-(size-mm)^2/(2*ssd))
      p=F.mort*selG
    }
    else{
      a=-10.85
      b=0.411
      selT=exp(a+b*size)/(1+exp(a+b*size))
      p=F.mort*selT
    }
  }
  return(1-exp(-p))
}

```

```

# FUNCTION:
# Predator fish uptake: consists of prey selectivity and quantified uptake of fish by
  bottlenose dolphin

```

```

# Predation equation and probability of being eaten with Holling type 2
  functional response
Pred2=function(N, e, a, h, d, pinit, CC)
{
  n=N/CC
  PredDens=pinit*exp((e*a*n)/(1+h*a*n)-d)
  return(PredDens)
}

```

```

# Predator's kill rate
Prey2=function(ET, a, h, N, pinit, CC)
{
  if(ET<2) {pred.mort=0} # predation mortality
  else{
    n=N/CC
    pred.mort=a*pinit/(1+h*a*n)}
  return(pred.mort)
}

# Predation equation and probability of being eaten with Holling type 3
  functional response
Pred3=function(e, a, h, d, pinit, N, CC)
{
  n=N/CC
  PredDens=pinit*exp(e*a*n^2/(1+h*a*n^2)-d)
  return(PredDens)
}

# Predator's kill rate
Prey3=function(ET, a, h, N, CC, pinit)
{
  n=N/CC
  if(ET<2) {pred.mort=0} # predation mortality
  else{
    pred.mort=(a*pinit*n^(2-1))/(1+h*a*n^2)
  }
  return(pred.mort)
}

# FUNCTION: Growth time (i.e. density effect on growth)
growth.time=function(BM,CC){
  a=10
  b=-a/0.90
  p=exp(a+b*BM/CC)/(1+exp(a+b*BM/CC))
  return(p)
}

# FUNCTION: Juvenile production as a function of mother's weight
numb.juv=function(size,GT){
  wg=0.00000659*size^3.001721
  zero_rec=round(6.353771726*wg)
  juv_prob=rbinom(1,zero_rec,0.10) # survival of 0 yr old recruits
  juv=round(juv_prob*GT)
}

```

```

    return(juv)
}

# FUNCTION: Length-weight relationship
sizeTOweight=function(size){
  wg=0.00000659*size^3.001721
}

# INITIALIZATION:

# Prey biological parameters
N=4000    # size of initial population
Pmin=0    # upper boundary for phenotypic trait value
Pmax=30   # lower boundary for phenotypic trait value
Pvar=3.5  # SD for normal distribution, scales heritability
CC=6000   # prey carrying capacity
Lo=2.5    # size at birth
mat.th=0.51 # fraction of asymptotic length at which fish become mature
M=0.1     # natural mortality among individuals 2 yrs and older
mat.mort=0.1 # mortality as reproductive cost
min.th=0  # minimum landing size (MLS); if set to 0 no MLS is considered
evolution=TRUE or FALSE #evolutionary processes

# Fishing parameters and fishing intensity
F.mort=0.15 # fishing mortality of the fully selected size class
dome=F     # if T then it is the dome shaped (gillnet); F is for logistic curve (trawl)
quota=T    # fishing with F.mort or quota
prop.quota=T # proportional or absolute quota
prop.fish=1-exp(-0.15) #fixed proportional fishing quota from the total biomass
Fquota=NA  #fixed fishing quota in kilos

# Prey-predator model parameters
a=0.07    # attack or discovery rate
e=0.90    # assimilation efficiency
d=0.06    # predator death rate
h=0.5     # handling time
pinit=0.30 # initial predator density

# Predation mortality and uptake based on the type of functional response
pred.sel2=TRUE or FALSE
pred.sel3=TRUE or FALSE

#INITIALIZATION: simulation parameters
#output directory
output='...'

```

```

Nstep=600 # total number of simulated timesteps
Nfish=600 # start of fishing
NendF=600 # end of fishing
Npred=600 # start of predation
NendP=600 # end of predation
Tpred=length(Npred:NendP) # the length of the predation period
start.fit=40 # start of fitness recording

# Lower and upper boundaries to initial genotypic trait distributions used to
# speed up adaptation
in.low=10 # lower genotypic value
in.up=15 # upper genotypic value

#INITIALIZATION: simulation data, i.e. initial population
simdata=read.table("recorded_populations.txt", header=TRUE, dec=".", sep=" ",
  stringsAsFactors = FALSE) # loading recorded adapted populations

# Output created in case when recorded populations are not used
#simdata=data.frame(size=rep(o,N),ET=rep(o,N),GT=rep(o,N),maturity=rep(o,N)
# ,sex=rep(o,N),KK=rep(o,N),LL=rep(o,N),mat.th=rep(o,N),reftrait.G=rep(o,N),r
# efrtrait.P=rep(o,N),locus1=rep(o,N),locus2=rep(o,N),locus3=rep(o,N),locus4=re
# p(o,N),locus5=rep(o,N),locus6=rep(o,N),locus7=rep(o,N),locus8=rep(o,N),locu
# s9=rep(o,N),locus10=rep(o,N),cum.juv=rep(o,N),ET.mat=rep(o,N),size.mat=re
# p(o,N))

for(i in 1:N){
  simdata$sex[i]=rbinom(1,1,0.5) # assigning sex
  simdata$reftrait.G[i]=sample(in.low:in.up,1) # assigning genotype within
  # determined genotypic range value
  #simdata$reftrait.G[i]=sample(o:20,1) # flat distribution over all possible
  # genotypic trait values

  ind=1
  while(ind==1){
    for(j in 10:19){
      simdata[i,j]=rbinom(1,2,simdata$reftrait.G[i]/20) # sums are 0, 1 or 2 for 1 loci
    }
    if(simdata$reftrait.G[i]==sum(simdata[i,10:19])){ind=0}
  }
}

for(i in 1:N){
  #simdata$reftrait.G[i]=sum(simdata[i,10:19])
  temp=fromGtoP(simdata$reftrait.G[i],Pvar=Pvar,Pmin=Pmin,Pmax=Pmax)
  simdata$reftrait.P[i]=temp$reftrait.P
  simdata$KK[i]=temp$KK
  simdata$LL[i]=temp$LL
  simdata$size[i]=simdata$LL[i]-(simdata$LL[i]-Lo)*exp(-
    simdata$KK[i]*simdata$GT[i])
}

```

```

mat.th[i]=simdata$size.mat[i]/simdata$LL[i]
if(simdata$size[i]>mat.th[i]*simdata$LL[i])
{
  simdata$maturity[i]=1
}
}

```

```
# SIMULATION PROCEDURE
```

```
# Output variables
```

```

year.aver.matsize=rep(o,Nstep)
year.aver.matsizeF=rep(o,Nstep)
year.aver.matsizeM=rep(o,Nstep)
year.aver.matage=rep(o,Nstep)
year.aver.matageF=rep(o,Nstep)
year.aver.matageM=rep(o,Nstep)
year.aver.matLL=rep(o,Nstep)
year.aver.matKK=rep(o,Nstep)
year.aver.LL=rep(o,Nstep)
year.aver.KK=rep(o,Nstep)
year.N=rep(o,Nstep)
year.N.mat=rep(o,Nstep)
year.N.dens=rep(o,Nstep)
year.females=rep(o,Nstep)
year.BM=rep(o,Nstep)
year.BM.mat=rep(o,Nstep)
year.N.juveniles=rep(o,Nstep)
year.LL.juveniles=rep(o,Nstep)
year.KK.juveniles=rep(o,Nstep)
year.heritability=rep(o,Nstep)
year.recruitment=rep(o,Nstep)
year.reftrait.G=rep(o,Nstep)
year.reftrait.P=rep(o,Nstep)
year.growth.time=rep(o,Nstep)
year.age.maturation=rep(o,Nstep)
year.size.maturation=rep(o,Nstep)
year.mortality=rep(o,Nstep)
year.catchN=rep(o,Nstep)
year.catchBM=rep(o,Nstep)
year.mortalityF=rep(o,Nstep)
year.fem.ratio=rep(o,Nstep)
year.mat.th=rep(o,Nstep)

```

```
# Predation-related output variables
```

```

PredDens.array=array(o,Tpred)
year.Pred.N=rep(o,Tpred)

```

```

year.eatenN=rep(o,Tpred)
year.eatenBM=rep(o,Tpred)
year.mortalityP=rep(o,Tpred)

# Parents dataframe (empty dataframe created here)
# parents=read.table("recorded_populations.txt", header=TRUE, dec=".", sep="",
  stringsAsFactors = FALSE) #used in case of non-evolutionary scenario

#used for evolutionary scenarios
parents=data.frame(size=rep(o,o),ET=rep(o,o),GT=rep(o,o),maturity=rep(o,o),sex
  =rep(o,o),KK=rep(o,o),LL=rep(o,o),mat.th=rep(o,o),reftrait.G=rep(o,o),reftrait
  .P=rep(o,o),locus1=rep(o,o),locus2=rep(o,o),locus3=rep(o,o),locus4=rep(o,o),lo
  cus5=rep(o,o),locus6=rep(o,o),locus7=rep(o,o),locus8=rep(o,o),locus9=rep(o,o)
  ),locus10=rep(o,o),cum.juv=rep(o,o),ET.mat=rep(o,o),size.mat=rep(o,o))

# Simulation loop over years

for(tt in 1:Nstep)
{

  # 0) Age increases with one year
  simdata$ET=simdata$ET+1

  # 1) Natural mortality
  # Recording population size for >2 year old fish
  ind=which(simdata$ET>2)
  Npop=length(ind)

  deads=rep(o,o)

  for(i in 1:length(simdata[,1])){

    p.mort=mort.nat(ET=simdata$ET[i],M=M,maturity=simdata$maturity[i],mat.
      mort=mat.mort)
    if(simdata$ET[i]>12){p.mort=1}
    ind.dead=rbinom(1,1,p.mort)
    if(ind.dead==1){deads=rbind(deads,i)}
  }

  if(tt>start.fit){

    write.table(cbind(simdata$reftrait.G[deads],simdata$cum.juv[deads],rep(tt,len
      gth(deads)),simdata$sex[deads],simdata$ET[deads],simdata$ET.mat[deads],si
      mdata$size.mat[deads],simdata$LL[deads],simdata$mat.th[deads],simdata$K
      K[deads],simdata$size[deads],rep(o,length(deads))),paste(output,"gtrait_juv_
      nat", ns, ".txt",sep=""),col.names=F,row.names=F,append=T)
  }
}

```

```

# removal of dead individuals
simdata=simdata[-deads,]

# Recording the fraction of dead individuals
Ndead=length(deads)
year.mortality[tt]=Ndead/Npop

# Setting annual fishing quota based on fixed fishing mortality procentage
if(prop.quota==T){
  Fquota=prop.fish*sum(sizeTOweight(simdata$size[which(simdata$ET>=3)]))
}

# 2) Fishing mortality

# Fishing with F.mort

if(quota==F){
  if(tt>Nfish & tt<NendF){

    ind=which(simdata$ET>3)
    Npop=length(ind)
    deads=rep(0,0)

    for(i in 1:length(simdata[,1])){

      p.mort=mort.fish(ET=simdata$ET[i],size=simdata$size[i],min.th=min.th,F.mort=F.mort)
      ind.dead=rbinom(1,1,p.mort)
      if(ind.dead==1){deads=rbind(deads,i)}
    }

    write.table(cbind(simdata$reftrait.G[deads],simdata$cum.juv[deads],rep(tt,length(deads)),simdata$sex[deads],simdata$ET[deads],simdata$ET.mat[deads],simdata$size.mat[deads],simdata$LL[deads],simdata$mat.th[deads],simdata$KK[deads],simdata$size[deads],rep(1,length(deads))),paste(output,"gtrait_juv_noQ", ns, ".txt", sep=""),col.names=F,row.names=F,append=T)

# N of caught fish per year/time step
year.catchN[tt]=length(deads)
# Biomass of caught fish per year/time step
year.catchBM[tt]=sum(sizeTOweight(simdata$size[deads]))
# Fishing mortality of hake per year/time step
year.mortalityF[tt]=year.catchBM[tt]/sum(sizeTOweight(simdata$size))
# removal of dead individuals
simdata=simdata[-deads,]

```

```

}}

# Fishing with quota
if(quota==T)
{
  if(tt>Nfish & tt<NendF)
  {
    ind=which(simdata$ET>3)
    Npop=length(ind)
    deads=rep(0,0)
    cum_quota=0

    inds_fish=1:length(simdata[,1])
    while(cum_quota<Fquota)
    {
      i=sample(inds_fish,1,replace=F)

      p.mort=mort.fish(ET=simdata$ET[i],size=simdata$size[i],min.th=min.th,F.mo
rt=F.mort)
      ind.dead=rbinom(1,1,p.mort)
      if(ind.dead==1)
      {
        deads=rbind(deads,i)
        cum_quota=cum_quota+sizeTOweight(simdata$size[i])
        inds_fish=inds_fish[-which(inds_fish==i)]
      }
    }

    write.table(cbind(simdata$reftrait.G[deads],simdata$cum.juv[deads],rep(tt,len
gth(deads)),simdata$sex[deads],simdata$ET[deads],simdata$ET.mat[deads],si
mdata$size.mat[deads],simdata$LL[deads],simdata$mat.th[deads],simdata$K
K[deads],simdata$size[deads],rep(1,length(deads))),paste(output,"gtrait_juv_
Q", ns, ".txt",sep=""),col.names=F,row.names=F,append=T)

# N of caught fish per year/time step
year.catchN[tt]=length(deads)
# Biomass of caught fish per year/time step
year.catchBM[tt]=sum(sizeTOweight(simdata$size[deads]))
# Fishing mortality of hake per year/time step
year.mortalityF[tt]=year.catchBM[tt]/sum(sizeTOweight(simdata$size))
# removal of dead individuals
simdata=simdata[-deads,]

}}

#####
# 3) Predators' numbers, selectivity and uptake
# Type 2 functional response

```



```

# Predator population
if(pred.sel2==TRUE){

  eaten=rep(o,o) # an object where all eaten individuals should be stored
  ind=which(simdata$ET>2) #focussing predation on individuals over two years
                        old which are well under the size range targeted by
                        predators

  if(tt==Npred)
  {
    PredDens.array[tt]=Pred2(pinit=pinit, N=length(simdata[,1]), e=e, a=a, d=d,
    h=h, CC=CC)
  }

  if (tt>Npred && tt<=NendP){
    PredDens.array[tt]=Pred2(pinit=PredDens.array[tt-1], N=length(simdata[,1]),
    e=e, a=a, d=d, h=h, CC=CC)
  }

# Mortality by predation
if (tt>=Npred && tt<=NendP){
  for (i in 1:length(simdata[,1])){
    if((simdata$size[i]>21) && (simdata$size[i]<51)){ # prey size selectivity
      ind.eaten=which(simdata$ET>2)
      pred.mort=Prey2(ET=simdata$ET[i], a=a, h=h, pinit=PredDens.array[tt],
      CC=CC, N=length(simdata[,1])) # probability of being eaten by predator
      ind.eaten=rbinom(1,1,pred.mort)
      if(ind.eaten==1)
      {
        eaten=rbind(eaten,i)
      }
    }
  }
}

write.table(cbind(reftrait.G=simdata$reftrait.G[eaten],cum.juv=simdata$cum.j
uv[eaten],sex=simdata$sex[eaten],ET=simdata$ET[eaten],ET.mat=simdata$ET.
mat[eaten],size.mat=simdata$size.mat[eaten],LL=simdata$LL[eaten],mat.th=s
imdata$mat.th[eaten],KK=simdata$KK[eaten],size=simdata$size[eaten]),paste
(output,"eaten_ind",ns,.txt",sep=""),col.names=TRUE,row.names=FALSE,appe
nd=FALSE)

# Recording of the fraction of the fish that has been eaten
# number of individual exposed to mortality caused by predation
Npop=length(ind.eaten)
# number of eaten fish by predators
Neaten=length(eaten)
# proportion of population eaten by predator
year.eatenN[tt]=Neaten/Npop
# eaten biomass of prey by predation

```

```

year.eatenBM[tt]=sum(sizeTOweight(simdata$size[eaten]))
# fish mortality caused by predation
year.mortalityP[tt]=year.eatenBM[tt]/sum(sizeTOweight(simdata$size))
# predator abundance per time step
year.Pred.N[tt]=round(PredDens.array[tt]*K)

# removal of eaten individuals
simdata=simdata[-eaten,]

}}

#####
# Type 3 functional response
if(pred.sel3==TRUE){

eaten=rep(0,0)
ind=which(simdata$ET>2)

if(tt==Npred)
{
  PredDens.array[tt]=Pred3(pinit=pinit, N=length(simdata[,1]), CC=CC, e=e,
a=a, d=d, h=h)
}

if (tt>Npred && tt<=NendP){
  PredDens.array[tt]=Pred3(pinit=PredDens.array[tt-1], N=length(simdata[,1]),
CC=CC, e=e, a=a, d=d, h=h)
}

# Mortality by predation
if (tt>=Npred && tt<=NendP){
  for (i in 1:length(simdata[,1])){
    if((simdata$size[i]>21) && (simdata$size[i]<51)){ # prey selectivity
      pred.mort=Prey3(ET=simdata$ET[i], a=a, h=h, pinit=PredDens.array[tt],
CC=CC, N=length(simdata[,1])) # probability of being eaten
      ind.eaten=rbinom(1,1,pred.mort)
      if(ind.eaten==1)
      {
        eaten=rbind(eaten,i)
      }
    }
  }
}

write.table(cbind(reftrait.G=simdata$reftrait.G[eaten],cum.juv=simdata$cum.j
uv[eaten],sex=simdata$sex[eaten],ET=simdata$ET[eaten],ET.mat=simdata$ET.
mat[eaten],size.mat=simdata$size.mat[eaten],LL=simdata$LL[eaten],mat.th=s
imdata$mat.th[eaten],KK=simdata$KK[eaten],size=simdata$size[eaten]),paste

```

```

(output,"eaten_ind",ns,".txt",sep=""),col.names=TRUE,row.names=FALSE,appe
nd=FALSE)

# Recording of the fraction of the fish that has been eaten
# number of individual exposed to mortality caused by predation
Npop=length(ind.eaten)
# number of eaten fish by predators
Neaten=length(eaten)
# proportion of population eaten by predator
year.eatenN[tt]=Neaten/Npop
# eaten biomass of prey by predation
year.eatenBM[tt]=sum(sizeTOweight(simdata$size[eaten]))
# fish mortality caused by predation
year.mortalityP[tt]=year.eatenBM[tt]/sum(sizeTOweight(simdata$size))
# predator abundance per time step
year.Pred.N[tt]=round(PredDens.array[tt]*K)

# removal of eaten individuals
simdata=simdata[-eaten,]

}}

# 4) Growth of each individual based on population density and individual
growth parameters
temp.year.BM=sum(sizeTOweight(simdata$size))
year.GT=growth.time(BM=temp.year.BM,CC=CC)

for(i in 1:length(simdata[,1])){
  simdata$GT[i]=simdata$GT[i]+year.GT
  simdata$size[i]=simdata$LL[i]-(simdata$LL[i]-Lo)*exp(-
  simdata$KK[i]*simdata$GT[i])
}

# 5) Maturity: those reproduce who have reached their size at maturation
(calculated from LL)
for(i in 1:length(simdata[,1])){
  mat.th[i]=simdata$size.mat[i]/simdata$LL[i]
  if(simdata$size[i]>(mat.th[i]*simdata$LL[i]) && simdata$ET.mat[i]==0){
    simdata$ET.mat[i]=simdata$ET[i]
    simdata$size.mat[i]=simdata$size[i]
  }
  if(simdata$size[i]>mat.th[i]*simdata$LL[i]){simdata$maturity[i]=1}
}

# 6) Reproduction: individual by individual, number of offspring and Lo from
mother's size

```

```

juveniles=data.frame(size=rep(o,o),ET=rep(o,o),GT=rep(o,o),maturity=rep(o,o),sex=rep(o,o),KK=rep(o,o),LL=rep(o,o),mat.th=rep(o,o),reftrait.G=rep(o,o),reftrait.P=rep(o,o),locus1=rep(o,o),locus2=rep(o,o),locus3=rep(o,o),locus4=rep(o,o),locus5=rep(o,o),locus6=rep(o,o),locus7=rep(o,o),locus8=rep(o,o),locus9=rep(o,o),locus10=rep(o,o),cum.juv=rep(o,o),ET.mat=rep(o,o),size.mat=rep(o,o))

```

```

matF=which(simdata$sex==1&simdata$maturity==1)
matM=which(simdata$sex==0&simdata$maturity==1)

```

```

# Going through mature females
for(i in matF){ # each mature females produces a clutch of juveniles
  Njuv=numb.juv(simdata$size[i],GT=year.GT)
  simdata$cum.juv[i]=Njuv+simdata$cum.juv[i]
  mate=sample(matM,1) # one male can father several clutches
  simdata$cum.juv[mate]=Njuv+simdata$cum.juv[mate]
}

```

```

# Dataframe for one clutch

```

```

temp.juveniles=data.frame(size=rep(Lo,Njuv),ET=rep(o,Njuv),GT=rep(o,Njuv),maturity=rep(o,Njuv),sex=rep(o,Njuv),KK=rep(o,Njuv),LL=rep(o,Njuv),mat.th=rep(o,Njuv),reftrait.G=rep(o,Njuv),reftrait.P=rep(o,Njuv),locus1=rep(o,Njuv),locus2=rep(o,Njuv),locus3=rep(o,Njuv),locus4=rep(o,Njuv),locus5=rep(o,Njuv),locus6=rep(o,Njuv),locus7=rep(o,Njuv),locus8=rep(o,Njuv),locus9=rep(o,Njuv),locus10=rep(o,Njuv),cum.juv=rep(o,Njuv),ET.mat=rep(o,Njuv),size.mat=rep(o,Njuv))

```

```

# Pool of genotypes used in case there are no evolutionary processes

```

```

if(evolution==F){
  ind=which(parents$sex==1)
  mg=sample(ind,1)
  ind=which(parents$sex==0)
  fag=sample(ind,1)
}

```

```

if(Njuv>=1){
  for(juv in 1:Njuv){ # each juvenile in the clutch produced
    # alleles from mother
    for(locus in 10:19){
      if(evolution==F){
        if(parents[mg,locus]==2) {temp.juveniles[juv,locus]=1}
        if(parents[mg,locus]==1) {temp.juveniles[juv,locus]=rbinom(1,1,0.5)}
        if(parents[mg,locus]==0) {temp.juveniles[juv,locus]=0}
      }
      else{
        if(simdata[i,locus]==2) {temp.juveniles[juv,locus]=1}
        if(simdata[i,locus]==1) {temp.juveniles[juv,locus]=rbinom(1,1,0.5)}
      }
    }
  }
}

```

```

    if(simdata[i,locus]==0) {temp.juveniles[juv,locus]=0}
  }}

  # alleles from father
  for(locus in 10:19){
    if(evolution==F){
      if(parents[fag,locus]==2)
        {temp.juveniles[juv,locus]=temp.juveniles[juv,locus]+1}
      if(parents[fag,locus]==1)
        {temp.juveniles[juv,locus]=temp.juveniles[juv,locus]+rbinom(1,1,0.5)}
      if(parents[fag,locus]==0)
        {temp.juveniles[juv,locus]=temp.juveniles[juv,locus]+0}
    }
    else{
      if(simdata[mate,locus]==2)
        {temp.juveniles[juv,locus]=temp.juveniles[juv,locus]+1}
      if(simdata[mate,locus]==1)
        {temp.juveniles[juv,locus]=temp.juveniles[juv,locus]+rbinom(1,1,0.5)}
      if(simdata[mate,locus]==0)
        {temp.juveniles[juv,locus]=temp.juveniles[juv,locus]+0}
    }
  }}

  temp.juveniles$refrait.G[juv]=sum(temp.juveniles[juv,10:19])

temp=fromGtoP(temp.juveniles$refrait.G[juv],Pvar=Pvar,Pmin=Pmin,Pmax=P
max)
  temp.juveniles$refrait.P[juv]=temp$refrait.P
  temp.juveniles$KK[juv]=temp$KK
  temp.juveniles$LL[juv]=temp$LL
  temp.juveniles$sex[juv]=rbinom(1,1,0.5)
}}
# Printing information of each clutch
# Clutch will be joined to juvenile population
juveniles=rbind(juveniles,temp.juveniles)
}

# Juveniles will be joined to the entire population
simdata=rbind(simdata,juveniles)

# Population metrics calculated for each year
year.aver.matsize[tt]=mean(simdata$size[which(simdata$maturity==1)])
year.aver.matage[tt]=mean(simdata$ET[which(simdata$maturity==1)])
year.aver.matLL[tt]=mean(simdata$LL[which(simdata$maturity==1)])
year.aver.matKK[tt]=mean(simdata$KK[which(simdata$maturity==1)])
year.aver.LL[tt]=mean(simdata$LL)
year.aver.KK[tt]=mean(simdata$KK)

```

```

year.N[tt]=length(simdata[,1])
year.N.mat[tt]=sum(simdata$maturity)
year.N.dens[tt]=length(simdata[,1])/CC

year.fem.ratio[tt]=length(simdata[,1][which(simdata$sex==1)])/length(simdata[,1][which(simdata$sex==0)])
year.females[tt]=sum(simdata$sex)/year.N[tt]
year.BM[tt]=sum(sizeTOWeight(simdata$size))

  year.BM.mat[tt]=sum(sizeTOWeight(simdata$size[which(simdata$maturity==1)]))
year.N.juveniles[tt]=length(juveniles[,1])
year.LL.juveniles[tt]=mean(juveniles$LL)
year.KK.juveniles[tt]=mean(juveniles$KK)
year.heritability[tt]=(sd(simdata$refrait.G)^2)/(sd(simdata$refrait.P)^2)
year.recruitment[tt]=length(which(simdata$ET==0))
year.refrait.G[tt]=mean(simdata$refrait.G)
year.refrait.P[tt]=mean(simdata$refrait.P)
year.growth.time[tt]=year.GT
year.age.maturation[tt]=mean(simdata$ET.mat[simdata$ET.mat>0])
year.size.maturation[tt]=mean(simdata$size.mat[simdata$size.mat>0])
year.mat.th[tt]=mean(simdata$mat.th)

# Recording fully adapted population (last 30 years before fishing)
if(evolution==F){
  if(tt>369 & tt<=400){
    ind=which(simdata$maturity==1)
    parents=rbind(parents,simdata[ind,])
  }
}

# Recording adapted population for the 150 yrs before simulation end
if(tt>2849 & tt<=3000){
  write.table(simdata,paste(output,"adapted_population",tt,".txt",sep=""),
    col.names=T,row.names=F,sep="\t")
  write.table(simdata,paste(output,"adapt_popslast150.txt",
    sep=""),col.names=T,row.names=F,sep="\t")
}

# Printing simulation progress
print(tt)
print(year.N[tt])
print()
}

output.data=data.frame(
  N=year.N,
  N.mat=year.N.mat,

```

```

N.dens=year.N.dens,
BM=year.BM,
BM.mat=year.BM.mat,
BMtoCC=year.BM/CC*100,
heritability=year.heritability,
refrait.G=year.refrait.G,
refrait.P=year.refrait.P,
N.juveniles=year.N.juveniles,
recruitment=year.recruitment,
LL.juveniles=year.LL.juveniles,
KK.juveniles=year.KK.juveniles,
LL=year.aver.LL,
KK=year.aver.KK,
aver.matsize=year.aver.matsize,
aver.matage=year.aver.matage,
aver.matLL=year.aver.matLL,
aver.matKK=year.aver.matKK,
fem.mal.ratio=year.fem.ratio,
females=year.females,
growth.time=year.growth.time,
aver.maturET=year.age.maturation,
aver.matur.size=year.size.maturation,
mortality=year.mortality,
mortalityF=year.mortalityF,
RL=year.mat.th,
catchN=year.catchN,
catchBM=year.catchBM)

```

```

# Calculation of selection differential

```

```

RR=rep(NA,length(output.data[,1]))

```

```

SS=rep(NA,length(output.data[,1]))

```

```

for(i in 2:length(output.data[,1])){

```

```

  RR[i]=output.data$refrait.G[i]-output.data$refrait.G[i-1]

```

```

  SS[i]=RR[i]/output.data$heritability[i-1]

```

```

}

```

```

output.data=data.frame(output.data,SS=SS)

```

```

# Preparation for the predator output (removing NAs)

```

```

PredDens.array=PredDens.array[!is.na(PredDens.array)]

```

```

year.Pred.N=year.Pred.N[!is.na(year.Pred.N)]

```

```

year.eatenN=year.eatenN[!is.na(year.eatenN)]

```

```

year.eatenBM=year.eatenBM[!is.na(year.eatenBM)]

```

```

year.mortalityP=year.mortalityP[!is.na(year.mortalityP)]

```

```

predator=data.frame(PredDens=PredDens.array, Pred.N=year.Pred.N,

```

```
eatenN=year.eatenN, eatenBM=year.eatenBM, Predation.M=year.mortalityP)
```

```
# Population parameters output per time step
```

```
write.table(output.data,paste(output,"simulation", ns,  
".txt",sep=""),col.names=T,row.names=F,sep="\t")
```

```
# Parameters output per individual
```

```
write.table(simdata,paste(output,"last_year", ns, ".txt",sep=""),  
col.names=T,row.names=F,sep="\t")
```

```
# Predator output
```

```
write.table(predator,paste(output,"Predator", ns, ".txt",  
sep=""),col.names=T,row.names=F,sep="\t")
```

```
#####
```