ALMA MATER STUDIORUM
UNIVERSITÀ DI BOLOGNA

DOTTORATO DI RICERCA IN

TECNOLOGIE INNOVATIVE E USO SOSTENIBILE DELLE RISORSE DI PESCA E BIOLOGICHE DEL MEDITERRANEO (FISHMED-PHD)

Ciclo 36

Settore Concorsuale: 05/C1 - ECOLOGIA

Settore Scientifico Disciplinare: BIO/07 - ECOLOGIA

ADAPTIVE LIFE HISTORY STRATEGIES OF THE ADRIATIC COMMERCIAL GADIFORMES FACING FISHING PRESSURE AND CLIMATE CHANGE

Presentata da: Federico Calì

Coordinatore Dottorato

Prof. Stefano Goffredo

Supervisore

Dr. Alberto Santojanni

Co-supervisori

Prof. Carlotta Mazzoldi

Dr. Mario La Mesa

Prof. Michele Casini

Prof. Stefano Goffredo

Esame finale anno 2024

Recommended citation:

Calì, Federico (2024) Adaptive life history strategies of the Adriatic commercial Gadiformes facing fishing pressure and climate change. Ph. D. Thesis, Università di Bologna, FishMed-PhD.

Credit cover and Figure 1.1: Raimondo Quagliana graphic

Credit fish species drawings: Gaia La Rosa

A smooth sea never made a skilled sailor

Franklin D. Roosevelt

Ringraziamenti/ Agradecimientos/Acknowledgments

ITA

Dal momento che non so come iniziare questa sezione e ho esaurito tutta la mia fantasia scrivendo la tesi, inizierò tirando un bel sospiro di sollievo che determina la fine di quello che metaforicamente posso considerare un bel tuffo profondo in apnea…

Phew!

(Si, si scrive proprio così nello slang fumettistico e, no, non è così che si dovrebbe respirare dopo un tuffo tirato al limite).

Pensando al mio percorso di dottorato ed agli ultimi tre faticosi anni, mi vengono in mente tante, troppe persone da ringraziare per il loro contributo e supporto psicologico/fisico/lavorativo, ma voglio e provo a farlo sperando di non dimenticare nessuno. Inizierò ringraziando di cuore i miei tre supervisori Alberto Santojanni, Carlotta Mazzoldi e Mario La Mesa. Fin dall'inizio non avevo dubbi riguardo il neoformato gruppo di lavoro "gadifriends", ma i risultati ottenuti dimostrano ulteriormente il buon funzionamento ed il potenziale futuro di questa collaborazione. Grazie Alberto (per me questo è ormai il decimo anno di collaborazione insieme mantenendo sempre in vita l'asse Ancona-Chioggia), per il supporto scientifico, la sempre pronta risposta e la ricerca con lanternino dei lavori scannerizzati. Grazie Carlotta, per avermi sempre supportato, creduto in me (e più di me stesso) fin dall'inizio, alimentato la mia curiosità ed aver tenuto sempre aperta la porta della tua persona e dell'Università di Padova, che considero come una famiglia e sono davvero grato ed orgoglioso di farne parte. Ed infine Grazie Mario, farei prima a dire le pochissime cose per cui non lo ringrazio (es. non essere ancora venuto a farmi visita in Sicilia), per aver rappresentato da sempre, specialmente in questi ultimi tre anni, un punto di riferimento costante, sicuro e sempre disponibile per qualsiasi dubbio, necessità o scambio di idee relativo a qualsivoglia tematica, riuscendo sempre perfettamente ad alternare con disinvoltura le vesti di grande professionista a quelle di grande amico.

Passiamo adesso alla sopracitata famiglia Stazione Idrobiologica-UniPd, da veterano *stationlabber* posso dire che negli anni ci sono stati diversi cambi di formazione ma l'atmosfera familiare e il supporto reciproco sono sempre stati una costante. Ringrazio in particolare il team supporto psicologico/misurazione pesci ed estrazione otoliti formato da: Cristina, Giulia, Emily, Jacopo, Mercedes, Mattia, Gabbo, Martina, Filippo; non può mancare Andrea, che ha sempre trovato una soluzione rapida ed efficace a qualsiasi strana esigenza (es. piastra raffreddagonadi e supporto bruciaotoliti). Grazie FedePoli per i consigli dispensati e i caffè improvvisati della mattina, momenti sempre molto intensi e che hanno scandito i vari momenti del percorso. Grazie Licia, non solo per aver estratto un bel po' di otoliti, ma soprattutto per non esserti mai stancata di chiedermi se avevo bisogno di una mano (e per stimolare la produzione di sfincione). Grazie Matteo, per i momenti ludici e di discussioni profonde, nonché per aver fatto da "compare di PhD" per un periodo. Grazie FedeStranci per aver condiviso la passione per il merlano (tanto sfigato quanto interessante), nonché per aver accettato di consumarti unghia e polpastrelli levigando otoliti. Ringrazio anche gli altri familiari Unipd come Laura, Davide, Serena, Joana, Robin per i bei momenti passati insieme negli ultimi 3 anni davanti ad uno spritz oppure a zappare lo station-orto o parlare di tematiche contadine e/o alimentari. Grazie Alberto per il supporto ed i consigli sempre pronti, le nostre chiaccherate sono state leggere ma allo stesso tempo significative. Grazie Cami per i momenti di confronto a distanza e per condividere la passione per i gadidi. Grazie Carlo per essere stato un altro "compare di PhD" nonché colui che mi ha iniziato al mondo dei cluster HPC, hanno davvero dato una svolta alla mia esperienza di ricerca a Palma di Maiorca! Ringrazio infine Davide, Sofi e Riccardo perché siete fatti volere bene (Davide anche per la concessione all'uso del microscopio).

Adesso devo obbligatoriamente fare una parentesi chioggiotta, ringraziando i pescatori e commercianti di Chioggia che negli ultimi tre anni ho disturbato di più ma che non mi hanno mai mandato a quel paese, tenendomi da parte i preziosi campioni che hanno costituito la spina dorsale della tesi: Sandro e Riccardo Zennaro, Daniele Padoan, Elio Dall'Acqua, Michelangelo Cavallarin, Cristian Bonaldo, Augusto Lombardo. Ringrazio Vito per il costante supporto logistico al campionamento e le partitelle di tennis. Infine, non resta che ringraziare Paolo, il mio primo vero amico chioggiotto, nonché compare di pescasub, per i bei momenti passati insieme e le innumerevoli volte che mi ha invitato ad andare a pescare negli ultimi anni e si è sentito rispondere quasi sempre di no (colpa del dottorato soprattutto, si).

Adesso passo all'altra grande famiglia che è il CNR-IRBIM di Ancona, che ho frequentato regolarmente ad intervalli random e informando tutti del mio arrivo sempre all'ultimo minuto (scusatemi). Grazie Fortunella, per il contributo attivo nella tesi, il tuo supporto affettivo sempre presente, gli aggiornamenti e le utilissime ramanzine. Grazie Monica, per il supporto morale e la passione condivisa per gli stomaci dei naselli. Grazie Michela e "nazionale sgambi" (Roberto, Lorenzo, Giovanni, Matteo, Filippo, Giordano, Peppe) per il supporto nel campionamento, i surveys Pomo hanno scandito il passare degli ultimi tre anni. Grazie a tutti i "CNR juveniles": Laura, Martina, Enrico, Francesco, Daniel, Andrea, Giada, Marina, Marco, tutti a turni alterni avete allietato i miei giorni anconetani sia durante che dopo la giornata di lavoro (in particolare a chi mi ha ospitato a dormire 😊), mi dispiace che ci siano 261 km a tenerci separati. Infine, Grazie Carmen, abbiamo avuto modo di conoscerci solo recentemente ma mi ha colpito subito la tua disponibilità e vicinanza nell'aiutarmi a trovare alloggio a Palma, como la auténtica isleña que eres.

Ringrazio Michele Casini per il supporto come co-supervisore e per aver dispensato ottimi consigli durante il percorso di dottorato, primo fra tutti quello sulla persona giusta da contattare per il periodo all'estero. Grazie anche a FedeMaioli, per il supporto sui modelli e il contributo di collaborazione, che ne dici di un thinning 10000?.

Concludo tornando alla mia terra d'origine, ringraziando di cuore la mia famiglia: Papis, Mamma, Rosalia e Raimondo (quest'ultimo anche per supporto grafico e fototolitigrafico). Mi avete sempre sostenuto moralmente ed economicamente (data l'esigua borsa di dottorato), oltre che avermi cresciuto ed educato in maniera impeccabile. Grazie ai miei fratelli Manu, Lorenzo e szwagierka Zofia per il supporto psicologico e perché siete belli. Grazie Giorgia e Salvatore (che considero madrina e padrino scientifici, nonché familiari), perché avete sempre tifato per me fin dall'inizio della mia carriera. Grazie ai miei amici di sempre, inossidabili: Gaetano, Marco, Iguana, Fabio, Alessandra, Giulia, Valentina, Alessio, Angelo, Giovanni, Michele, Ciccio, Tevez per essere stati sempre presenti anche

a distanza.
E infine, ringrazio Gaia per essere stata sempre al mio fianco nei momenti belli ed in quelli bui, mettendocela tutta per supportarmi, consolarmi, proteggermi e farmi sorridere anche quando era l'ultima cosa che volevo fare (oltre che per i fantastici disegni che inaugurano i capitoli). Grazie anche a Pippo, Giusi e Nicola per il supporto grazie ai bei momenti passati insieme, le pescate e i pranzi domenicali che hanno sempre accompagnato le vacanze sicule degli ultimi anni.

ESP

Y ahora vamos a agradecer a las fantásticas personas que he conocido durante la(s) experiencia(s) española(s). Comienzo con Manolo, al que considero un supervisor más (¡y qué supervisor!), además de un amigo. Aunque el tiempo que pasamos juntos acumulado no fue mucho, pero siempre fue muy intenso y de gran calidad, creo que es difícil encontrar gente tan buena tanto científica como humanamente. Espero que nuestra colaboración pueda continuar en los próximos años. Agradezco Marta por su amistad, charlas intensas durante los viajes en coche y permitirme a veces el lujo de sentirme como un verdadero mallorquín (aunque me falta participar en una "matanza" para tener el título official, verdad?). Agradezco Patricia por su apoyo en el trabajo y los buenos momentos en compañía, comiendo o pegando sacos hasta la muerte. Agradezco Marina por su fantástica compañía y sensibilidad, siempre dispuesta a hacer algo por los demás. Agradezco Georgios por su compañía siempre agradable en la biblio, momentos de gossip y también de fiesta nocturna. Agradezco Andrea porque fuiste mi compañera de resistencia del COB cuando esto estaba desierto y por invitarme a menudo a hacer fiesta juntos. Ahora solo porque creo que no iría a terminar nunca (perdóname si no lo hago individualmente), agradezco las otras personas maravillosas que hicieron que mi experiencia en Mallorca fuera única: Alicia, Virginia, Alex, Inma, Natalia, Safo, Vicenç, Mar, Melissa, Diego, PatriciaR, Pilar, Biel, Gloria, Federico, Julia, Gavino, Jil, Luis, Eko, Io, Eirini, Angel y todo el equipo GRECO-COB-IEO (realmente me sentí como uno de ustedes). Creo que no podría haber deseado una experiencia mejor que ésta, y espero de verdad que después de la primera y segunda vez, haya una tercera vez en Palma. Dejo un trozo de mi corazón en esta fantástica isla.
Os invito y os espero a todas/os ya sea en Chioggia (paralelo 45° norte) o en Sicilia (paralelo 38° norte), según el clima y el mar preferidos.

ENG

And last but not least, I would like to thank the biblioffice compañeras/o of the last three months I spent in Palma: Rachel, Marion, Siadbh and Ian (even if you are Catalan I put you here because you are polyglot and part of this group). It was a big pleasure to meet you and spending time together, you made me have so much fun (and made me feel younger).
Finally, I need to thank Georg Engelhard, Caroline Cusack and Cóilín Minto. Even if we met only once or in few occasions over the last three years, your suggestions and the interest you have shown towards my research activities and gadids spurred me on to give my all and be proud of my achievements. I hope we will have the opportunity to meet again soon.

Table of contents

Extended Abstract

Understanding the biology, ecological interactions, and population trends of key marine species is essential for comprehending ecosystem dynamics and achieving sustainable marine resource management through an ecosystem-based approach. This is particularly true for those basins characterised by high levels of anthropogenic impacts (i.e., pollution, habitat degradation, and overfishing) and high susceptibility to climate change, whose effects can be interactive, amplifying their negative consequences. The response of species to stressors is influenced not only by the characteristics of the stressor and the environmental context but also by species-specific attributes, which ultimately determine varying levels of vulnerability. There is increasing concern about the condition of numerous commercial species that have shown spectacular declines in landings over the last decades, as in the case of cold-water species inhabiting the northern sectors of the Mediterranean Sea. Among these, the Adriatic Sea is the one showing the highest warming trend over the last 20 years, although it is considered a cold refugium due to its unique combination of hydrographic and environmental features. However, for most of the species with an affinity for cold waters, data are not routinely collected, and there is a lack of knowledge about their life cycles and the effects of sea warming on their population dynamics.

This thesis focuses on some commercial species belonging to the cold-water group of Gadiformes in the Adriatic Sea and on their biological responses to increasing sea temperatures and high fishing exploitation. I used an experimental approach to investigate the life history traits of three key gadid species (whiting, blue whiting, and poor cod) and compare them with samples collected between 1985 and 1991, to investigate the presence of variations potentially related to fishing and/or climate change. To complement and support the experimental part of the thesis, I then applied a joint species distribution model to explore the influence of some environmental factors (including sea bottom temperature) on the abundance of five Adriatic gadiforms (whiting, blue whiting, poor cod, silvery pout, and European hake), using data from the MEDITS surveys carried out between 1998 and 2020.

The experimental results provided novel and updated information on the biology of the three species investigated in the Adriatic area, highlighting both common and species-

specific variation patterns between recent and old samples. Whiting and blue whiting exhibited a reduction in size and growth performances, which seem to be attributable to the direct and indirect effects of climate change, respectively. In poor cod, the decrease in size was instead coupled with an increased growth rate at the early stages and trunked age structures, revealing a potential impact due to fishing exploitation. The model results highlighted the significant influence of depth in determining the occurrence pattern of gadiform species, while the abundance models revealed varying contributions from all the environmental covariates. The comparison of models fitted to two distinct thermal regimes allowed me to detect an increased influence of thermal covariates in the most recent (and warm) period, suggesting an increase in the sensitivity of species to temperature. Interestingly, the correlation pattern between abundance and sea bottom temperature was species-specific, though almost all the species showed a negative impact of increasing temperature except for European hake, which showed a positive relationship. Moreover, the species-specific responses to temperature resulting from the models indicated that whiting and blue whiting are potentially more vulnerable to increasing temperature compared to poor cod, confirming the hypotheses drawn from the experimental results.

In summary, this thesis integrates different methodological approaches and a combination of intra- and inter-specific comparisons to provide a comprehensive understanding of the impacts of fishing and climate change on gadiform species in the northern-central Adriatic Sea. The different responses observed in both experimental and modelling approaches indicate that even within a small group of closely related species, there can be different levels of vulnerability to fishing and climate change. European hake, an exception among the studied species, is the only species with the adaptive potential to thrive in a warming scenario, and consequently, a possible increase in its population is expected in the Adriatic area. The results of the present study provide valuable insights into the adaptive mechanisms of these species and underscore the importance of ecosystem-based management approaches for sustainable marine resource management.

1 General Introduction

1.1 Evolution of life history traits and strategies

The life history traits encompass several aspects of the life cycles of organisms, including growth mode, maximum size, reproductive investment, size and age at sexual maturity, number and size of offspring, longevity, sexual pattern, maximum age and type of sexual determination. These biological features represent the evolutionary outcome of multiple environmental pressures under the driving force of natural selection (Roff, 1992). The principles underlying this process are the fundamentals of the theory of evolution: variability, inheritance of individual characters and natural selection, which lead to evolutionary change in populations (Stearns, 1992). The variability in life history traits among animals and plants is clearly observable in nature at both intra-specific and inter-specific levels. Differences can be noticed in patterns of growth cycle, lifespan, and reproduction at various levels of taxonomic organization. For example, at the interspecific level, within the fish family Pleuronectidae, there are species that reach maximum sizes of a few centimetres and are sexually mature within the first year of life, and other species (e.g. *Hippoglossus hippoglossus* or halibut) that exceed two metres and generally are sexually mature at around ten years of age. Similarly, at intraspecific level, dwarf halibut populations in Scotland reach sexual maturity at three years of age, while in Newfoundland the same species reaches maturity at fifteen years of age. The differences observed are strongly influenced by the environmental and ecological context (Roff, 2002).

The life history theory aims to explain how evolution shapes organisms to achieve the survival and reproductive success (Darwin 1871), a concept that can be summarised by the term 'fitness'. Throughout evolution, natural selection has acted within the genetic variability present in each population, favouring those traits that in a given environment maximise the fitness of the individuals possessing them. Although the classic approach used in the past was to study life history traits under the concept of optimality, recently non-equilibrium approaches (involving frequency-dependence, density-dependence, evolutionary game theory, adaptive dynamics, and explicit population dynamics) have supplanted optimization as the preferred approach. Moreover, looking at ecological studies, there is increasing evidence that population dynamics and interspecific interactions have impacts on the evolutionary process

(Stearns, 2000). In addition to the external constraints, there are also the internal ones, determined by interactions between traits and physiology. Indeed, since the available resources can be limited, investing energy in one trait implies less investment in another, resulting then in a “trade-off”. Adaptive strategies can be described as sets of trade-offs, which represent the linkages between traits that constrain their simultaneous evolution. For example, delaying the age at sexual maturity allocates more energy for juvenile growth or having low fecundity allows the production of large-sized offspring (Fonseca and Cabral, 2007). In general, when the trade-off involves genotypic characteristics, it is called "strategy", whereas, if the variation pattern is shaped by phenotypic plasticity in response to environmental changes, it is called "tactic." (Stearns, 1989).

The external factors can create intense selection pressures for certain life history traits and strategies. For example, in areas with high predation pressure, organisms may evolve faster growth rates and earlier reproductive ages to increase their chances of survival and pass on their genes before being preyed upon. On the other hand, in environments with limited resources, organisms with slower growth rates and delayed reproduction may maximize their chances of survival and reproduction when resources become available (Wilbur and Rudolf, 2006). Overall, the interplay between environmental factors and life history traits is crucial in shaping the survival and reproductive success of organisms. Since ecological conditions act as a selective agent in favouring the type of reproductive strategy, similarities between some traits are often observed in species living in the same environment. For example, in the marine environment, a negative correlation has been observed between water temperature and the size of eggs produced by many species (Laptikhovsky, 2006). Egg size is generally species-specific, although it can vary intraspecifically depending on the size of the female, food availability and breeding season. In general, while at low and intermediate latitudes species producing eggs of different diameters are found, in polar regions only species producing large eggs are observed (Laptikhovsky, 2006). This trend was described and theorised in the 1940s, initially for marine gastropod molluscs ('Thorson's rule'; Thorson, 1936) and marine teleosts ('Rass's rule'; Rass, 1935). According to Thorson's theory, the tendency to produce larger eggs is linked to low water temperature and consequently reduced water productivity, which limits the growth and survival of many species with planktotrophic larval stages (feeding on plankton from their early life stages). Consequently, lecithotrophic larvae (which feed on yolk in the early larval stages), which survive even in the absence of external nourishment, have higher survival success compared to planktotrophic larvae. Rass's rule explains the same phenomenon, but in other terms, and with particular reference to marine fish. In fact, the size of the eggs is related to the temperature at which the reproduction of a species takes place. In particular, the lower the temperature of the water, the longer it takes for the stages of oogenesis and embryonic development to occur. This causes the species-specific size of the eggs and the hatching size to increase, as reported from the multiple comparisons within the family Carangidae and Liparidae (Rass, 1986), where, in both cases, species living at higher latitudes produce larger eggs. Although these trends have been demonstrated and extensively discussed, temperature and trophic factors are currently considered to be only some of the factors involved in determining egg size (Clarke, 1992; Levin and Bridges, 2001). In fact, there are several exceptions to this general rule, which are the result of other factors, such as biotic interactions.

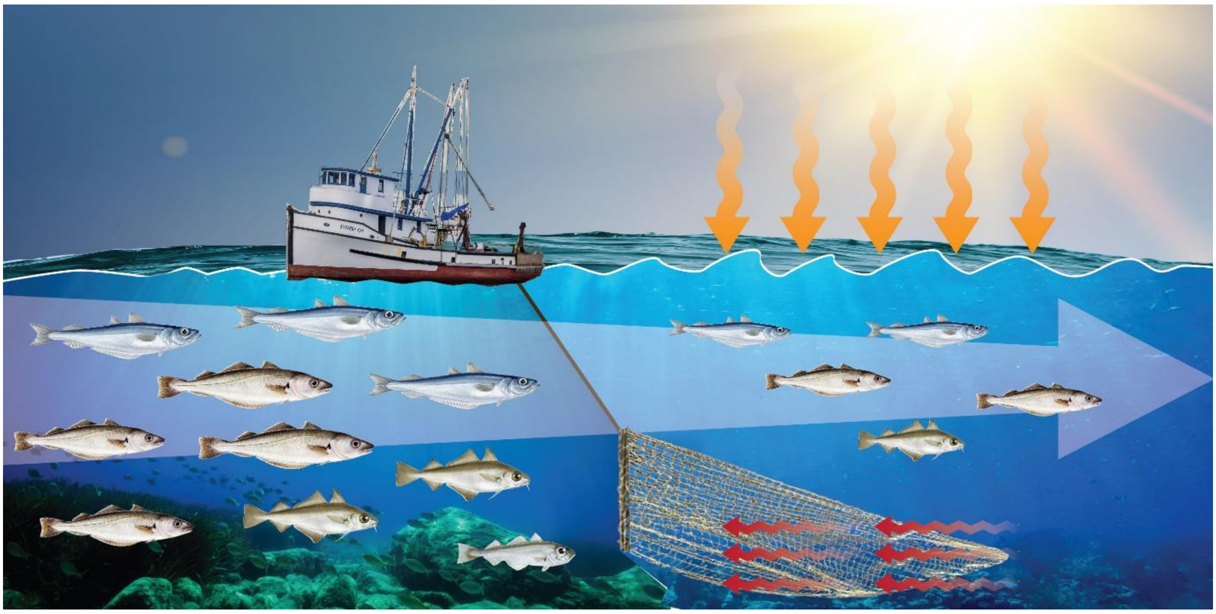


Figure 1.1. Schematic representation of the typical effects of fishing and climate change on marine fish populations, frequently leading to reduced biological productivity and sizes in cold and temperate regions.

1.1.1 Effects of climate change and fishing on fish populations and life history traits

The intricate interplay between climate change, fishing, and their consequential impacts on fish life history traits represents a multifaceted ecological challenge that demands thorough investigation. Human-induced climate change has emerged as a global force, determining shifts in environmental parameters such as temperature, precipitation, and oceanic conditions (IPCC, 2014a). These alterations profoundly influence the physiological, behavioural, and reproductive dynamics of fish species, ultimately shaping critical life history traits. Concurrently, intensified fishing practices, driven by escalating global demand for seafood, subject fish populations to selective pressures that induce evolutionary changes in their life history strategies (Heino et al., 2013). As a consequence, these stressors interact to produce a complex network of challenges, potentially leading to cascading effects throughout aquatic ecosystems (Figure 1.1). Their simultaneous occurrence, often showing synergistic effects, determines different outcomes and complexity scales depending on the local context (Genner et al., 2010; Hidalgo et al., 2012; Engelhard et al., 2014; O'Connor et al., 2015).

Over the last century, intensified fishing practices have led to a range of ecological consequences worldwide. One of the most immediate impacts is overfishing, which occurs when the rate of fish extraction exceeds the population's ability to replenish resulting in the depletion of targeted species and disruptions in trophic cascades (Pauly et al., 1998). This can lead to the collapse of entire fisheries, compromising the livelihoods of communities dependent on marine resources. Currently, 35% of global marine stocks are being overexploited, a trend that has been steadily increasing in recent decades. Besides, 57% of the stocks are being exploited at the maximum sustainable levels and only 7% of stocks are under-fished, a significant decrease from the 40% observed in 1975 (FAO, 2022). Furthermore, certain fishing practices, such as bottom trawling, can cause physical damage to seafloor habitats, impacting benthic communities and reducing overall biodiversity (Watling and Norse, 1998). The selective targeting of specific species can also trigger shifts in the composition of marine ecosystems, potentially leading to the proliferation of certain species and the decline of others (Jennings and Kaiser, 1998). Moving on a closer scale, the selective harvesting of larger individuals, a prevalent practice in many fisheries, has been identified as a driver of alterations in reproductive- and growth-related traits (Jørgensen et al., 2007; Enberg et al., 2012). Reproduction and growth are among the most important life history traits determining fish population dynamics and therefore productive potential at different temporal scales. Firstly, the direct negative effects of a reduction in age/size of fish populations induced by fishing are evident by considering the positive relationship between fecundity and female size (Barneche et al., 2018). Indeed, the relative fecundity (number of eggs per unit of body mass) of fish increases with their size, meaning that a population with larger individuals will have a higher reproductive output compared to a population with smaller individuals, given the same amount of biomass (Bohnsack, 1994). Moreover, if fishing artificially limits the reproductive lifespan of fishes, their capacity for reproduction will not be fully achieved. Secondly, at a longer temporal scale, it is worth mentioning that selective harvesting has determined also evolutionary effects on fish populations, even if this process is challenging to investigate in wild populations due to the difficulty of distinguishing it from the effects of the phenotypic plasticity in response to both biotic and abiotic factors (Heino et al., 2002). Well-known examples of fisheries-induced modification of life history traits are related to size/age at maturity and growth rate, which were widely investigated over the last decades. In the case of the maturation pattern, the common trend reported is a decrease of size/age of maturity in harvested fish populations (Mollet et al., 2007; Albo-Puigserver et al., 2021). On the other hand, although early literature on fish-induced growth variation was dominated by the hypothesis that fishing favours the slow-growing specimens (for which fishing mortality is lower), several studies over the last two decades highlighted more complex dynamics, with more factors involved, keeping the scientific debate still open (Enberg et al., 2012; Pauly, 2021).

While overfishing is widely recognised as the main factor behind the decline of marine populations, there is mounting evidence indicating that climate change also plays a significant role in influencing fish population dynamics. Climate change has profound effects on the life history traits of fish species, impacting their physiology, behaviour, and overall population dynamics. The consequences of climate change on fish life history traits are complex and varied, with potential implications for fisheries, ecosystems, and the livelihoods of communities dependent on marine resources. Rising water temperatures, a direct consequence of climate change, have a direct influence on the metabolic rates of fish. Warmer temperatures can accelerate growth rates and affect the timing of key life history events, such as hatching, larval development, and age at maturity (Cheung et al., 2010). In addition, considering the Gill-Oxygen Limitation Theory (Pauly and Cheung, 2018), fish body growth is constrained by gill capability to supply oxygen through their surface. Consequently, in a situation where sea temperature rises, it is expetced that the body size of fish will decrease (Audzijonyte et al., 2020). This is because the solubility of oxygen in water decreases as temperature increases (Forster et al., 2012). On the other hand, changes in temperature and environmental cues can influence the timing and location of spawning. Altered reproductive behaviours, including shifts in spawning grounds and changes in the timing of reproductive events, have been observed in response to climate-induced changes in the marine biota (IPCC, 2014b). Fish species often exhibit specific thermal and habitat preferences. As climate change alters sea temperature, fish may respond by shifting their distribution ranges and migration patterns to stay within their thermal optima (Perry et al., 2005). Climate change can further influence the abundance and distribution of plankton and prey species, affecting the availability of food for fish. Changes in trophic interactions, such as mismatches between the timing of fish spawning and the peak abundance of prey species, can impact the survival and growth of fish populations (Hare et al., 2010). As already discussed for fishing, fish populations may undergo adaptive responses and evolutionary changes in their life history traits to cope with changing environmental conditions. Rapid evolution in traits such as size at maturity and reproductive strategies has been documented in response to climate-driven selective pressures (Sheridan and Bickford, 2011; Alvarez-Noriega et al., 2023).

Understanding the distinct effects of these stressors and their interactions is essential for informed conservation and management strategies. Integrated approaches that consider both fishing and climate change impacts are necessary to ensure the sustainable use and preservation of fish populations and the ecosystems they inhabit (Free et al., 2019).

1.2 The unique features of the Adriatic Sea within the Mediterranean context

The Adriatic Sea, located in the centre of the Mediterranean Basin, represents a dynamic and diversified ecosystem with ecological and oceanographic features that are both distinct and closely linked with the broader Mediterranean context (Tortonese, 1964). This semi-enclosed sea, situated between the Italian and the Balkan Peninsulas, extends approximately 800 kilometres from north to south and is characterized by a remarkable mosaic of oceanographic processes, biological diversity, and human activities. The distinctive set of oceanographic characteristics and ecological phenomena arising from its geographical location and complex bathymetry make it a unique microcosm within the Mediterranean Basin. The Adriatic Sea has distinct morphological variations, with the western section characterised by a predominantly uniform and sandy composition, with a gentle slope. In contrast, the eastern coastline displays an irregular topography, characterised by numerous islands and a steeply sloping bathymetry composed of rocky formations (Russo and Artegiani, 1996). Based on the bathymetric features, the basin is divided into three sub-basins along its latitudinal axis (Figure 1.2).

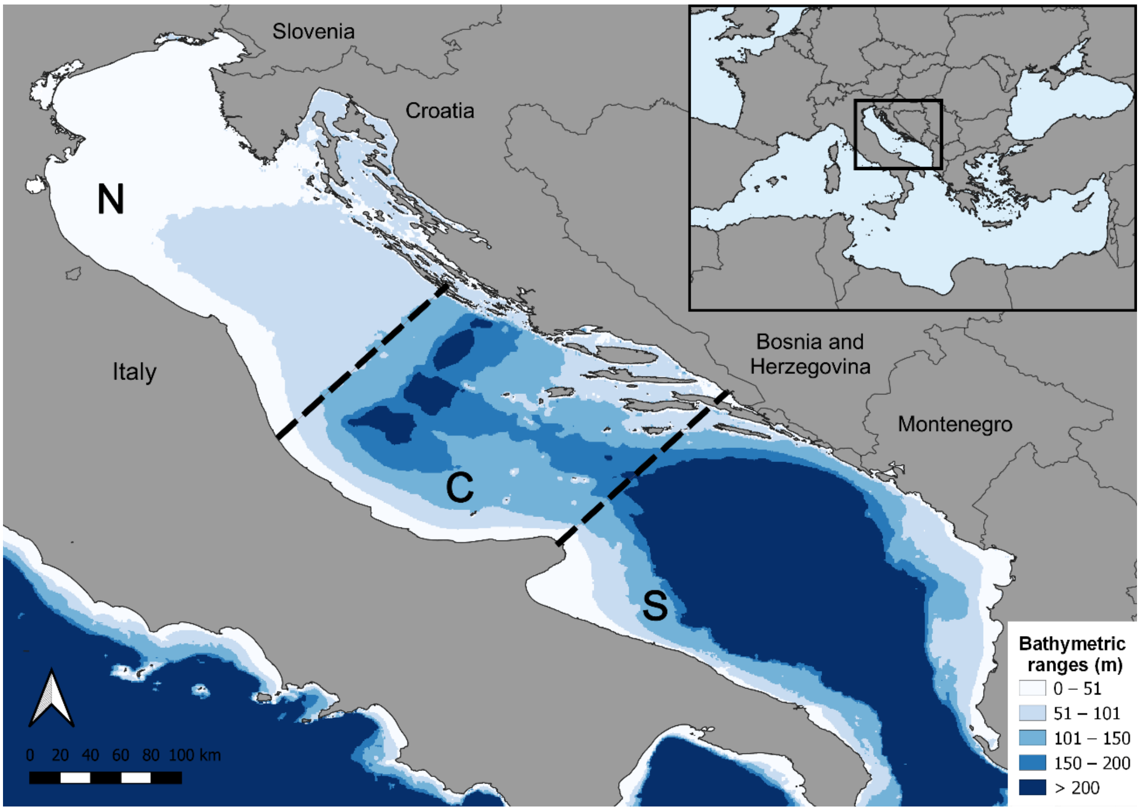


Figure 1.2. Map of the Adriatic Sea showing the bathymetric features, which serve as the basis for dividing the area into three sub-basins (Russo and Artegiani, 1996). N = northern sub-basin; C = central sub-basin; S = southern sub-basin.

The northern sub-basin extends from its northernmost point to a depth of 100 m and is distinguished by a notably shallow average depth of approximately 30–50 m. Additionally, it is marked by the presence of strong river runoffs. It is thought that Po and other rivers in northern Italy contribute approximately 20% of the overall Mediterranean river runoff (Hopkins, 1992). Conversely, the southern sub-basin is characterised by a narrow continental shelf, measuring 20–30 km in width. Beyond this point, there is a steep continental slope that descends to a depth of 1000 m. The area then transitions into a relatively flat abyssal plain, with a maximum depth of 1270 m, often known as the South Adriatic Pit. The middle Adriatic is a transition zone between the northern and the southern sub-basins which shows some open sea conditions, with an average depth of 100–150 m and characterised by two depressions (maximum depth 270 m), known as Pomo/Jabuka Pits (Russo and Artegiani, 1996).

Strong salinity gradients are observable in all seasons, mainly along the western coast, related to the river runoff. During the spring-summer period, the freshwater waters entering the northern Adriatic Sea extend in a south-eastern direction, intruding into the open sea. The highest salinity levels are observed in winter when homogeneous values of about 38 psu are measured over all offshore areas of the whole basin. On the other hand, in summer, minimum values are observed, due to stratification processes that prevent the vertical mixing of fresh and salty waters (Artegiani et al., 1997b). The temperature of the sea bottom exhibits a pronounced seasonal pattern, with coastal waters experiencing a range of variation from 7 °C (winter) to 27 °C (summer), while deeper places exhibit a range of variation from 10 °C (winter) to 18 °C (summer) (Russo et al., 2012). The physical properties and circulation patterns of the Adriatic Sea are significantly affected by atmospheric forces and in particular by wind regimes (Russo and Artegiani, 1996), with strong differences between summer and winter. During the cold season, low temperatures combined with the strong and dry north-easterly wind (Bora) trigger the formation of cold and dense waters in the northern sub-basin. The newly formed waters deepen and move southward, first reaching the Pomo/Jabuka Pits and then the Adriatic Pit (Marini et al., 2016). Finally, these waters reach the Ionian Basin, from where they spread south and east close to the bottom, supplying the Mediterranean thermohaline circulation system (Roether and Schlitzer, 1991). The Adriatic Sea, together with other northern (and cold) sectors of the Mediterranean Sea (Gulf of Lions, north Aegean Sea) are key regions where intermediate and deep-water convection is regularly observed, leading to vertical recirculation, which is essential to sustain the Mediterranean thermohaline circulation (Roether et al., 1996). Having the biggest contribution to the Mediterranean deep-water formation, the Adriatic Sea plays a pivotal role, being the area where the eastern Mediterranean Deep Water originates (Civitarese et al., 2005).

1.2.1 Vulnerability of the northern-central Adriatic Sea: trends of fishing and sea warming over the last decades

Recent studies employing AIS (Automatic Identification System) technology have identified the northern-central Adriatic Sea as the most heavily trawled region in the entire Mediterranean Sea (Ferrà et al., 2018; Merino et al., 2019), and potentially even in the globe (Pitcher et al., 2022). Several are the reasons why this area is particularly suited to the development of intense fishing activities, which date back, at least, to the beginning of the 19th century (Botter et al., 2006). Firstly, the high nutrient inputs characterising the northern and central parts of the Adriatic Sea promote the development of short trophic chains and facilitate efficient energy transfer between trophic levels, leading to high biological productivity (Fanelli et al., 2023). Secondly, this area has one of the largest continental shelves of the Mediterranean Sea and, being characterised by shallow waters and muddy/sandy bottoms, a large amount of its surface is exploitable by trawled gears (i.e., otter trawls, hydraulic dredges, and rapido trawls) (Pranovi et al., 2005). Here, fishing activities underwent an industrialization process after the Second World War, thanks to the introduction of the engine propeller. Concurrently, advanced fishing equipment (e.g., iron-teethed dredges and mid-water pelagic trawls) and new technologies such as freezer trawlers, radar, and echo sounding were adopted, further enhancing the efficiency of fishing activities. Although by the end of the 19th century fishing exploitation was already considered responsible for some stock declines, only at the beginning of the 20th century was proved to be linked with some changes in the fish community (Fortibuoni et al., 2010). Nowadays, fishing pressure is known to have played a primary role in the local decline of fish resources and the strong reduction of some vulnerable species, such as the elasmobranch community (Barausse et al., 2011; Coll et al., 2009; Fortibuoni et al., 2017; Lotze et al., 2011; Sguotti et al., 2022).

Another factor recently recognised as a major threat to the Adriatic ecosystem is represented by climate change. Indeed, in addition to the highest fishing exploitation level, this basin shows the highest warming trend in the Mediterranean Sea (García-Monteiro et al., 2022). The main reasons for which this basin is considered highly vulnerable compared to other areas are its geographical conformation and bathymetry. Indeed, being a land-locked sea extended along the latitudinal axis, it gives few migratory options to the sensitive species, i.e. the so-called cold-water species that are more abundant in this area than in the other regions of the Mediterranean Sea (Tortonese, 1964; Ben Rais Lasram et al., 2010). Distribution shifts poleward represent one of the first biological responses of stenothermal organisms to climate change (O’Connor et al., 2014) and the rapid increase of temperature, together with the geographical conformation, represent a severe threat to the survival of these species. Moreover, the northern-central Adriatic Sea, due to its shallowness, is strongly affected by air temperature variations, showing the greatest seasonal thermal gradient in the Mediterranean Sea (Russo and Artegiani, 1996; Bonacci and Vrsalovic, 2022). Recent estimations of Sea Surface Temperature trends in the Mediterranean Sea between 2003 and 2019 highlighted an increase of 1.12 °C of the mean temperature value in the Adriatic Sea, with the highest peaks observed in the northern part (García-Monteiro et al., 2022). Another effect of climate change in the northern-central Adriatic Sea has been observed by investigating the frequency and intensity of winter storms, which have undergone a decreasing trend over the second half of the 20th century (Lionello et al., 2012). The occurrence of winter storms, associated with strong northerly winds, is essential to maintain the dynamics of water circulation formation of cold and dense waters, which contribute to the overall thermal balance not only at the Adriatic but also at the Mediterranean scale (Schroeder et al., 2017). Consequently, climate variations occurring in these regions can have huge impacts, with serious consequences for the marine ecosystems, as already reported in other Mediterranean areas (Danovaro et al., 2001).

1.3 The Order of Gadiformes

The order of Gadiformes, also known as “gadoid” or “cod-like” fishes, is a taxonomically diverse and biologically intriguing assemblage of aquatic species belonging to the class Actinopterygii. Within the broader hierarchy of biological classification, Gadiformes is classified under the subclass Neopterygii, which includes all the modern bony fishes. This order comprises 500 species included in 85 genera representing several morphologically divergent families: Ranicipitidae, Euclichthyidae, Macrouridae, Moridae, Melanonidae, Lotidae, Bregmacerotidae, Muraenolepididae, Phycidae, Merlucciidae and Gadidae (Van Der Laan et al., 2014). Each family exhibits unique adaptations that have allowed them to thrive in some of the most challenging and remote aquatic environments on Earth. From the well-known Atlantic cod to the bizarre grenadiers found in the deepest ocean trenches, Gadiformes inhabit a wide range of habitats (from deep-sea to shore, in estuarine and even freshwater habitats), displaying an array of intriguing life history traits, and play vital ecological roles in marine ecosystems (Cohen et al., 1990). The species within the Gadiformes order are known for their similarities to cod and they are generally characterized by elongated bodies and barbels on their chins (Figure 1.3A). The exceptional adaptability of gadiform species is the key factor behind their success. These fish display a remarkable range of physical and biological characteristics that have enabled them to flourish in various habitats. From specialized jaw structures and sensory adaptations to the capacity to withstand extreme pressures in the abyssal depths, the adaptations within this order are a testament to the “evolutionary plasticity” of these species. Recent studies, especially those using molecular phylogenetic techniques, have provided deeper insights into the evolutionary relationships within Gadiformes. DNA analysis has helped clarify the relationships between different species and genera, which were previously ambiguous based on morphology alone (Figure 1.3B). This molecular approach has revealed new evolutionary lineages and has helped in understanding the timing and pattern of diversification within the group (Roa-Varòn and Ortì, 2009).

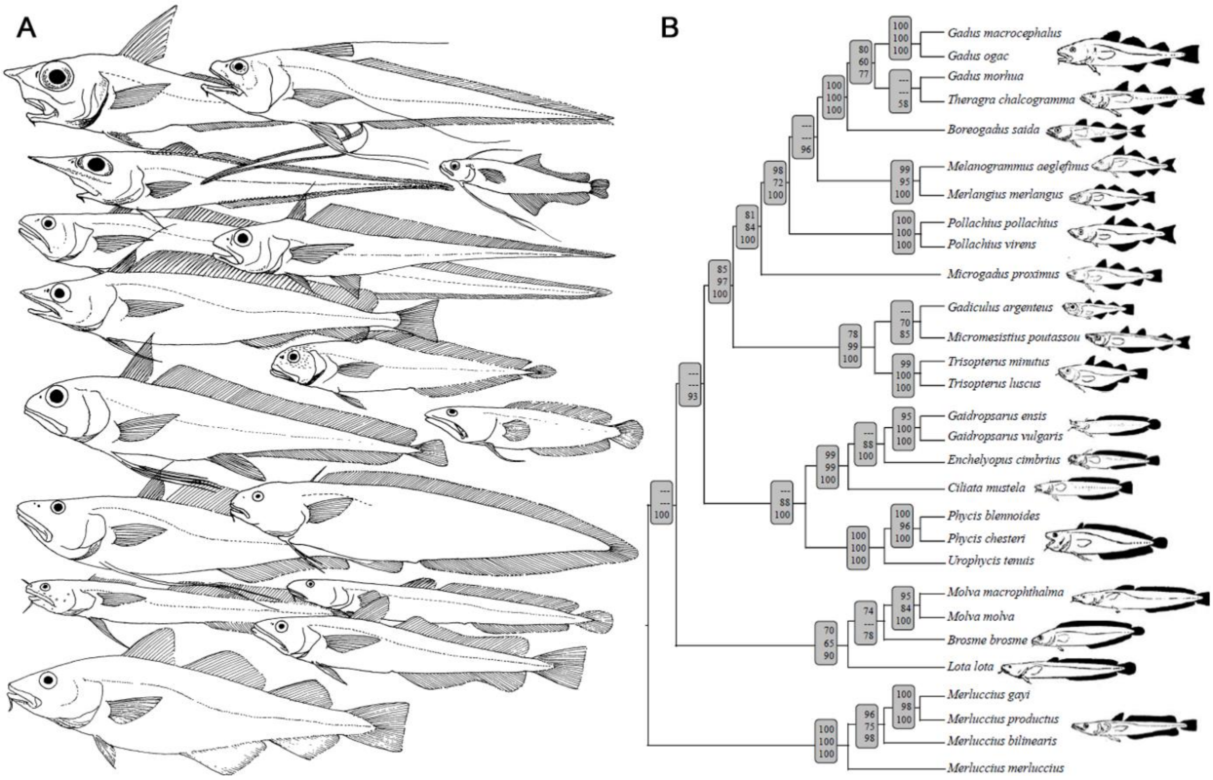


Figure 1.3. A) Examples of gadiform fishes showing the morphological features of the major taxonomic groups (modified from Howes 1991); B) Phylogenetic relationships of some representative Gadiformes. The frames at nodes indicate the bootstrap values for different methods of phylogenetic inference used in the analysis, respectively: Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian analysis and (modified from Teletchea et al., 2006).

The first hypothesis on the biogeography of a relevant part of Gadiformes species (gadids, merlucciids, ranicipitids, bregmacerotids and morids) was given by Svetovidov (1948), based on the history of geological and climatic changes, time and place of fossil records, and ecological information. Later on, the biogeography of “gadoids” (Gadiformes minus Macrouridae and Macrouronidae) has been widely investigated (Endo, 2002), and currently, the most credited hypothesis is that of Howes (1991), which was later confirmed by Endo (2002). According to it, the discontinuous bipolar distribution pattern observed among gadoids (focused on the Atlantic) is the outcome of the fragmentation of a previously widespread distribution. The gadoids found in the northern Pacific are the result of recent dispersals of derived taxa, while the circumglobal distribution primarily found in primitive taxa is considered to be a plesiomorphic (ancestral) character.

Concerning the ecological role, Gadiformes, as predators and prey, play significant roles within marine food webs. They serve as a critical link in the transfer of energy within ecosystems, influencing the abundance and distribution of prey species. Understanding the ecological roles and interactions of Gadiformes is crucial for comprehending the dynamics of marine ecosystems, as changes in their populations can ripple through entire food webs, affecting the abundance and distribution of numerous species. Large-sized species, such as cod and haddock, are formidable predators feeding on a variety of prey species (fish and invertebrates) and their predatory activity helps to control the populations of these prey, preventing unchecked growth that could disrupt ecosystem balance (Rudstam et al., 1994). In this way, large Gadiformes play a regulatory role, helping to maintain the diversity and structure of marine communities. On the other hand, small- and medium-sized species, occupying an intermediate position in marine food chains, play a key role in converting energy from lower trophic levels (e.g. small fish) into their biomass (Worm et al., 2009). This energy transfer is a critical component of marine energy flow, as it allows energy to move from primary producers (such as phytoplankton) up through the food web, ultimately supporting larger predators, including marine mammals and seabirds.

Gadoid fisheries, targeting species such as cod, haddock, and pollock, hold profound historical, economic, and ecological significance. These fisheries have played pivotal roles in the cultural heritage of coastal communities, for example shaping the exploration and settlement of North America (Kurlansky, 1997). Economically, they contribute substantially to livelihoods worldwide, offering products ranging from fresh fillets to fishmeal. Despite some gadoid stocks, such as Atlantic cod, have experienced severe declines due to overexploitation and climate change, some species are still among the most important fish resources worldwide. Indeed, according to the latest FAO report (2022a), blue whiting and Atlantic cod are the sixth and the twelfth finfish species in terms of global marine capture production, accounting for 1487 and 1078 thousand tonnes in 2020, respectively. In the Mediterranean Sea, the group identified as “cods, hakes, haddocks” accounted for 27 thousand tonnes (3.7% of the total landings) in the period 2018–2020. Out of this amount, 19 thousand tonnes (2.7% of the total landings) were attributable to the sole contribution of the European hake, which is the most important finfish species caught by the Mediterranean bottom trawlers (FAO, 2022b).

1.3.1 Study species

The gadiform families that inhabit the Mediterranean Sea are limited to Gadidae, Phycidae, Lotidae, Merlucciidae and Moridae. Taking into consideration the ecological and commercial value of this species group in the Adriatic Sea, this thesis focuses on the following species: *Merlangius merlangus* (whiting)*, Micromesistius poutassou* (blue whiting)*, Trisopterus capelanus* (poor cod) and *Gadiculus argenteus* (silvery pout) for the family Gadidae; *Merluccius merluccius* (European hake) for the family Merluccidae.

It is worth mentioning that the genera *Gadiculus*, *Trisopterus*, *Micromesistius* and *Merlangius* are regarded as the most primitive genera within the subfamily Gadinae (family Gadidae), and they are the only species distributed both in Atlantic and Mediterranean areas. It was hypothesised that the retention of a plesiomorphic trait for a wider thermal range determined the spread of these species in the Mediterranean Sea after the climatic crisis in the late Miocene about 6 million years BP (Endo, 2002). On the other hand, the more recent genera of Gadinae (classification based on stratigraphic ranges of gadoid fossil otoliths) show a strict Atlantic distribution. Although their slightly warmer water preference than the others allowed these four genera to successfully colonise the Mediterranean Sea, the primitive genera show cold-water preference, likewise the other gadiform members (Svetovidov, 1948). This feature is clearly noticeable when looking at the preferred temperature ranges of whiting, blue whiting, poor cod and silvery pout (Froese and Pauly, 2023), whose upper limits are close to the minimum winter value in the Mediterranean Sea, around 13 °C (Salat et al., 2019). For this reason, they are considered cold-water species within the Mediterranean context, as further supported by their spawning seasons, occurring during the winter months. Among the study species, the only one showing a broader thermal range is the European hake (Dulvy et al., 2008), which is the only Mediterranean member of the family Merluccidae. The inclusion of this species as an outgroup allowed us to compare the responses of some gadiform species with different temperature sensitivities to the environmental variations caused by climate change.

Whiting (*Merlangius merlangus*)

Preferred thermal range: 7 −11.9 °C

Preferred bathymetric range: 10 − 150 m

Figure 1.4. Whiting, *Merlangius merlangus.*

Whiting, *Merlangius merlangus* (Linnaeus, 1758) (Figure 1.4), is a benthopelagic species widespread mainly in the northeastern Atlantic Ocean and in the northern sub-basins of the Mediterranean and Black Seas (namely Adriatic, Aegean, Marmara, and Azov Sea) (Figure 1.5). The restricted occurrence of whiting in the cold Mediterranean area represents the living trace of the spread of Atlantic species in the Mediterranean Sea during past glaciations (Panayotova and Todorova, 2015), after which there has been a contraction of the distribution area coupled with the increase in temperatures. The uniqueness of the whiting distribution range is strictly linked to its thermal optimum, which is the least heat-tolerant among the Mediterranean Gadinae (Froese and Pauly, 2023). The species is common on mud and gravel bottoms from 30 to 100 meters depth, with juveniles inhabiting shallow waters. Whiting can grow up to 70 cm, but its usual length in catches is from 30 to 40 cm. Females are usually bigger than males of the same age (Jardas, 1996). The whiting spawns in the winter period, from December to March (Giovanardi and Rizzoli, 1984; Jardas, 1996; Vallisneri et al., 2004), and the larvae are pelagic. Sexual maturity occurs when the fish attain a length of 18−20 cm (Vallisneri et al., 2004), after the first year of life (Giovanardi and Rizzoli, 1984).

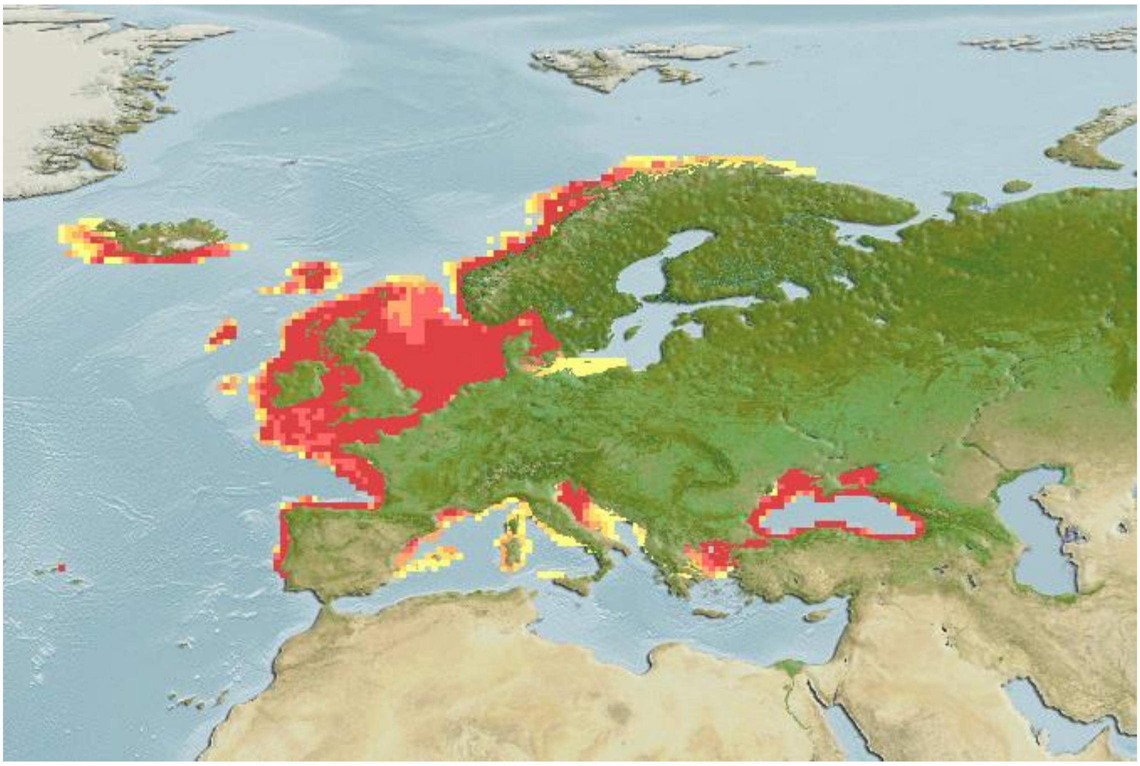


Figure 1.5. Distribution range of whiting. The colour intensity from yellow to red indicates the probability of occurrence (source: Kaschner et al., 2022).

While for the Black and Aegean Sea official long-term landings data are available at a Geographical Sub Area (GSA 17) level, in the Adriatic Sea the only data available at this scale starts from 2005 (FAO, 2023), not allowing to track back the exploitation history of whiting in the Adriatic area. Likewise, standardized estimations of its biomass from the Italian MEDITS survey are available only from 1994, giving a partial picture of the temporal trend of this species over the last decades (Figure 1.6B). The only data series covering at least the last 50 years is represented by landings data from Chioggia's fishing fleet (Figure 1.6A), which operates in the northern Adriatic Sea and represents the major Adriatic fleet and one of the most developed in the Mediterranean Sea (FAO 2022b). Both data sources highlight a fluctuating pattern of landings/biomass, which seemed to be stronger in landings before 1990. This pattern, together with the absence of a clear directional trend suggests that this species is strongly affected by environmental variability, which can, for example, favour the recruitment success as already reported in other gadid species (Mir-Arguimbau et al., 2022a).

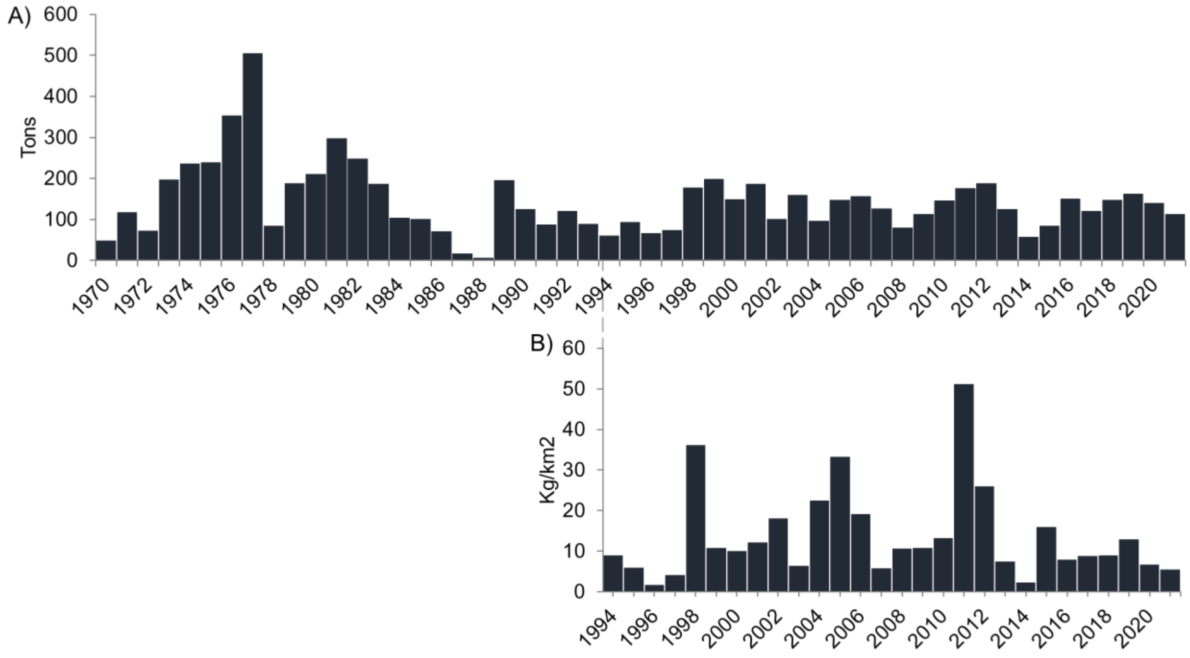


Figure 1.6. A) Temporal trend of the whiting landings (in tons) of the Chioggia port from 1970 to 2021 (Clodia database, 2022); B) Temporal trend of the whiting biomass index (in Kg/km^2) from 1994 to 2021, based on the MEDITS surveys carried out in the northern-central Adriatic Sea (Italian side). The grey dotted line indicates the year 1994, from which the temporal coverage of landing and survey data overlaps.

Blue whiting (*Micromesistius poutassou*)

Preferred thermal range: 3.1 − 13.9 °C

Preferred bathymetric range: 150 − 1000 m

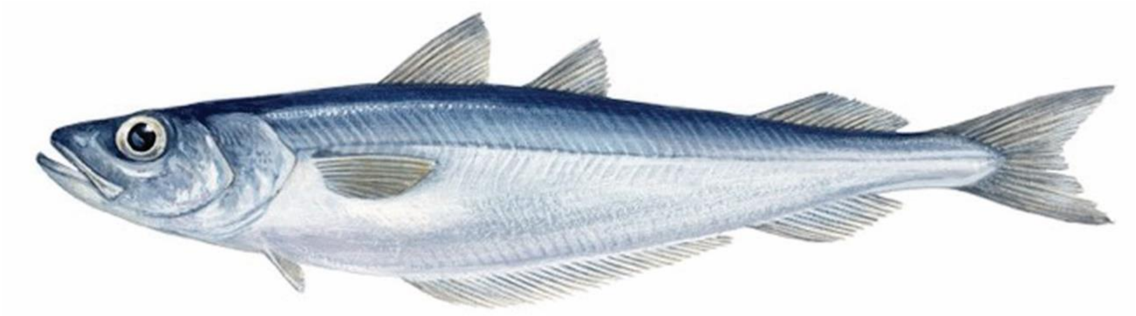


Figure 1.7. Blue whiting, *Micromesistius poutassou.*

Blue whiting, *Micromesistius poutassou* (Risso, 1827) (Figure 1.7), is a deep-water mesopelagic species broadly distributed along the continental slope of the North Atlantic and the Mediterranean Sea (Figure 1.8), inhabiting mainly the continental slope and shelf from 150 to more than 1000 m (Bailey, 1982). It is known that this species undergoes seasonal migration in the North Atlantic, moving towards the northern edge of its distribution (Faroes, Iceland, and Norway) during the summer (Cohen et al., 1990). In the Mediterranean Sea, there are no indications of seasonal migrations, although it has been observed that the species performs diel vertical migrations and is captured more efficiently during daylight when it is closer to the bottom than at night (Martin et al., 2016). The spawning of this species occurs at temperatures between 11−13 °C, which represent the minimum values in the Mediterranean Sea. While in the North Atlantic, the spawning season starts in January, showing a wide temporal lag in relation to the latitudinal temperature gradient (Bailey, 1982), in the Mediterranean Sea it is restricted between January and March (Froglia and Gramitto, 1981; Serrat et al., 2019a). Despite cold-water species living in deep habitats usually exhibit slow growth and late maturity (Lloret et al., 2021), the Mediterranean blue whiting shows fast growth and early maturity, being sexually mature at the end of the first year of life at around 20 cm TL (Froglia and Gramitto, 1981; Serrat et al., 2019a, Mir-Arguimbau et al., 2020).

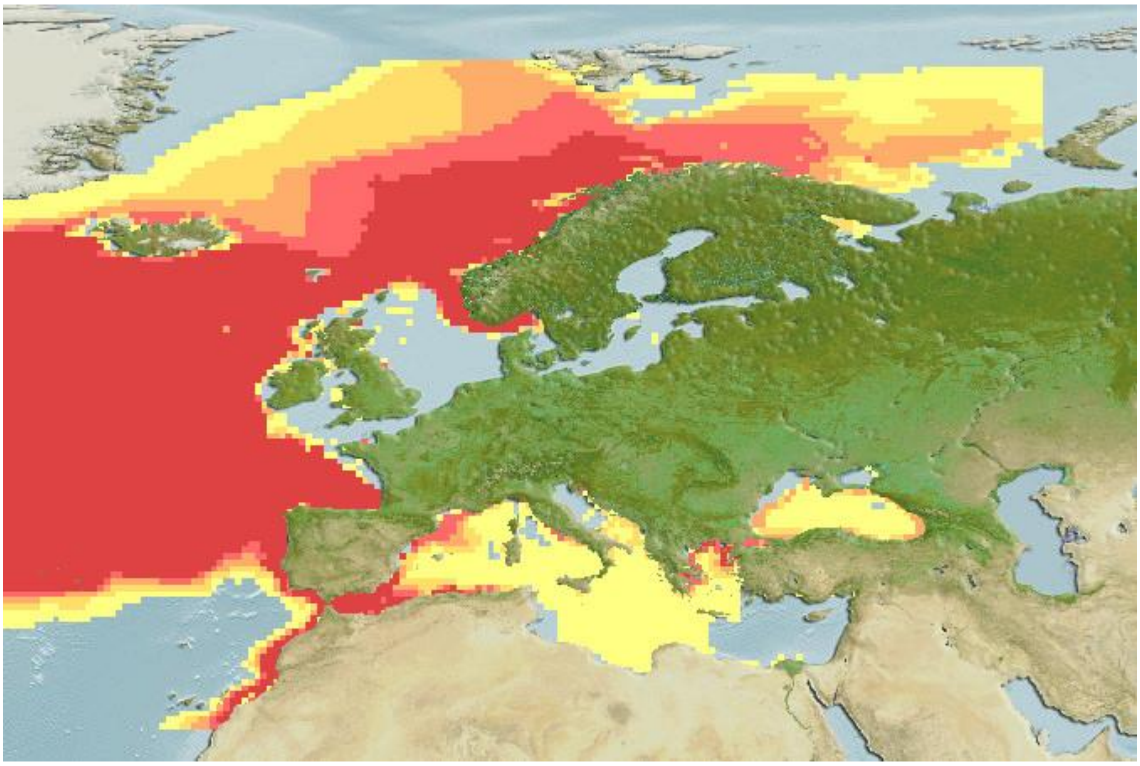


Figure 1.8. Distribution range of blue whiting. The colour intensity from yellow to red indicates the probability of occurrence (source: Kaschner et al., 2022).

Landing data of the northern-central Adriatic Sea from 1970 to 2020 highlight relatively stable landings with fluctuations until 1990. Then, a decline in landings started by the beginning of the 1990s, with a slight recovery around 1999 followed by a persistent decline from 2004 onwards, with landings always lower than 200 tons (Figure 1.9A). Standardized estimations of its biomass from the Italian MEDITS survey, available from 1994, give a partial picture of the temporal trend of this species over the last decades (Figure 1.9B). Survey data show an oscillatory pattern in the biomass index, which is stronger in the period 2010−2021.

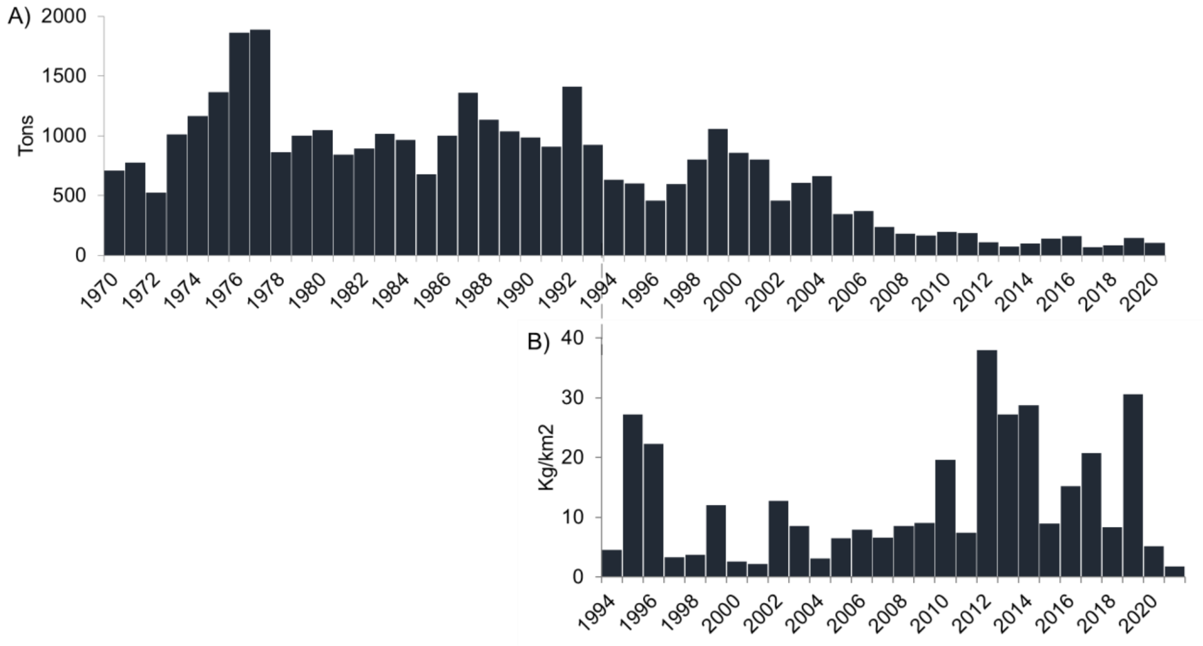


Figure 1.9. A) Temporal trend of the blue whiting landings (in tons) of the northern-central Adriatic Sea from 1970 to 2020 (FAO, 2023); B) Temporal trend of the blue whiting biomass index (in Kg/km^2) from 1994 to 2021, based on the MEDITS surveys carried out in the northern-central Adriatic Sea (Italian side). The grey dotted line indicates the year 1994, from which the temporal coverage of landing and survey data overlaps.

Poor cod (*Trisopterus capelanus*)

<u>Preferred thermal range:</u> 7.2 − 13 °C*

<u>Preferred bathymetric range:</u> 15 − 400 m*

*values referred to *T. minutus* because no specific data were collected for *T. capelanus* (from the Mediterranean Sea) after its identification as a distinct species.

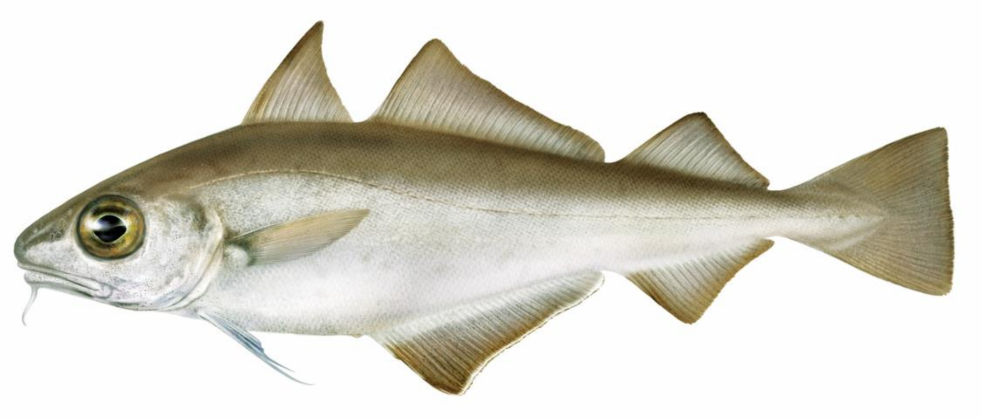


Figure 1.10. Poor cod, *Trisopterus capelanus.*

Poor cod, *Trisopterus capelanus* (Lacepède, 1800) (Figure 1.10), is a benthopelagic species widespread throughout the Mediterranean and along the western coasts of the Black Sea (Figure 1.11). It is more abundant in the western basin, in the northern-central Adriatic, and along the northern coast of the Aegean Sea (Sbrana, 2017). The benthopelagic behaviour of poor cod is characterised by a close association with the sea bottom, particularly for trophic purposes (Gramitto, 1999). From a depth of 20 m to over 400 m, the species lives on muddy and sandy bottoms forming small shoals, with greater abundances between 40 and 120 m. Likewise many other gadiform species, the poor cod shows a peak of spawning during the winter, except for the exception of having an extended residual spawning activity with a variable duration of five to seven months after the peak (Politou and Papacostantinou, 1991; Vallisneri et al., 2003). Poor cod shows fast growth and early maturity, being sexually mature at the end of the first year of life at around 13 cm TL (Froglia, 1981; Politou and Papacostantinou, 1991; Vallisneri et al., 2003). This species in the past was known as *Trisopterus minutus capelanus* and considered a subspecies of the Atlantic species *Trisopterus minutus.* The taxonomic revision of the genus done by Delling et al. (2011), based on morphological and molecular analysis, recognised that Mediterranean specimens belong to a distinct species, *T. capelanus.*

Figure 1.11. Distribution range of poor cod (modified from Gaemers, 2016). Since the recent recognition of the Mediterranean species of poor cod (*Trisopterus capelanus)*, specific data are not enough to build a detailed distribution map.

The only landings data available at the Adriatic scale starts from 2005 (FAO, 2023), not allowing to track back the exploitation history of whiting in the GSA. The only data series covering at least the last 50 years is represented by landings data from Chioggia's fishing fleet (Figure 1.12A), which operates in the northern Adriatic Sea and represents the major Adriatic fleet and one of the most developed in the Mediterranean Sea (FAO 2022b). Standardized estimations of its biomass from the Italian MEDITS survey, available from 1994, give a partial picture of the temporal trend of this species over the last decades (Figure 1.12B). Both data sources highlight a fluctuating pattern of landings/biomass before 2000, followed by a striking decline in landings/biomass, which remained at unusually low levels over the last 20 years (Figure 1.12B). The observed consistent trend indicates that this species experienced a substantial decrease in the Adriatic region over the last decades.

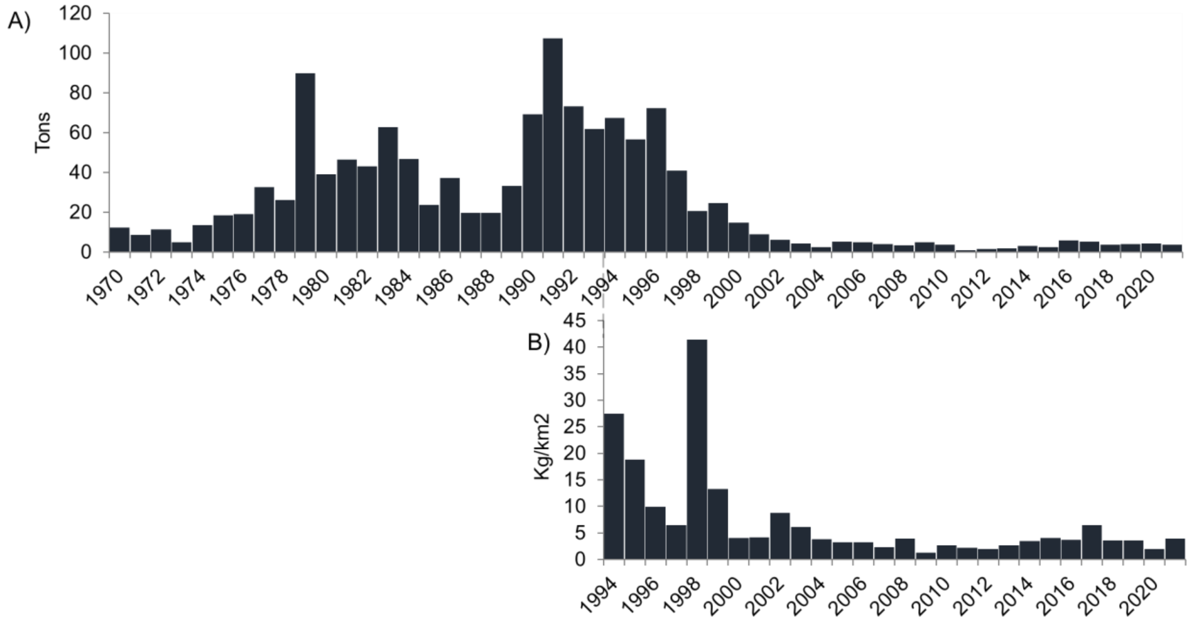


Figure 1.12. A) Temporal trend of the poor cod landings (in tons) of the Chioggia port from 1970 to 2021 (Clodia database, 2022); B) Temporal trend of the poor cod biomass index (in Kg/km^2) from 1994 to 2021, based on the MEDITS surveys carried out in the northern-central Adriatic Sea (Italian side). The grey dotted line indicates the year 1994, from which the temporal coverage of landing and survey data overlaps.

Silvery pout (*Gadiculus argenteus*)

Preferred thermal range: 3.4 – 13.9 °C

Preferred bathymetric range: 110 − 1000 m

Figure 1.13. Silvery pout, *Gadiculus argenteus.*

Silvery pout, *Gadiculus argenteus* (Guichenot, 1850) (Figure 1.13), is a deep-water mesopelagic fish common over the edge of the continental shelf in the European North Atlantic Ocean and the western Mediterranean Sea (Figure 1.14). It occurs in large schools over mud, muddy sand, gravel, and rock bottoms, from 110 to 1000 m, but mostly from 200 to 400 m in the northern Mediterranean and from 300 to 600 m off Tunisia. The spawning season is from December to January in the Mediterranean, and from mid-winter to spring in northern Europe. The major spawning grounds are located in the western part of the Mediterranean, on both sides of the Straits of Gibraltar, in deep waters. The silvery pout typically has a lifespan of less than 3 years. At its largest, it can reach a length of 15 cm. In its northern distribution, it usually grows to about 13 cm, while in the Mediterranean Sea, it typically measures between 7 and 10 cm (Cohen et al., 1990). As in the case of poor cod, a recent study recognised the existence of two species within the genus *Gadiculus*: the northern silvery pout (*G. thori*), widespread in the Northeast Atlantic at latitudes higher than 45°; the southern silvery pout (*G. argenteus*), widespread in the East Atlantic and Mediterranean Sea at latitudes lower than 45° (Figure 1.14) (Gaemers and Poulsen, 2017).

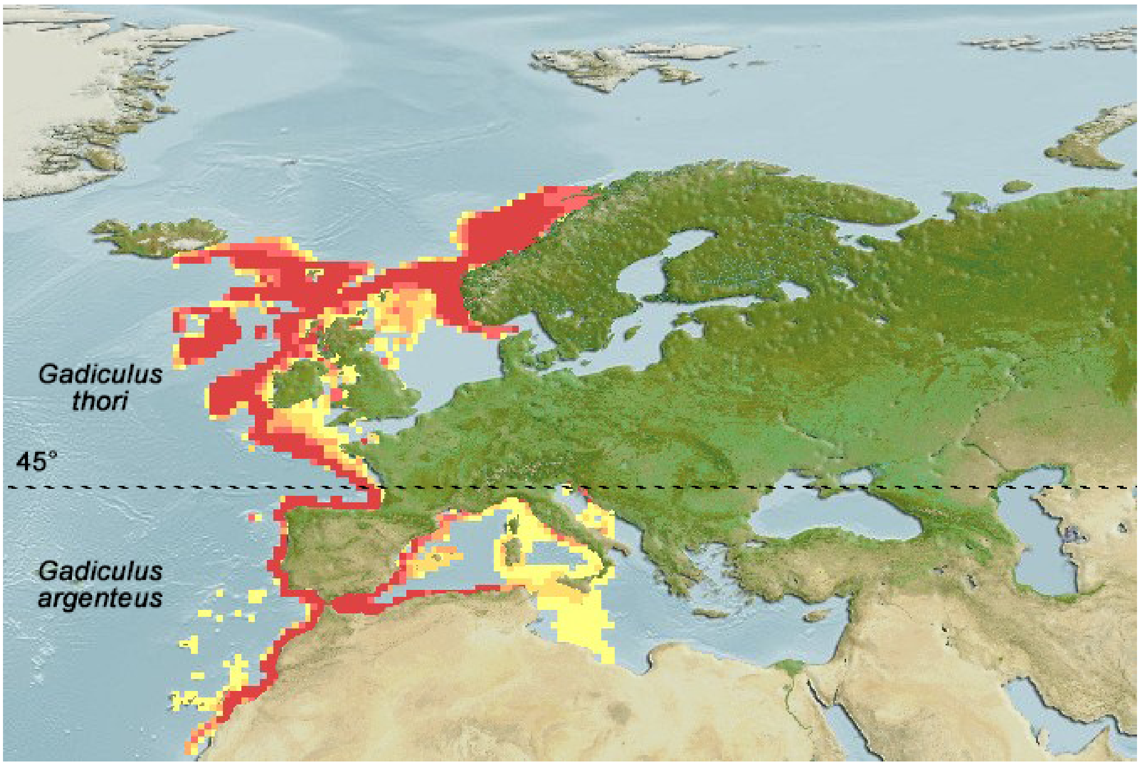


Figure 1.14. Distribution range of silvery pout. The colour intensity from yellow to red indicates the probability of occurrence (modified from Kaschner et al., 2022). According to Gaemers and Poulsen (2017), the most probable distribution of *Gadiculus argenteus* is at lower latitudes than 45° (black dashed line), while only *Gadiculus thori* would be present in the northern sector.

Although most gadid species are economically important, silvery pout has limited commercial value due to its small size (it is the smallest species of Gadidae) and predominantly artisanal exploitation in some Mediterranean countries. For this reason, official landing data on this species are not available from any source. Standardized estimations of its biomass from the Italian MEDITS survey, available from 1994, highlight a fluctuating pattern of biomass before 2008, followed by consistently low values until 2020 (Figure 1.15).

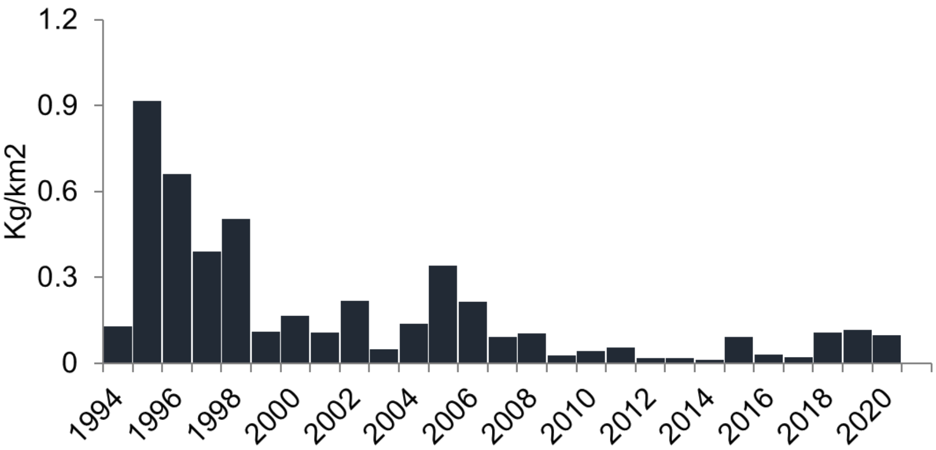


Figure 1.15. Temporal trend of the silvery pout biomass index (in Kg/km^2) from 1994 to 2020, based on the MEDITS surveys carried out in the northern-central Adriatic Sea (Italian side).

European hake (*Merluccius merluccius*)

Preferred thermal range: 6.9 – 15.4 °C

Preferred bathymetric range: 30 − 1000 m

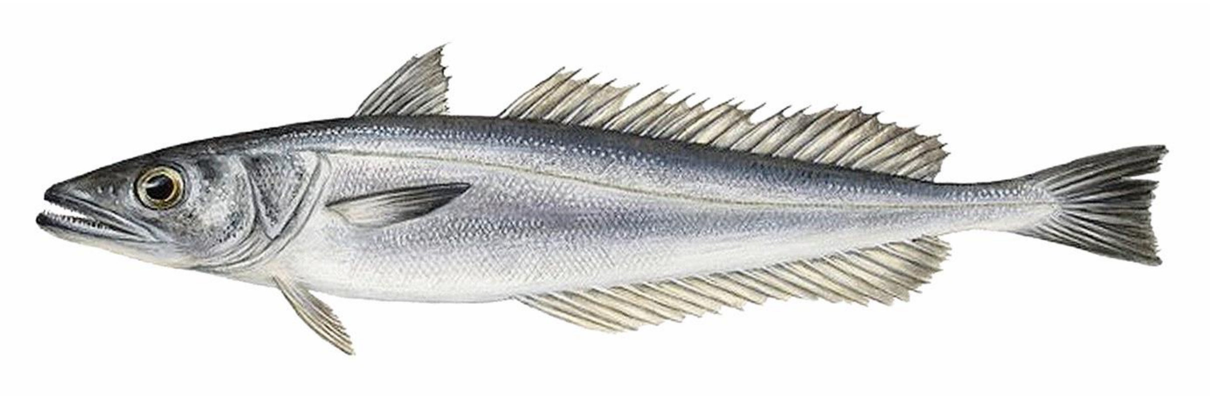


Figure 1.16. European hake, *Merluccius merluccius.*

European hake, *Merluccius merluccius* (Linnaeus, 1758) (Figure 1.16), is a demersal species widely distributed across the eastern side of the North Atlantic and the Mediterranean Sea (Figure 1.17), found from inshore water (30 m) to 1000 m. It is known that this species performs diel vertical migrations, living close to the bottom during daytime and moving away from the bottom at night (Cohen et al., 1990). The spawning period is extended throughout the year and shows different seasonal peaks depending on the area (Follesa and Carbonara, 2019). There are marked differences in the life history traits of the Atlantic and Mediterranean populations in terms of size and growth. For example, in the Atlantic populations, first maturity is reached at around 40 cm and 57 cm in males and females, respectively; in the Mediterranean populations, males mature at around 26 cm, females at 36–40 cm. The Mediterranean populations show slow growth (Cohen et al., 1990). European hake is a long-lived species and, although in this species assessing the age by means of the otoliths is particularly challenging, the use of radiocarbon dating allowed to estimate a maximum age of 25 years (Vitale et al., 2016).

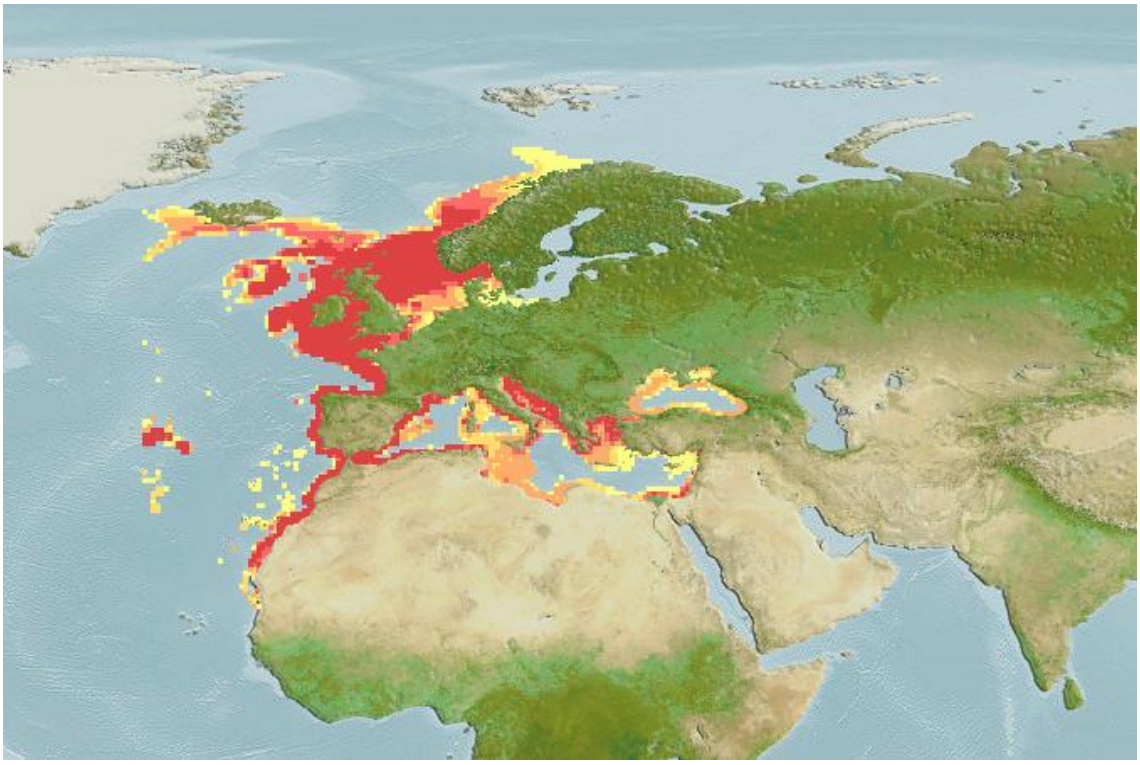


Figure 1.17. Distribution range of European hake. The colour intensity from yellow to red indicates the probability of occurrence (source: Kaschner et al., 2022).

Among the Mediterranean gadiform species, the European hake is the most important fish resource in terms of commercial value, and it has been an important food resource for the European population throughout historic times (Cohen et al., 1990). Landing data of the northern-central Adriatic Sea from 1970 to 2020 highlight relatively stable landings with some peaks over the last 50 years (Figure 1.18A). Standardized estimations of its biomass from the Italian MEDITS survey, available from 1994, show the same pattern and a high degree of overlap with the landing data (Figure 1.18B). Analysing more in detail the biomass temporal trend an oscillatory pattern is more evident compared to the landings.

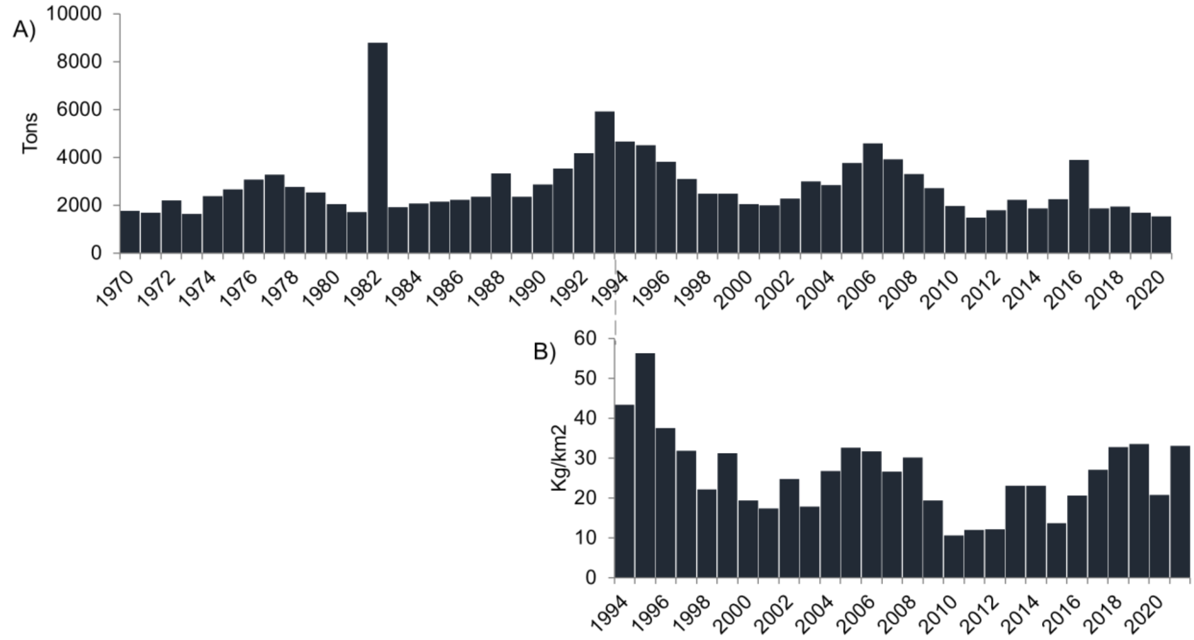


Figure 1.18. A) Temporal trend of the European hake landings (in tons) of the northern-central Adriatic Sea from 1970 to 2020 (FAO, 2023); B) Temporal trend of the European hake biomass index (in Kg/km^2) from 1994 to 2021, based on the MEDITS surveys carried out in the northern-central Adriatic Sea (Italian side). The grey dotted line indicates the year 1994, from which the temporal coverage of landing and survey data overlaps.

1.4 Motivation and Aims of the Thesis

The stress experienced by marine fish species with an affinity for cold waters that are being exploited may be exacerbated by the combined impacts of climate change and overfishing. This condition is expected to be particularly severe in enclosed basins where migration opportunities are reduced, such as the Adriatic Sea. Considering the aforementioned statement, the main motivation behind this thesis is the limited knowledge of the biological response to warming and the population status of cold-water fish species that are exploited in the northern-central Adriatic Sea. In order to fully comprehend the population state of species and their susceptibility to external influences, it is crucial to have detailed data on some key life history traits. Furthermore, given the significant fishing exploitation and rising temperatures experienced by the Adriatic Sea in recent decades, it is crucial to compare some key biological traits between current and past populations to determine if there have been any adaptive mechanisms to mitigate their impact.

The overall aim of this thesis is to investigate some life history traits of commercial gadiform species of the Adriatic Sea, performing a historical comparison of growth performances (and thus stock productivity potential) and trying to relate the variation patterns to the effects of environmental changes and fishing pressure. Moreover, through the use of a modelling approach (joint species distribution models), it is assessed how the occurrence and abundance of these species have been influenced by some environmental factors. The outputs of biological evidence are integrated with information coming from the spatio-temporal analysis and compared with the available literature to investigate the occurrence of modifications in the population dynamics of gadiform species over the last decades. By combining the information coming from the experimental and modelling approaches, it is possible to gather new insights into population resilience, adaptation, and vulnerability to external pressures. This is essential for effectively managing and conserving cold-water species that are being exploited (Lloret et al., 2013).

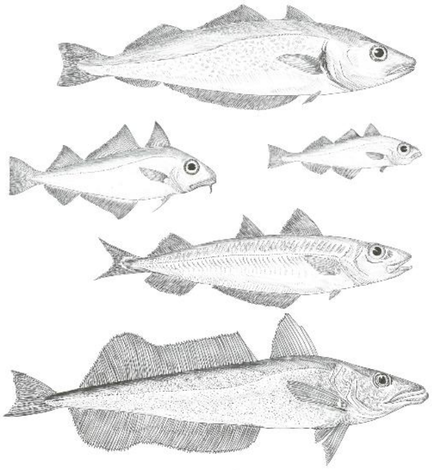
In order to achieve the overall aim, the following specific objectives are addressed throughout the thesis:

i) to describe the population dynamics and some reproductive parameters (spawning season, size at sexual maturity, and fecundity) of whiting, blue whiting, and poor cod for a better understanding of their life cycles, essential to fishery management through an ecological approach (Case studies I, II, III);

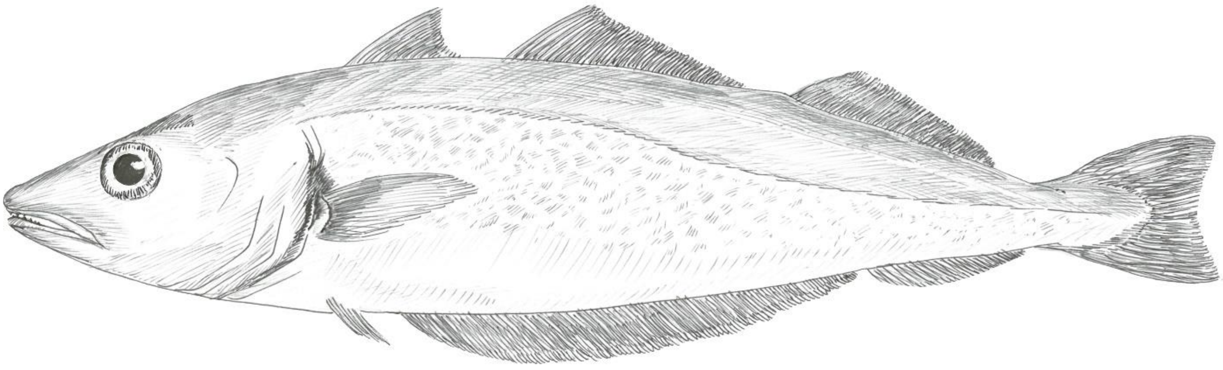
ii) to analyse the current age/size structures and growth performances of whiting, blue whiting, and poor cod, performing a comparison between samples collected in comparable areas with a time shift of 30–35 years (Case studies I, II, III);

iii) to investigate the spatio-temporal patterns of occurrence and how the abundance of key gadiform species has responded to some environmental factors, in particular, the increase in sea temperature over the last 20 years (Case study IV);

iv) to integrate data coming from different approaches (single-species/experimental and multi-species modelling) to shed light on the adaptive strategies ongoing in this cold-water species group, using a comparative approach to evaluate their vulnerability to climate change and fishing pressure (Case studies I, II, III, IV).



2 Case study I – Whiting (*Merlangius merlangus*)



Whiting (M*erlangius merlangus*) grows slower and smaller in the Adriatic Sea: new insights from a comparison of two populations with a time interval of 30 years

Federico Calì[1,2,3,4], Federica Stranci[3], Mario La Mesa[4], Carlotta Mazzoldi[3], Enrico Arneri[2], Alberto Santojanni[2]

[1]Department of Biological, Geological, and Environmental Sciences (BiGeA), Alma Mater Studiorum - University of Bologna, Italy

[2]National Research Council – Institut e for Marine Biological Resources and Biotechnologies (CNR-IRBIM) Ancona, Italy

[3]Department of Biology, University of Padova, Italy

[4]National Research Council - Institute of Polar Sciences (CNR-ISP) Bologna, Italy

Published in *Fishes*, *8*(7), 341 (June 2023);
https://doi.org/10.3390/fishes8070341

Abstract

Nowadays, overexploitation and climate change are among the major threats to fish production all over the world. In this study, we focused our attention on the Adriatic Sea (AS), a shallow semi-enclosed sub-basin showing the highest exploitation level and warming trend over the last decades within the Mediterranean Sea. We investigated the life history traits and population dynamics of the cold-water species whiting (*Merlangius merlangus*, Gadidae) 30 years apart, which is one of the main commercial species in the Northern AS. The AS represents its southern limit of distribution, in accordance with the thermal preference of this cold-water species. Fish samples were collected monthly using a commercial bottom trawl within the periods 1990–1991 and 2020–2021. The historical comparison highlighted a recent reduction in large specimens (> 25 cm total length, TL), which was not associated with trunked age structures, therefore indicating a decrease in growth performance over a period of 30 years ($L_{\infty 90–91}$ = 29.5 cm TL; $L_{\infty 20–21}$ = 22.8 cm TL). The current size at first sexual maturity was achieved within the first year of life, at around 16 cm TL for males and 17 cm TL for females. In the AS, whiting spawns in batches from December to March, showing a reproductive investment (gonadosomatic index) one order of magnitude higher in females than in males. Potential fecundity (F) ranged from 46,144 to 424,298, with it being heavily dependent on fish size. We hypothesize that the decreased growth performance might be related to a metabolic constraint, possibly related to the increased temperature and its consequences. Moreover, considering the detrimental effects of size reduction on reproductive potential, these findings suggest a potential endangerment situation for the long-term maintenance of whiting and cold-related species in the AS, which should be accounted for in setting management strategies.

Keywords: Adriatic Sea; whiting; otolith; growth models; cold-water species; demersal resources; bottom trawling

2.1 Introduction

During the last century, marine fish species have suffered increasing levels of impact due to human activity, such as habitat degradation and fishing exploitation. Meanwhile, climate change has produced great modifications in marine ecosystems, e.g., changing species distributions and trophic dynamics (Casini et al., 2010; Cheung et al., 2013b; Micheli et al., 2013; Azzurro et al., 2019). The dramatic and long-term effects of overfishing have been widely reported all over the world, leading to altered and less productive ecosystems (Pauly et al., 1998; Barausse et al., 2011; Kuparinen and Hutchings, 2012; Fortibuoni et al., 2017). Overfishing is considered the primary cause of the decline in marine populations, and its consequences on ecosystems started occurring centuries ago. In particular, analyses of historical data have revealed that a stronger decline has been observed for large-sized, long-lived, and late sexual maturing species, such as large marine vertebrates (Jackson et al., 2001). Among bony fish, the Atlantic cod, *Gadus morhua* Linnaeus, 1758, underwent the most dramatic collapse in the early 1990s in the north western Atlantic Ocean, also determining strong negative impacts on socio-economic systems (Pauly et al., 2002). On the other hand, over the 21st century, increasing evidence of the significant role of sea warming in affecting fish ecology and fishing yields has been provided. In response to increased temperatures, marine organisms have shifted their distribution ranges (generally towards higher or colder latitudes), changed their phenology, and reduced their body size (Poloczanska et al., 2016; Pauly and Cheung, 2018). Despite this, the net effect of these changes on species abundance is not only determined by the specific thermal tolerance but is also dependent on the ecoregion, taxonomy, and exploitation history (Hidalgo et al., 2014; Free et al., 2019; Moullec et al., 2019). Accordingly, temperate fish (experiencing strong seasonal variation) are expected to be more tolerant compared to their polar and tropical counterparts, which are adapted to stable cold and warm environments, respectively (Cheung and Pauly, 2016). Moreover, marine organisms are often subjected to both fishery exploitation and climate change, which may play synergistic or antagonistic roles depending on the context, and disentangling their effects is often difficult (Genner et al., 2010; Hidalgo et al., 2012; Engelhard et al., 2014; O'Connor et al., 2015).

The Mediterranean Sea has been defined as a sea “under siege” (Coll et al., 2012), because of its long history of exploitation and the higher rate of water warming compared to other marine regions (Colloca et al., 2017; Azzurro et al., 2019). It is considered a biodiversity hotspot, hosting more than 17000 species, many of them endemic to the Mediterranean area (Coll et al., 2012). The contemporary presence of high species diversity and multiple sources of impact determines an increasing concern about the management of fish resources in relation to the current level of fishing exploitation. It was recently highlighted that 90% of the Mediterranean commercial stocks were assessed as being out of safe biological limits (Colloca et al., 2017). In addition, rapid sea warming, combined with the expansion of non-indigenous species, is modifying the habitat suitability for commercial species, with detrimental effects on their resilience to fishing (Walther et al., 2002, 2009; Bazairi et al., 2010). Despite the introduction of regulations according to the European (EU) Common Fisheries Policy and Regulation 1967/2006 in EU countries (e.g., fishing capacity and effort limitations, regulation of mesh size, and spatial/temporal closures), Mediterranean resources have not shown signs of recovery (Colloca et al., 2017). The failure of fisheries policies is mainly related to a low level of compliance and non-enforcement of rules in the whole Mediterranean area, where there has always been a disagreement between scientific advice and national management plans (Cardinale et al., 2017). Moreover, increasing evidence is showing that climate change affects the productivity potential of fish stocks at a global scale (Free et al., 2019), suggesting a significant role of environmental factors in the failure to recover fish resources. The colder regions (high latitude) show higher vulnerability and economic loss from climate change, particularly in shallow and enclosed basins, which could be less resilient to climate and human stressors (Moullec et al., 2019).

The Adriatic Sea (AS) is the basin showing the highest exploitation and sea warming rate in the Mediterranean Sea, making it an ideal model to study the simultaneous effects of fishing and climate change on fish species (Barausse et al., 2011; Moullec et al., 2019; García-Monteiro et al., 2022). This semi-enclosed basin represents the northernmost part of the Mediterranean Sea; it is subjected to the cold Bora wind (north east direction) and receives cold waters from many alpine rivers, determining a suitable habitat for those species typical of the Atlantic waters, the so-called "boreal species" (Tortonese, 1964; Ben Rais Lasram et al., 2010). An example is represented by the whiting, *Merlangius merlangus* (Linnaeus, 1758) (Gadidae), a benthopelagic species widespread mainly in the northeastern Atlantic Ocean and in the northern sub-basins of the Mediterranean and Black Seas (Adriatic, Aegean, Marmara, and Azov Sea). Despite its commercial importance at a local scale, with it being one of the main bony fish resources caught by bottom trawlers, the biological traits of this species in the AS are still poorly known (Vallisneri et al., 2004, 2006), and most of the available literature comes from the Atlantic Ocean and the Black Sea. Knowledge of fish biology is essential to estimate the vulnerability and resilience to the external stressor of the fish species already assessed, as well as to increase the number of species to be assessed, which is currently less than 5% of the fish species worldwide (Reynolds et al., 2005). This is particularly true for exploited species with narrow geographical ranges whose biological traits and population dynamics may differ between geographical areas depending on the environmental, ecological, and fishing features.

This work aims to investigate the life history traits of *M. merlangus* in the Northern AS (NAS), focusing on the historical comparison of two populations sampled in the same area with a time interval of 30 years. Population dynamics and age/length structures were examined through length–frequency distributions (LFDs) analysis and otolith readings, respectively. We investigated the reproductive cycle and fecundity to provide information useful to shed light on the life cycle of this species in the NAS. The historical comparison enabled us to infer the effect of fishing or environmental changes on the growth performance and reproductive potential of this species. To evaluate the phenotypic plasticity and spatial variation of whiting life history traits, in the discussion, we compared our data with the Atlantic Ocean and Black Sea populations. Considering the potential vulnerability of whiting due to the combined effect of overexploitation and sea warming, the further aim of this study was to provide new insights to underpin more comprehensive management strategies under an ecosystem approach.

2.2 Materials and Methods

2.2.1 Study area

The study area comprises the northern part of the AS, a semi-enclosed basin located in the Central Mediterranean Sea (Figure 2.1). Based on the bathymetric differences along its latitudinal axis, three sub-basins can be identified and are roughly characterized by sandy shores on the western side and rocky shores and islands on the eastern side (Russo and Artegiani, 1996). The northern sub-basin encompasses the northernmost part down to the 100 m bathymetric line and is characterized by an extremely shallow mean depth (about 30 m) and strong river runoffs. Indeed, the Po and the other northern Italian rivers are the source of about 20% of the total Mediterranean river runoff (Hopkins, 1992; Ludwig et al., 2009). Primary productivity is very high along the northwestern side and decreases southward and eastward due to the scarcity of rivers along the Croatian coastline (Fonda Umani, 1996). The sea bottom temperature shows a strong seasonal cycle in winter and summer, ranging from 7 to 27 °C and from 10 to 18 °C in coastal and deep waters, respectively (Russo et al., 2012). The physical properties and dynamics of the area are strongly influenced by atmospheric forces and river discharge, displaying marked temporal and spatial variations (Russo and Artegiani, 1996; Supić et al., 2004).

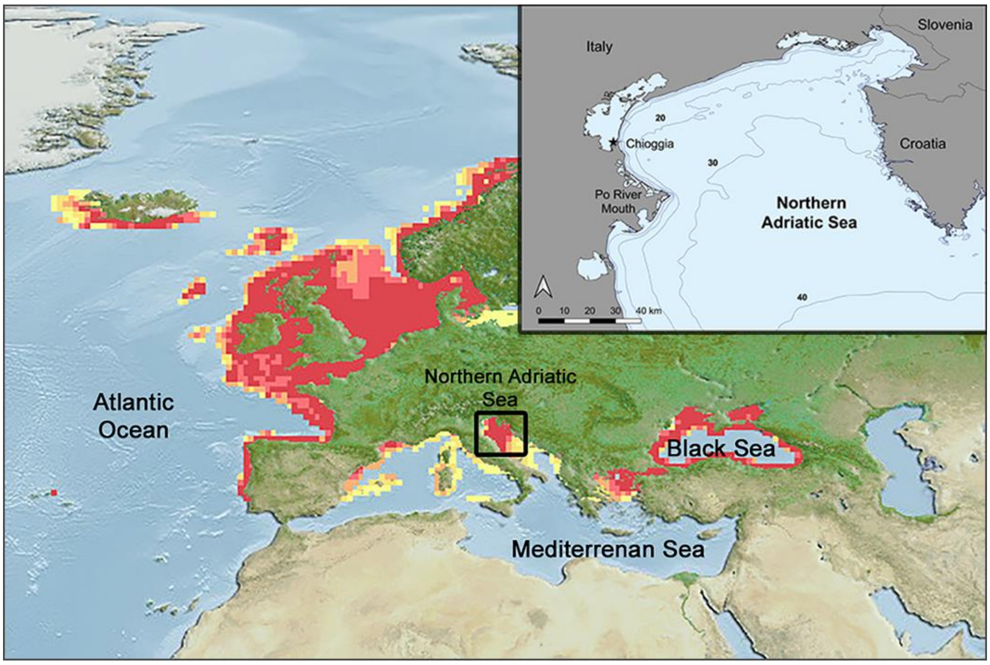


Figure 2.1. Distribution range of *Merlangius merlangus* and study area (black square). Colour intensity from yellow to red indicates the probability of occurrence (modified from Kaschner et al., 2022). Top-right square: detailed map of the study area with bathymetric lines, showing the location of the Chioggia's harbour (★) and the Po River Mouth.

2.2.2 Sampling design and population parameters

The fish samples were collected monthly in the same fishing ground in front of the Po River mouth during two different sampling periods (1990–1991 and 2020–2021). The first was carried out between March 1990 and December 1991; the second one was carried out between November 2020 and November 2021. No samples were available from February and May 1990–1991 and from August of both periods due to the annual ban on trawling activities. The fish samples were caught using an Italian-type commercial fishing net (otter bottom trawl, *tartana*) with a cod-end mesh size of 40 mm, towed between 15 and 35 m depth. In 2020–2021, juveniles were collected bi-weekly from April to June, aiming to thoroughly assess the timing and duration of recruitment. Moreover, when sampling on board was not possible, whiting samples were collected at the landing sites of the Chioggia trawling fleet from local fishers exploiting the same fishing ground. All of the sampled individuals were measured to the nearest half cm (total length, TL) to obtain the length frequency distributions (LFD) of each sample. A monthly subsample of 40–60 specimens representative of the whole size range was randomly selected for biological examination. The following measures were taken: TL to the nearest mm, total weight (TW) to the nearest 0.1 g, and gonad weight (GW, only in the 2020–2021 sample) to the nearest 0.01 g. Sex was assigned macroscopically in specimens > 12 cm TL, and only in the 2020–2021 sample the gonad maturity stage was evaluated using the standard ICES (2008) six-point scale: (1) immature; (2) maturing; (3) spawning; (4) spent; (5) and resting/skip of spawning; (6) abnormal. Since it was not possible to determine the sex macroscopically in individuals smaller than 12 cm TL, they were treated as unsexed juveniles. The sagittal otoliths were removed, cleaned, and stored dry in vials for ageing purposes. Sex ratios, expressed as the percentage of females in relation to the number of males, were calculated and the difference between the sampling periods was tested using a χ^2 test for proportions. The condition factor (K) was calculated using the following relationship, $K = 10^3\ (TW/TL^b)$, where b is 3 or ≠3 in the case of isometric or allometric growth, respectively (Bolger and Connolly, 1989). Differences in K values between the two samplings were tested by the Mann–Whitney test.

To assess the reproductive investment in gonads, the GW was used to calculate the gonadosomatic index (GSI = GW/TW × 100). In 2020–2021, the ovary subsamples were weighed and fixed in 10% seawater formaldehyde for fecundity estimation in pre-spawning females from the whole size range. Furthermore, ovaries from stage 2/3 females were stored in Dietrich solution (900 mL distilled water, 450 mL 95% ethanol, 150 mL 40% formaldehyde, and 30 mL acetic acid) for histological analyses.

2.2.3 Age estimation

From the whole fish sample, a representative subsample was selected for each sampling period, grouping specimens in 1 cm TL classes. Age readings were performed on two males and two females per length class in each monthly sample to fully represent the population size range. The morphology of whiting sagittal otoliths makes age readings difficult on the whole otolith because of the thickness and the presence of bumps (Figure 2.2).

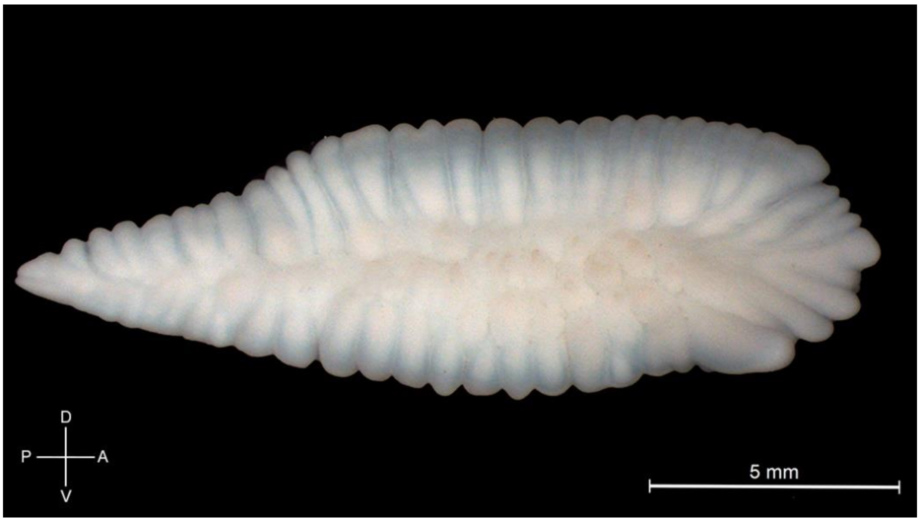


Figure 2.2. Right otolith of *Merlangius merlangus*, distal side view. D = dorsal axis; A = anterior axis; V = ventral axis; P = posterior axis.

An opacification process was noticed during dry storage, in that the otoliths of the individuals sampled in 1990–1991 were homogeneously white. After several trials, the "burning and breaking" technique was considered the most appropriate to establish a reliable age estimate (Vitale et al., 2019), removing the opacification effect and enhancing the annulation pattern in the otoliths from both sampling periods. The otoliths were burnt in an oven at 350 °C for 2–4 min (depending on size), embedded in resin (Crystalbond 509 Amber, Aremco products, Inc., New York, USA), ground using an abrasive paper, and polished on a lapping film with 0.05 µm alumina powder. Particular attention was given to obtaining a final reading plane passing across the nucleus, using the shape of *sulcus acusticus* as a reference. The otolith sections were fixed onto glass slides using resin and soaked in fresh water over a dark background to enhance the contrast between the translucent and opaque zones. The otolith readings were performed under reflected light, counting the rings from the nucleus to the distal margin of the section. The sections were read using a stereomicroscope (Leica MZ6) at low magnification (10×). Age was estimated as the number of completely formed annuli, consisting of one opaque and one neighboring translucent ring. The samples were blindly read twice and in random order by two operators independently, without any indication of the date of capture, sex, or fish size. The age and the edge type (translucent or opaque) of each otolith sample were recorded and, in case of disagreement between the readers, the sample was discarded. The edge condition (percentage of otoliths with an opaque margin each month) was analyzed to determine the periodicity and timing of ring formation, allowing the annual formation of the rings to be verified. To evaluate the ageing precision (Campana, 2001), the index of average percent error (APE) (Beamish and Fournier, 1981) and the mean coefficient of variation (CV) (Chang, 1982) were calculated by comparing readings within and between readers. Given the low number of classes, the age was estimated in months, establishing a conventional common birth date (1st January) according to the reproductive period (Vallisneri et al., 2006) and considering the capture date and the edge type. Since we observed an opaque deposition in fish smaller than 12 cm only, they were considered young of the year (YOY), and their age was calculated taking into account only the month of capture. The von Bertalanffy growth function (VBGF) was used to describe the growth of the population:

$$TL = L_\infty (1 - e^{-k(t-t_0)})$$

where TL is the length-at-age t, L_∞ is the asymptotic total length, k is the so-called Brody growth rate coefficient which determines how fast the fish approaches L_∞, and t_0 is the theoretical age at which the average length is zero. The VBGF was fitted to the observed length-at-age data pairs. The VBGF parameters were estimated for males, females, and sex combined, using Growth II software (PISCES Conservation Ltd., Lymington, UK). The unsexed juveniles were included in both female and male growth curves to improve the fitting of the model in the first period of growth. Differences in growth between the sampling periods and sexes were tested by applying the Kimura likelihood-ratio test (Kimura, 1980). The growth performance index ($\varphi = \log k + 2\log L_\infty$) was calculated to allow for comparison among the growth parameters estimated in different populations of whiting (Froese and Pauly, 2022).

2.2.4 Fecundity and maturity estimation

Fecundity was estimated in spawning females (macroscopic stage 3; (ICES, 2008)) at the beginning of the spawning season (December 2020–2021), assuming that spawning had not yet occurred. The gravimetric method was used by counting the number of the most advanced oocytes in a weighted subsample (Murua et al., 2003), representing 1–2% of the GW. To assess any possible difference in oocyte density across the ovaries, three subsamples were taken from different portions of the ovary (anterior, median, and posterior) from five specimens, and oocyte counts were compared among the three portions. As no significant difference in the number of oocytes/g of the ovaries among the portions was found ($\chi^2 = 2.8$, $df = 2$, $p = 0.24$, Friedman test for related samples), the portion of the ovary used in fecundity estimation was randomly chosen. After at least 20 days of fixation, each ovary subsample was first treated with a mixture of commercial sodium hypochlorite (30%) and seawater (70%) (Choy, 1985) for 3 min to facilitate the disintegration of ovarian lamellae, and then, they were immersed in filtered sea water in a Petri dish with a dark background. The oocytes were manually spaced and photographed with a digital camera (Leica DFC 420) connected to a stereomicroscope at low magnification (8×), keeping the camera settings standard for all images. Then, the ImagePro Plus version 6.0 imaging software (Media Cybernetics, Rockville, MD) was used to count and measure the oocytes semi-automatically, allowing the operator to check, modify, and set the measurement thresholds.

Pre-vitellogenic oocytes were identified and excluded from the counts, setting a threshold size of 150 µm, based on the histological analyses of ovaries. Following a standard protocol, the ovaries were taken from Dietrich solution, dehydrated, and embedded in paraffin wax (Paraplast®, Sigma-Aldrich, Burlington, USA). From each sample, transverse serial thin sections (7 µm) were mounted on slides and stained with Harris hematoxylin and eosin (Pearson, 1985). The tissue sections were observed under a light microscope (Leica DM4000B) using different magnifications to study oocyte development. Due to oocyte shrinkage during histological processing, a correction factor was applied to compare the diameters measured in the histological section with the formaldehyde-fixed ones (Saber et al., 2015).

With this species being a batch spawner with a “determinate” fecundity type (Murua and Saborido-Rey, 2003), it was possible to estimate the potential fecundity (F), the relative potential fecundity (F_{rel}), and the batch fecundity (F_b). The potential fecundity, defined as the standing stock of vitellogenic oocytes (Hunter et al., 1992), was estimated by applying the following equation:

$$F = (n/sw)\ GW,$$

where n is the number of vitellogenic oocytes in the subsample, sw is the weight of the subsample, and GW is the gonad weight. The F_b was calculated as the number of hydrated oocytes in the subsample multiplied by the ovary total weight. The F_{rel} and F_{brel} were then calculated as the number of vitellogenic and hydrated oocytes per gram of gutted body weight, respectively. The relationship between fish size and fecundity was assessed by applying a least squares regression analysis to $\log_{10}$-transformed data, applying the Shapiro–Wilk test to verify the assumptions of normality.

The size-at-first maturity L_{50}, i.e., the size at which 50% of individuals are sexually mature, was estimated by taking into account 242 females and 196 males, collected between November (when individuals in early maturation gonadal stages were observed) and March (when a few spawning individuals were still detected among post-spawner ones). Data on size and maturity stage were coupled to fit a predicted proportion of mature individuals (namely at stages 3 and 4) at size using a logistic model.

2.3 Results

3.1 Population structure

From the collected samples, the total number of analyzed specimens for the age readings was 511 (180 males, 190 females, and 141 unsexed) out of 1895 specimens for 1990–1991 and 476 (209 males, 240 females, and 27 unsexed) out of 742 for 2020–2021. The sex ratio did not differ significantly between the samplings (two-sample Z-test for proportions, $\chi^2 = 1.54$, $df = 1$, $p = 0.21$), with the ratios being 0.52 and 0.55 for 1990–1991 and 2020–2021, respectively. In both samplings, females were dominant in the population.

The LFDs of the sexed subsamples are reported in Figure 2.3. The LFDs were rather different in the two sampling periods (two-sample Kolmogorov–Smirnov test, $p < 0.05$), clearly showing a higher number of individuals larger than 25 cm TL in 1990–1991

(Figure 2.3). The maximum size was higher in individuals caught in 1990–1991 (males: 30 cm TL, females: 37 cm TL) compared to 2020–2021 (males: 24 cm TL, females: 31 cm TL) (Figure 2.3; Mann-Whitney test, $p < 0.05$). In the 1990–1991 sample, the distribution was unimodal around 18 cm for both sexes and skewed toward larger sizes, whereas, in 2020–2021, the modal class was 16 cm for males and 22 cm for females, showing divergent LFDs between the sexes. YOYs join the sampled population in April (at approximately 8 cm TL), producing a bimodal distribution in the LFD and showing fast growth over the spring and summer, with a mean growth of 3 cm TL per month (Supplementary Figure 2.1).

Comparing the mean condition factors (K) calculated for the same size classes (cm) in both sexes and sampling periods, they were higher in female individuals and in the 1990–1991 samples (Mann–Whitney test, $p < 0.05$).

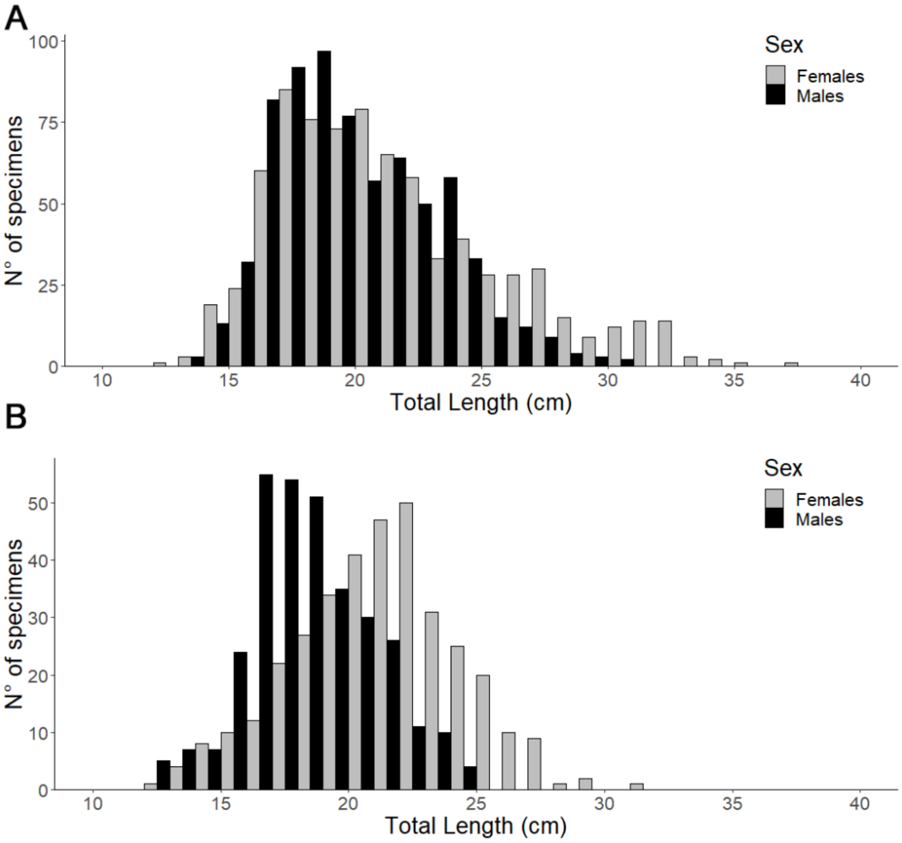


Figure 2.3. Length–frequency distribution (LFD) of the samples by sex. (A) 1990–1991 and (B) 2020–2021.

3.2 Growth

The otolith edge-zone analysis throughout the year revealed that the opaque layer is laid during the warmer months, confirming the annual deposition of one opaque ring plus one translucent ring (Figures 2.4 and 2.5). A difference in the deposition timing of the opaque ring was detected between the sampling periods, ranging from April to September in the 1990–1991 samples and from May to July in the 2020–2021 ones.

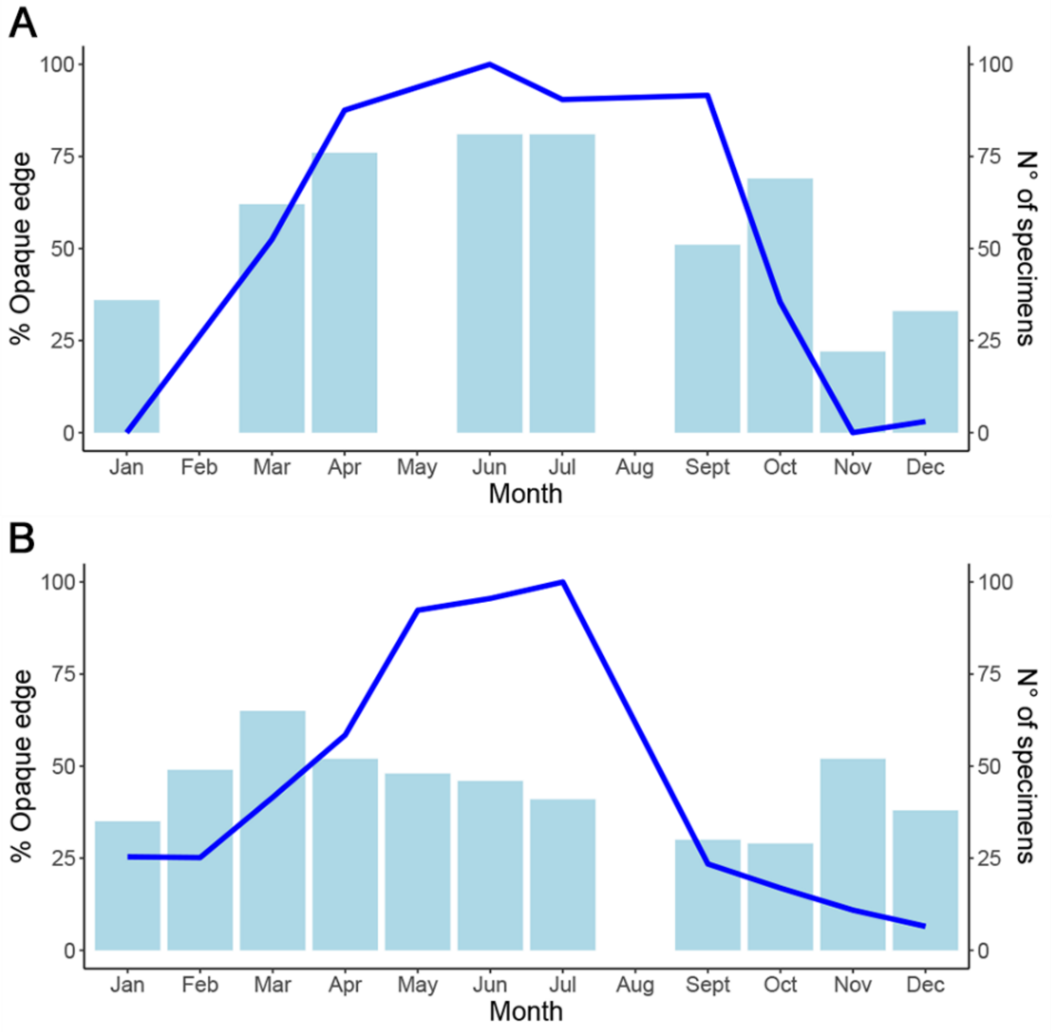


Figure 2.4. Monthly edge composition indicating the proportion of the population with opaque margin otoliths (%, blue lines) and the number of individuals (bars) sampled. (A) 1990–1991 and (B) 2020–2021.

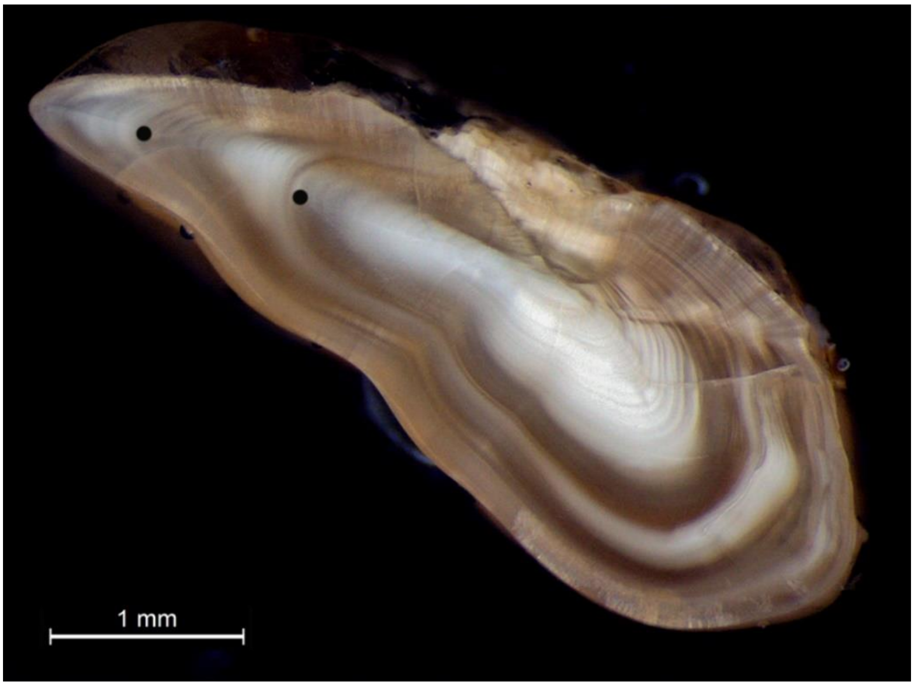


Figure 2.5. Transverse otolith section from a 2+ age class specimen (male, 28 cm TL) of *Merlangius merlangus* caught in October 1990, showing two completely formed annuli (black dots), consisting of one opaque and one neighbouring translucent ring.

The average percentage error (APE) and the coefficient of variation (CV) were low, at 0.9% and 1.3%, respectively, indicating high precision for the age readings. The age classes obtained from the otolith readings of the selected subsamples were three (age 0+, 1+, 2+); age estimates ranged from 2 to 32 months in the 1990–1991 samples and from 2 to 30 months in the 2020–2021 samples. The age–length keys of the two populations are reported in Tables 2.1 and 2.2. In Supplementary Tables 2.1 and 2.2, the age-length keys for males, females, and unsexed juveniles are reported. The year was divided into quarters to better visualize the population structure (quarters 3–9 = YOY; quarters 12–21 = 1+ age group; quarters 24–33 = 2+ age group). Significant differences were found in the mean sizes at age calculated for the two populations in both sexes (Wilcoxon signed-rank test; $Z = 2.60$, $p < 0.01$), with the 1990–1991 samples showing higher mean length-at-age than 2020–2021 across the whole age range.

Table 2.1. Age-length for combined sexes based on otolith readings of *Merlangius merlangus* sampled in the 1990–91 period in the Northern Adriatic Sea. N = total number; SD = standard deviation; TL = total length.

Age (quarters)	3	6	9	12	15	18	21	24	27	30	33	N
Total length (cm)												
3	1											1
4	7											7
5	21											21
6	35											35
7	12											12
8	8											8
9	1	4										5
10	1	3										4
11		6										6
12		8	1									9
13		22	4									26
14		41	14									55
15		6	8	2								16
16		5	8	2								15
17		7	8	4								19
18		7	8	5	2							22
19		8	8	6	3							25
20		5	8	8	4							25
21		4	8	9	6	1						28
22		3	7	7	5	1						23
23		1	7	8	6	2		1				25
24			4	3	5	4	1	3				20
25		1	1	4	3	2	3	2	1			17
26			4	8	5		2	3	1			23
27			1	4	5	4	2	2	1			19
28			1	2	2	3	2				1	11
29				1		3	1	1			1	7
30				1	1	3	1	1		1		8
31					1	2	1	1				5
32						2	2	3		1		8
33						1	1					2
34						1	1					2
35							1					1
37									1			1
N	86	131	100	74	48	29	18	17	4	2	2	511
TL mean (cm)	6.3	15.2	18.9	22.2	23.6	27.8	28.9	27.5	28.9	31.3	28.8	
TL SD	1.2	3.2	3.8	3.5	3.1	3.5	3.5	3.1	5.5	1.8	1.1	

Table 2.2. Age-length for combined sexes based on otolith readings of *Merlangius merlangus* sampled in the 2020–21 period in the Northern Adriatic Sea. N = total number; SD = standard deviation; TL = total length.

Age (quarters) Total length (cm)	3	6	9	12	15	18	21	24	27	30	33	N
3												0
4	1											1
5												0
6	13											13
7	15	1										16
8	11	2										13
9	5	2										7
10	2	2										4
11		3										3
12		6										6
13		10			1							11
14		9	2	4	3							18
15		5	7	10	10	2						34
16		7	6	10	12	2						37
17		8	8	12	11	3						42
18		4	7	11	15	6						43
19		1	5	12	10	7						35
20			8	9	10	10	1	3	1			42
21			3	8	10	9	2	3	2	1		38
22			4	5	7	10	2	2	2	1		33
23			1	4	7	4	2	4	2			24
24				3	3	5		2	2			15
25				2	3	6	1	3	2			17
26					1	1		2	3	1		8
27						2		5	2			9
28						1		1				2
29								1				1
30						1		1		1		3
31								1				1
32												0
33												0
34												0
35												0
37												0
N	47	60	51	90	103	69	8	28	16	4	-	476
TL mean (cm)	7.7	14.4	18.5	19	19.2	21.6	22.6	25.5	24.2	27.9	-	
TL SD	1.2	2.8	2.4	2.8	2.9	3	1.6	3.6	2.2	5	-	

According to the likelihood ratio test on the estimated VBGF parameters, the 1990–1991 population showed higher values of L_∞ and lower values of k compared to 2020–2021 (Kimura likelihood ratio test, Tables 2.3 and 2.4). The growth performance index was higher in the 1990–1991 population, providing further evidence of a greater growth capability, as already highlighted by the mean length-at-age comparison. A higher overlap between the size ranges associated with each quarter was observed in 2020–2021 (Figure 2.6), in particular in the 1+ age group (quarters 12–24). As expected, considering the sexual dimorphism in size, males showed a lower L_∞ than females in both populations (Table 2.3, Supplementary Tables 2.1 and 2.2).

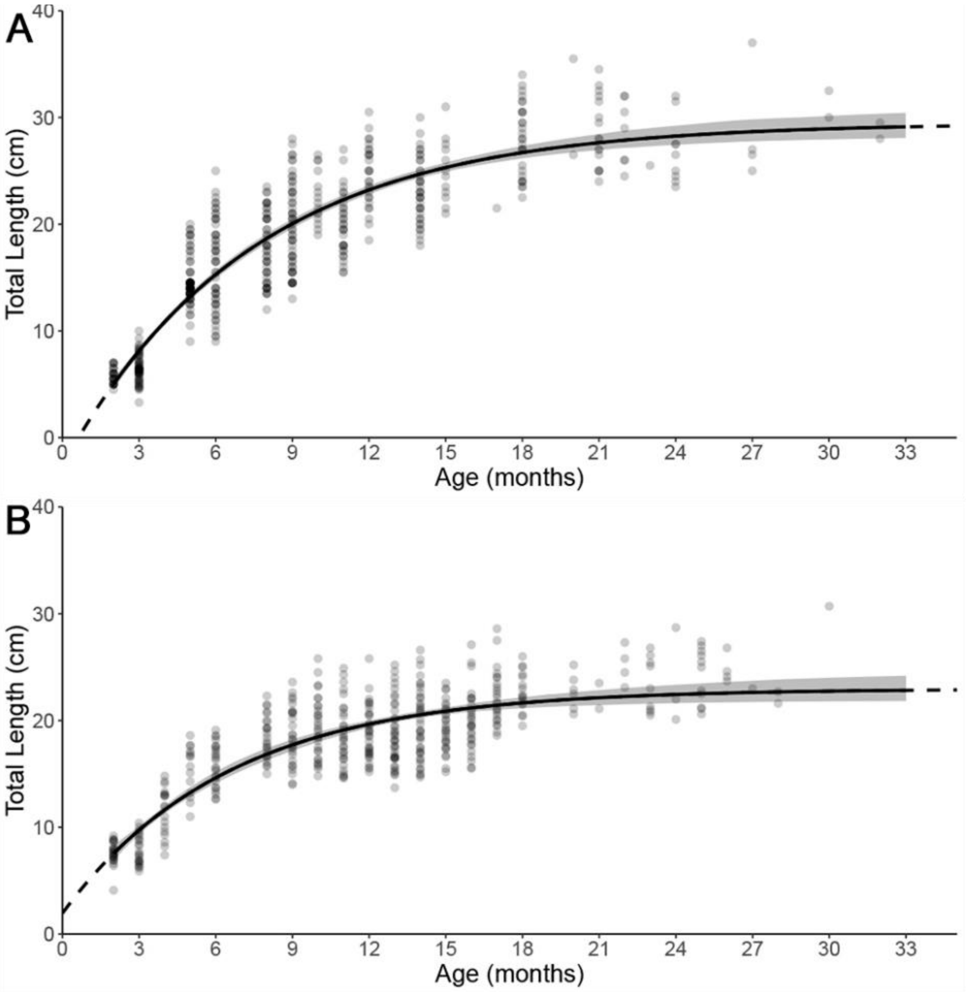


Figure 2.6. Von Bertalanffy growth models for the whole 1990–91 (A) and the 2020–21 (B) subsample of *Merlangius merl*angus collected in the Northern Adriatic Sea.

Table 2.3. *Merlangius merlangus* von Bertalanffy growth parameters estimates for both sampling periods in the Northern Adriatic Sea. The growth rate coefficient (k) and theoretical age at which the average length is zero (t_0) are expressed in years^{-1} and years, respectively. L_∞ = asymptotic total length; φ = growth performance index.

	L_∞	k	t_0	φ
1990–1991 combined sexes	29.47	1.633	0.052	3.15
2020–2021 combined sexes	22.84	1.889	−0.043	2.99
1990–1991 females	35.14	1.219	0.045	3.17
2020–2021 females	25.11	1.663	−0.04	3.02
1990–1991 males	26.7	1.831	0.059	3.11
2020–2021 males	20.52	2.236	−0.02	2.97

Table 2.4. Kimura's likelihood ratio test results, used to compare the von Bertalanffy growth parameters estimates for both sexes and sampling periods of *Merlangius merlangus* from the Northern Adriatic Sea. L_∞ = asymptotic total length; k = growth rate coefficient.

		χ^2	*p*-Value
1990–1991 vs. 2020–2021	L_∞	33.25	<0.01
	k	1.1	0.29
	Whole model	255.78	<0.01
Females vs. males 2020–2021	L_∞	19.23	<0.01
	k	2.5	0.11
	Whole model	94.62	<0.01
Females vs. males 1990–1991	L_∞	42.39	<0.01
	k	13.21	<0.01
	Whole model	80.07	<0.01
Females 2020–2021 vs. 1990–1991	L_∞	28.64	<0.01
	k	3.75	0.05
	Whole model	175.78	<0.01
Males 2020–2021 vs. 1990–1991	L_∞	29.16	<0.01
	k	1.45	0.23
	Whole model	177.69	<0.01

3.3 Maturity estimation and fecundity

According to the macroscopic observation of gonad maturation and GSI monthly patterns, the spawning season extended from December to March, with stronger activity at the beginning of winter. During the spawning peak in December, the GSI mean value was 11% (max 18%) for females and 1% (max 3%) for males, showing a striking difference in the reproductive efforts between the sexes (Figure 2.7). Based on the logistic model fitted to the proportion of sexually mature specimens, size-at-first maturity L_{50} was estimated at 16.1 ± 0.1 cm TL for males and 16.8 ± 0.5 cm TL for females.

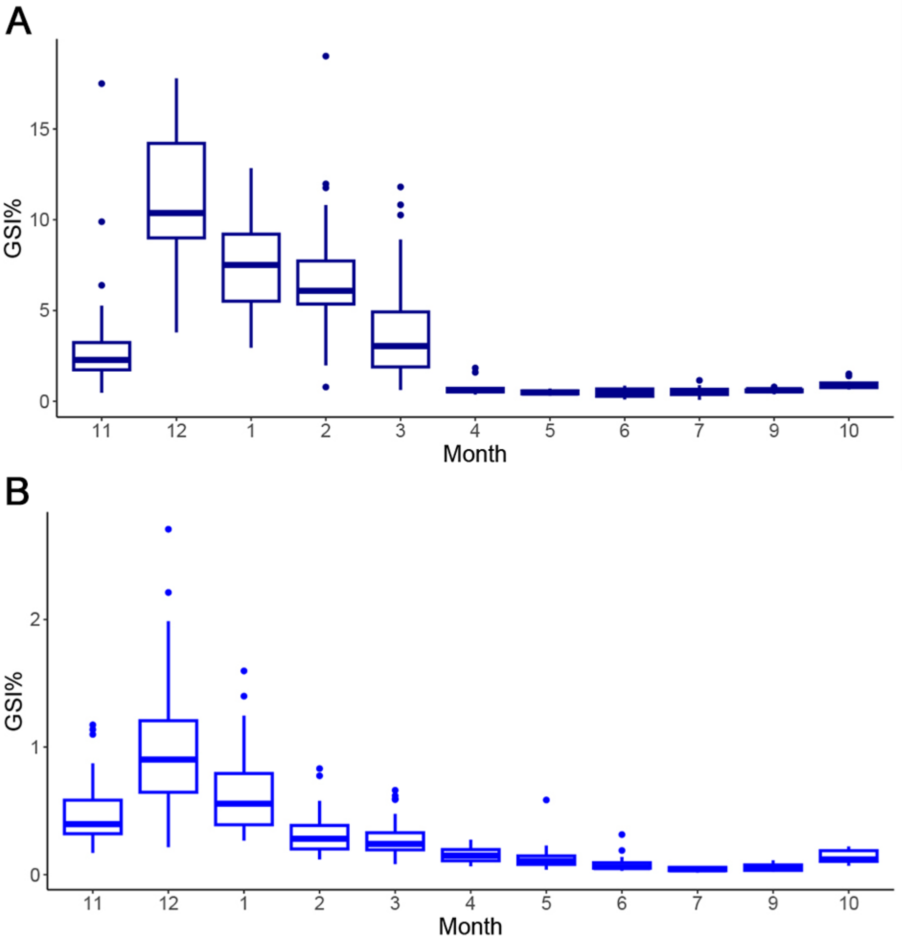


Figure 2.7. Monthly variation of the gonadosomatic index for *Merlangius merlangus* females (A) and males (B) across the 2020–21 sampling. Note the scale difference in y-axes.

A total of 15 females, ranging from 16.5 to 29 cm TL, were analyzed for fecundity estimation. Oocyte size frequency distributions (OFDs) in early spawning females indicated the presence of two or three modes corresponding to oocytes in different stages of vitellogenesis. The first mode ranged in diameter from 100 to 450 μm, the second one ranged in diameter from 450 to 700 μm, and the third one was > 700 μm, composed of hydrated oocytes. Different OFD patterns were observed in pre-spawning females depending on their gonadal development stage. Females in earlier developmental stages showed a higher overlap between the oocyte groups, while those in later stages showed a clear differentiation between modes (Figure 2.8). The maximum size of hydrated oocytes was 1300 μm in a 25 cm TL female.

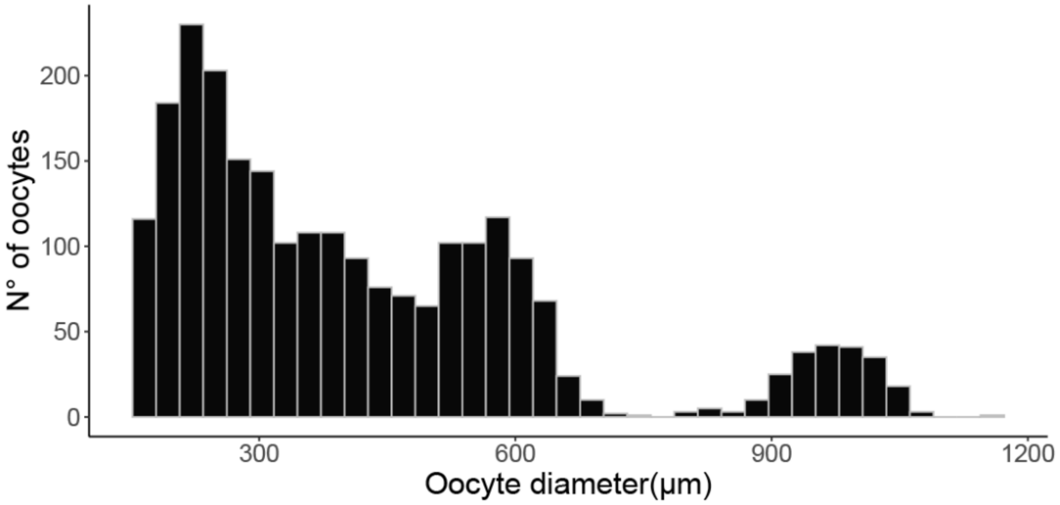


Figure 2.8. Size frequency distribution of vitellogenic oocytes for an early spawning female (macroscopic stage 3) showing three oocyte modes (TL = 20.6 cm).

The potential fecundity (F) ranged from 46,144 to 424,298 (201,035 ± 122,020) oocytes, and the relative potential fecundity (F_{rel}) ranged from 1362 to 3182 (2297 ± 546) oocytes g^{-1}. Batch fecundity was calculated on nine females, in which the mode of hydrated oocytes was markedly distinguishable from OFDs (Figure 2.8). Batch fecundity (F_b) ranged from 1293 to 22,949 (10,220 ± 6940), and the relative batch fecundity (F_{brel}) ranged from 31 to 206 (125 ± 63). The total number of vitellogenic oocytes was positively related to female size (TL) ($F = 128$, $df = 14$, $p < 0.001$). The relationship between TL and F is described by the equation:

$F = 0.8795 \times TL^{3.95}$; $r^2 = 0.91$.

2.4 Discussion

The present study provides a comprehensive picture of the biological cycle of the *M. merlangus* stock in the NAS, focusing on the population structure, growth parameters, and reproductive traits. For this area, to our knowledge, the growth parameters and fecundity values have never been reported before. Moreover, this is the first time that populations sampled with a time-shift of 30 years from the same fishing ground are compared in terms of population structure and growth.

2.4.1 Historical Comparison

The temporal comparison revealed a reduction of the mean size over the considered period, with a higher proportion of large individuals in the 1990–1991 sample with respect to the 2020–2021 ones. This finding confirms the declining trend in size reported for several fish stocks at different latitudes mainly due to fishing exploitation (Fisher et al., 2010). Fishing affects ecosystems by removing selectively larger specimens of commercial species, determining short-term (e.g., removal of spawners from the stock) and long-term effects (e.g., selection of fast-growing and early maturing specimens) (Bianchi et al., 2000; Shin et al., 2005; Hidalgo et al., 2012). Nevertheless, since fishing exerts selective pressure by removing larger and, consequently, older individuals (Yemane et al., 2008; Edwards and Plagányi, 2011), it was expected for the same difference in the age structure to be observed. Conversely, our data revealed that in both populations, the maximum age was similar (30–32 months). An effect on mean size-at-age was observed instead, with higher sizes per age class in the 1990–1991 sample compared to the 2020–2021 ones. These results together suggest that the observed reduction in length classes is related to different growth performances, which may be explained by metabolic or trophic constraints.

The physiological performance of marine fish, with them being ectotherms, is tightly controlled by water temperature, and their essential body functions (growth and reproduction) are optimal only within the thermal tolerance of the species (Pörtner and Knust, 2007). Oxygen consumption (i.e., metabolic rate) is higher in organisms living in warmer waters and it is proportional to body size (Atkinson and Sibly, 1997). Thus, as the water temperature increases, the maximum body size decreases to balance the increase in the metabolic rate (Pauly, 1998; Lindmark et al., 2022). Generally, the sensitivity to temperature changes in temperate species is low but it may vary depending on the specific location within its distribution range. Several studies have shown that under ocean warming, sensible species have been shifting their distribution towards higher latitudes and deeper waters to maintain physiological homeostasis (Engelhard et al., 2014; Poloczanska et al., 2016). However, sometimes a geographic constraint may prevent poleward migration, as in the case of enclosed seas, such as the Mediterranean Sea. Within this area, species distributions are highly clustered depending on the local features of water masses, and it is possible to find a wide range of species along the latitudinal axis: from the cold waters to the sub-tropical ones (Bianchi and Morri, 2000). The coldest parts of the Mediterranean Sea are the Gulf of Lion and the NAS. Being located in the northern limit of the Mediterranean latitudinal range, these areas are defined as "cul-de-sacs", from which cold-water species will have no possibility of escaping. Recent observational data showed that the AS, and in particular the NAS, is the sub-basin with the highest warming trend in sea surface temperature in the Mediterranean Sea over the last 20 years (Bonacci and Vrsalović, 2022; García-Monteiro et al., 2022) (Supplementary Figure 2.2), which could determine a strong reduction in cold-adapted species during the ongoing century and, in the worst case scenario, even their local extinction (Ben Rais Lasram et al., 2010). This phenomenon is probably occurring in the Adriatic population of whiting, whose distribution is restricted to the central and northern parts of the sub-basin, showing high abundance only in the northern part (Kaschner et al., 2022). Here, land boundaries could allow only a southward shift, which is prevented by the positive gradient of sea temperature and depth along the Adriatic latitudinal axis, creating a physical barrier. In fact, besides thermal tolerance, another peculiar feature of whiting is the preference for shallow waters, with the species being common at depths lower than 100 meters (Cohen et al., 1990). It is possible, therefore, to explain the observed difference in growth efficiency between populations in terms of a metabolic constraint due to the thermal tolerance of this species, limiting the increase in body size (Pörtner and Knust, 2007). Moreover, the observed trend confirms what is expected from the gill–oxygen limitation theory (Pauly and Cheung, 2018), according to which fish body growth is limited by gill capability to provide oxygen through their surface. As oxygen solubility in water decreases with temperature (Forster et al., 2012), body size is expected to decrease, through phenotypic plasticity, to maintain the scope for aerobic activity. This hypothesis is further corroborated by the reduction in the condition factor, which is associated not only with low oxygen levels but also with food limitations (Casini et al., 2016). Furthermore, considering the potential effects of oxygen limitation on size at maturity, GSI, and egg production as well (Kolding et al., 2008), it can thus be suggested that reproductive functions have undergone important changes over the last few decades. Unfortunately, no data about the reproductive traits were available from the 1990–1991 samples to test this phenomenon.

One interesting finding is that the timing of otolith seasonal depositions revealed a different pattern between the investigated periods. The edge-zone analysis pointed out a difference in the opaque deposition timing over the warm season, showing an opaque deposition rate > 90% from April to September in the 1990–1991 samples and from May to July in the 2020–2021 samples (no samples in August), therefore with a reduction in the length of the period. Several factors are known to influence the periodicity of opaque and translucent zones in otoliths, such as geographical distributions, life history events (settlement and reproduction), food availability, and water temperature (Panfili et al., 2002). Nevertheless, temperature is known to play a primary role in determining deposition patterns (Choat and Axe, 1996; Fablet et al., 2011; Vitale et al., 2019), and consequently, the increased temperature may have affected the biomineralization process negatively.

Another possible explanation for the decreased growth performance may be related to another environmental driver, primary production, which has been recognized as one of the main historical drivers in the Mediterranean ecosystem (Piroddi et al., 2017). For example, this is noticeable in the AS, where forage fish population dynamics can be influenced by river discharge, and consequently, by primary production (Santojanni et al., 2006). As a result, the declining trend in freshwater inputs observed in the Mediterranean Sea (Macias et al., 2014) could have played a significant role in the observed pattern, reducing the prey quantity or quality for mesopredatory species such as whiting.

We observed an unexpected outcome when comparing the LFDs by sex related to the marked sexual dimorphism in size featuring in the 2020–2021 sample. While in the 1990–1991 sample, the modal distributions of the two sexes mostly overlap (except for the largest length classes, dominated by females), a 5–6 cm gap was noticed between the sexes in TL modal classes in 2020–2021. As already reported for other areas, whiting females attain a larger size than males, showing higher L_∞ and lower k (Hussy et al., 2012; Lauerburg et al., 2015; Yildiz and Saadet Karakulak, 2019). The increased difference in size may suggest a sex-dependent response related to the different energetic investments in gamete production and the effect of body size for each sex

(Hayward and Gillooly, 2011; Barneche et al., 2018). Although to our knowledge, a similar finding has never been pointed out in previous studies, we hypothesize that the integrated effect of fishing and warming towards smaller sizes exerts a stronger influence on males because of their lower reproductive cost with respect to females. On the other hand, females, despite being subjected to the same conditions, are less subjected to size decrease because their reproductive output (i.e., quantity and possibly quality of offspring) is positively correlated with size (Barneche et al., 2018). Another possible explanation could be related to modifications in energy uptake patterns between males and females, controlled by sex-specific behaviour, as already reported for whiting by Lauerburg et al. (2015). Females ingest a significantly higher amount of food items and show lower percentages of empty stomachs compared to males. Fishing and warming could have acted in enhancing the degree of differentiation between these behavioral patterns, determining an increased dimorphism in growth rates over three decades.

Consideration must be made about the timing of the sample collection. Even if the same methodology was used, these results need to be interpreted with caution because of the longtime shift between sampling collection and its related issues. First, the samples came from two discrete sampling activities, thus providing detailed pictures of two restricted periods that were not appropriate to highlight a trend over three decades. The adaptive phenotypic plasticity may influence population dynamics even on a short-term scale, and it is favored by heterogeneous environments such as the AS (Hidalgo et al., 2014). Consequently, populations that are subjected to environmental variability may have natural oscillations in biological parameters in relation to external conditions. Finally, the skewed distribution observed in 1990–1991 is probably due to the higher proportion of specimens coming from the summer months, a period during which YOY are more abundant than adults (Giovanardi and Rizzoli, 1984). In addition, it may be also related to the high fishing pressure exerted in the late 20th century, being the typical length structure featuring heavily exploited stocks (Ottersen et al., 2006).

2.4.2 Population Biological Traits

The size range found was smaller than that previously observed in the AS (Vallisneri et al., 2004) and similar to the Black Sea (Bilgin et al., 2012; Mazlum and Bilgin, 2014).

As already reported for other gadoids (Mir-Arguimbau et al., 2020), the Mediterranean maximum size was much smaller than the Atlantic one (Gerritsen et al., 2003; Lauerburg et al., 2015; Timmerman et al., 2020). The presence of the opaque margin during the warmer months in the otoliths analyzed confirms the deposition pattern of the species, indicating that an opaque deposition is associated with the fast growth season (ICES, 1998; Ross and Hussy, 2013; Mir-Arguimbau et al., 2020).

The age classes and maximum age estimated in the present study were similar to those previously observed in the AS (Giovanardi and Rizzoli, 1984; Vallisneri et al., 2006) and lower than those reported in the Atlantic Ocean and Black Sea (Polat and Gümücs,1996; Gerritsen et al., 2003; Mazlum and Bilgin, 2014; Lauerburg et al., 2015). Surprisingly, despite similar length ranges, our age estimates are lower than the Black Sea population, indicating faster growth and shorter lifespan in the AS population. Moreover, this result is noticeable by comparing the growth rate and the growth performance between different areas, values of which in the AS population are the highest reported in the literature (Yildiz and Saadet Karakulak, 2019; Froese and Pauly, 2022) (Figure 2.9). In particular, our estimates of *k* were higher than those previously reported probably because of the inclusion of the YOY data in the VBGF, whose age estimation (in months) was validated through the analysis of the YOY LFDs collected between April and June (Supplementary Figure 2.1). Generally, it is difficult to obtain length-at-age data of juvenile stages (when the growth rate reaches its maximum), and this often leads to an underestimation of k values (Mir-Arguimbau et al., 2020). Another explanation for the difference in the age–length results could be attributed to the different methodologies used to perform the age readings. After several attempts, we obtained consistent results with the “burnt and broken” otoliths, but there is no general agreement about the best method to use, even if the latest ICES guidelines (Vitale et al., 2019) suggest using broken or sectioned preparations in this species. Additionally, age reading studies often lack a validation step (e.g., edge/length–frequency analysis, marking and recapturing, and tagging), limiting the comparability of the results.

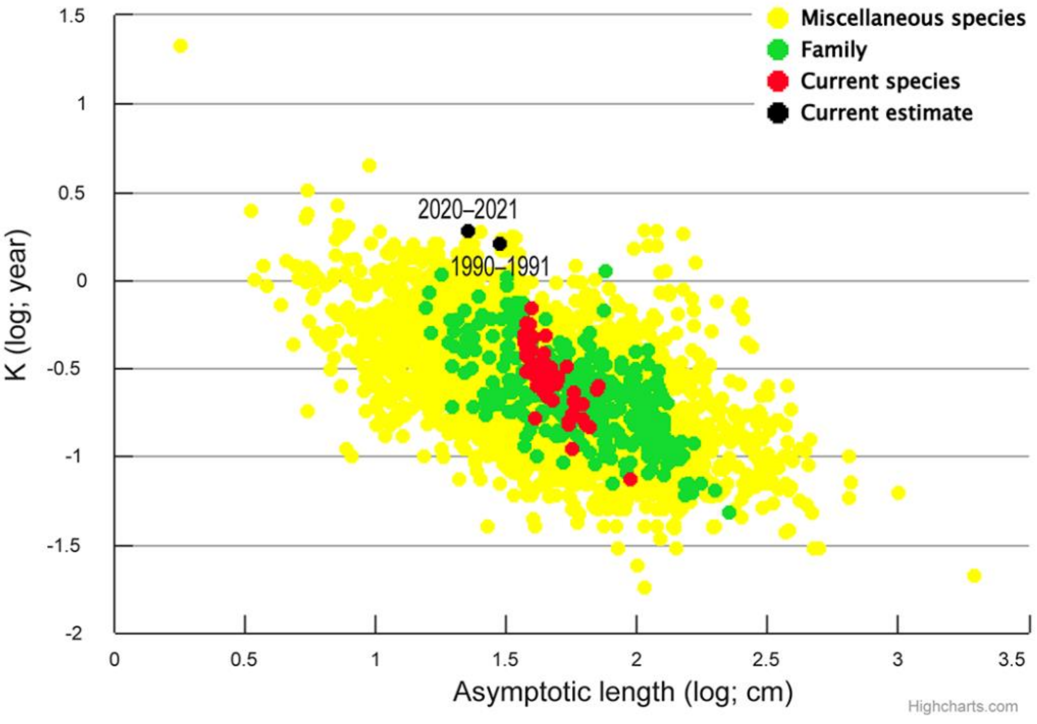


Figure 2.9. Auximetric plot for *Merlangius merlangus* and other gadid species that allows for comparison between the L_∞ and k estimated in this study (black) with other estimates obtained for the same species (red), other gadids (green), and other bony fish (yellow). Modified from (Froese and Pauly, 2022).

Sexual maturity is reached within the first year of life in males and females at 16.1 and 16.8 cm TL, respectively. These estimates are lower than previous observations carried out in the AS (Giovanardi and Rizzoli, 1984; Vallisneri et al., 2006) and, as expected, in the Atlantic Ocean (Gerritsen et al., 2003); on the other hand, our estimates were higher than those reported in the Black Sea (Yildiz et al., 2021). The difference observed between our updated data and the previous studies in the AS agrees with our expectations, considering the reduction in L_∞ and the positive relationship between L_∞ and L_{50} (Pauly, 2022). Macroscopic observations on gonads and GSI trends indicated clearly that spawning takes place in winter, showing a narrower spawning season compared to the Atlantic Ocean and Black Sea, where it occurs from January to September and throughout the year, respectively (Cohen et al., 1990; Yildiz et al., 2021). During the spawning peak (December), the mean GSI value of the females (11%) is one order of magnitude higher than the males (1%), confirming the highly different reproductive efforts between the sexes (Vallisneri et al., 2006; Yildiz et al., 2021).

The present study has provided fecundity estimates for the first time for whiting in the AS, which are within the range provided by previous studies carried out in the north east Atlantic Ocean and the Black Sea (Cohen et al., 1990; Ismen, 1995). Considering that whiting is a batch spawner (Murua and Saborido-Rey, 2003) and that the average F was 18.1 times higher than the average F_b, a female could potentially lay 18 batches during the spawning season. Regarding the OFDs, the presence of at least two separated modal groups was clear only in females in advanced ovarian developmental stages (with hydrated oocytes) and we often observed nonhomogeneous oocyte size distributions, without any recognizable modal group. Although whiting is considered to have a group-synchronous ovarian organization, our data suggest the possibility of an asynchronous organization (Murua and Saborido-Rey, 2003), but the low number (15) of females used may not be adequate to infer the spawning pattern of this species.

The differences in life history traits observed between the Mediterranean Sea and Black Sea populations can be related to the genetic divergence process. Previous studies, based on morphological and meristic features, revealed differentiation between the AS and the Black Sea, raising a debate about the existence of two subspecies (Tortonese, 1970; Ungaro et al., 1995). Recent molecular analyses have attempted to answer this question, stating that, despite some genetic differentiation between different sampling sites in the Black and Aegean Seas, there is no evidence supporting the existence of the presumed subspecies (Şalcıoğlu et al., 2020).

2.4.3 Conclusions

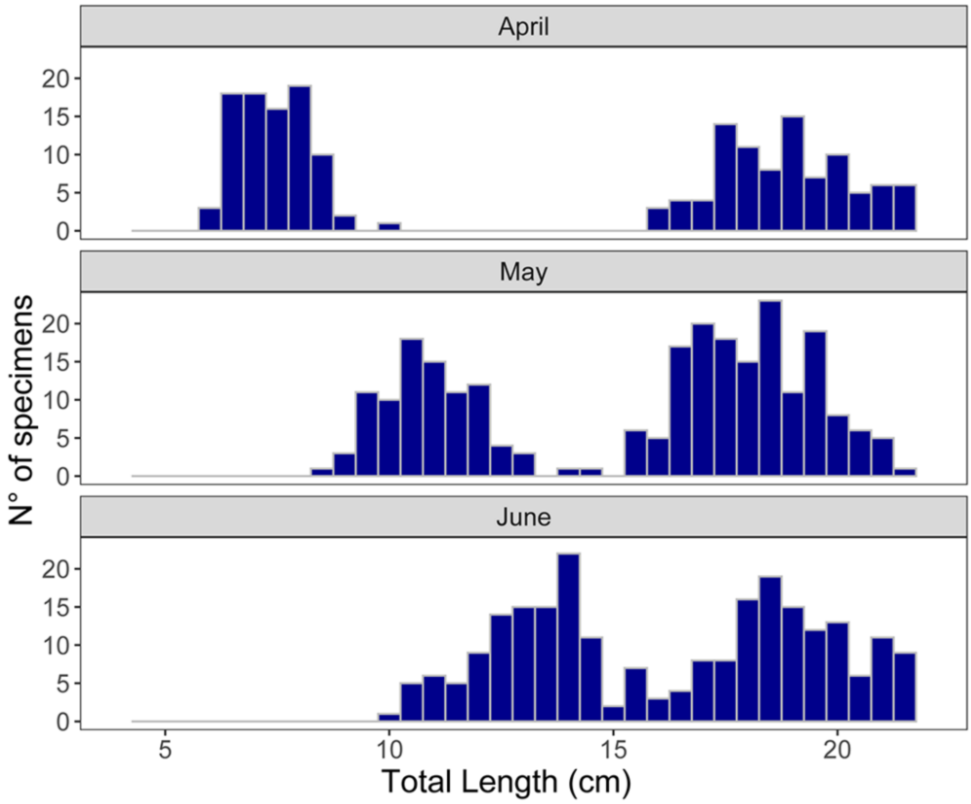
The present study provides a comprehensive picture of the biological life cycle and population parameters of the cold-water species *M. merlangus* in the AS. At the same time, it describes for the first time what seems to be a process of decreasing growth performance, depicting a current population composed of individuals with smaller sizes and lower body conditions than in 1990–1991. This process, together with the reduction in reproductive potential driven by the size dependency of fecundity values can lead to a more vulnerable and less resilient population, whose long-term stability is threatened by climate change and fishing exploitation. Surprisingly, we did not observe any difference in the age structure over the period considered, suggesting that fishing did not play a significant role in the observed species stock dynamics in the analyzed period. On the other hand, our evidence indicates that modified environmental parameters (first of all sea temperature) may have led to the observed modification pattern, as already reported in several fish stocks worldwide (Cheung et al., 2013a). Nevertheless, several questions about this phenomenon remain to be answered, for example, about the role of trophic ecology, which alone could explain such a growth variation through prey-predator interactions.

The study contributes to our understanding of the biological responses of fish populations to climate change and fishery impacts. Even if our data on whiting support that the main driver was represented by environmental pressures, it is well-known that interacting effects of climate change and fishing may be present, speeding up the declining trend of some groups of fish species, such as the cold-adapted ones living in the Mediterranean Sea (Lloret et al., 2015, 2021). Management policies need to consider these dynamics not only at the basin level but also at the local scale, providing adaptive measures based on the knowledge of interactions between the environment and the biota, which is the only way to achieve sustainable exploitation of fish resources.

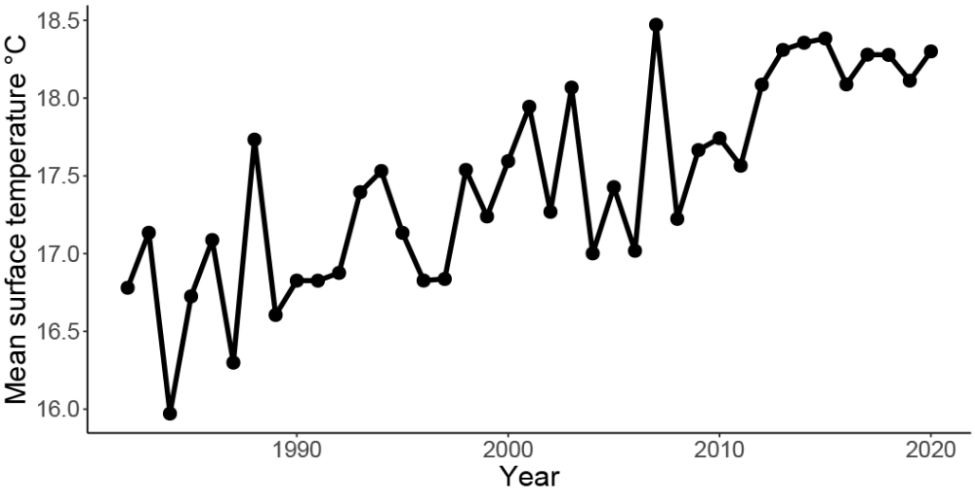
Acknowledgements

We thank all of the staff of the National Research Council (CNR) and the Hydrobiological Station Umberto D'Ancona (University of Padova), as well as the fishers involved for their essential contribution to the data collection and interpretation. The research leading to these results was conceived under the International Ph.D. program “Innovative Technologies and Sustainable Use of Mediterranean Sea Fishery and Biological Resources” (www.FishMed-PhD.org, accessed on 1 June 2023). This study represents partial fulfilment of the requirements for the Ph.D. thesis of Federico Calì.

Supplementary material



Supplementary Figure 2.1. Monthly length–frequency distribution of *Merlangius merlangus* in the springtime of 2021. The bimodal distribution is due to the joining of the young-of-the-year (YOY) in the sampled population.



Supplementary Figure 2.2. Historical trend of the mean annual values of surface temperature in the Adriatic Sea. Modified from García-Monteiro et al. (2022).

Supplementary Table 2.1. Age–length for females, males, and unsexed juveniles based on otolith readings of *Merlangius merlangus* sampled in the 1990–1991 period. N = total number; SD = standard deviation.

	Females											Males										
Age (quarters)	6	9	12	15	18	21	24	27	30	33	N	6	9	12	15	18	21	24	27	30	33	N
Total length (cm)																						
12	1	1									2											0
13	6	2									8	5										5
14	12	6									18	8	7									15
15	2	4									6	4	4	2								10
16	3	4									7	2	4	2								8
17	3	4	2								9	4	4	2								10
18	3	4	2								9	4	4	3	2							13
19	4	4	2	1							11	4	4	4	2							14
20	3	4	2	2							11	2	4	6	2							14
21	2	4	4	2							12	2	4	5	4	1						16
22	2	3	4	2							11	1	4	3	3	1						12
23	1	3	4	2							10		4	4	4	2		1				15
24		3	3	2	1						9		1		3	3	1	3				11
25		1	2	2		1					6	1		2	1	2	2	2	1			11
26		3	7	3							13		1	1	2		2	3	1			10
27		1	3	5	2	1					12			1		2	1	2	1			7
28		1	2	2	1	1					7					2	1				1	4
29			1		2		1				4					1	1				1	3
30			1	1	2	1	1				6					1				1		2
31				1	2	1	1				5											0
32					2	2	3		1		8											0
33					1	1					2											0
34					1	1					2											0
35						1					1											0
37								1			1											0
N	42	52	39	25	14	10	6	1	1	-	190	37	45	35	23	15	8	11	3	1	2	180
TL mean (cm)	16.7	19.3	23.6	25.0	30.1	30.9	31.2	37.0	32.5	-		16.8	18.7	20.6	22.2	25.6	26.4	25.5	26.2	30.0	28.8	
TL SD	3.0	4.1	3.4	3.1	2.7	3.4	1.2	-	-	-		3.0	3.2	2.9	2.3	2.7	1.8	1.3	1.0	-	1.1	

Unsexed juveniles

Age (quarters)	3	6	9	12	N
Total length (cm)					
3	1				1
4	7				7
5	21				21

6	35				35
7	12				12
8	8				8
9	1	4			5
10	1	3			4
11		6			6
12		7			7
13		11	2		13
14		21	1		22
N	86	52	3	-	141
TL mean (cm)	6.3	12.8	13.5	-	
TL SD	1.2	1.6	0.5	-	

Supplementary Table 2.2. Age–length for females, males, and unsexed juveniles based on otolith readings of *Merlangius merlangus* sampled in the 2020–2021 period. N = total number; SD = standard deviation.

	Females												Males											
Age (quarters)	3	6	9	12	15	18	21	24	27	30	33	N	3	6	9	12	15	18	21	24	27	30	33	N
Total length (cm)																								
6	1											1	4											4
7	1											1	4	1										5
8	3	2										5	3											3
9	1	1										2	2											2
10		2										2	2											2
11		1										1		2										2
12												0		6										6
13		5										5		5			1							6
14		5	2	2	1							10		4		2	2							8
15		2	2	2	3							9		3	5	8	7	2						25
16		4	2	4	4							14		3	4	6	8	2						23
17		4	4	5	4	1						18		4	4	7	7	2						24
18		2	4	6	7	2						21		2	3	5	8	4						22
19		1	3	5	5	2						16			2	7	5	5						19
20			4	6	6	4						20			4	3	4	6	1	3	1			22
21			3	6	7	5	1					22				2	3	4	1	3	2	1		16
22			4	5	7	7						23						3	2	2	2	1		10
23			1	4	6	4	1		1			17					1		1	4	1			7
24				3	3	4		1	1			12						1		1	1			3
25				2	3	6	1	3	2			17												0
26					1	1		2	3	1		8												0
27						2		5	2			9												0
28						1		1				2												0
29								1				1												0
30						1		1		1		3												0
31								1				1												0
32												0												0
33												0												0
34												0												0
35												0												0
36												0												0
37												0												0
N	6	29	29	50	57	40	3	15	9	2	-	240	15	30	22	40	46	29	5	13	7	2	-	209
TL mean (cm)	8.1	14.5	19.1	20.0	20.5	22.9	23.3	28.0	25.8	28.8	-		8.1	14.4	17.7	17.6	17.7	19.7	22.2	22.1	22.2	22.2	-	

TL SD	1.2	3.1	2.6	2.9	2.9	2.8	2.1	2.4	1.2	2.8	-	1.3	2.5	1.9	1.9	2.1	2.2	1.3	1.4	1.3	0.8	-

Unsexed juveniles

Age (quarters)	3	6	9	12	N
Total length (cm)					
4	1				1
6	8				8
7	10				10
8	5				5
9	2	1			3
N	26	1	-	-	27
TL mean (cm)	7.4	9.3	-	-	
TL SD	1.1	-	-	-	

References

Atkinson, D., and Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* 12, 235–239. doi: 10.1016/S0169-5347(97)01058-6.

Azzurro, E., Sbragaglia, V., Cerri, J., Bariche, M., Bolognini, L., Ben Souissi, J., et al. (2019). Climate change, biological invasions, and the shifting distribution of Mediterranean fishes: A large-scale survey based on local ecological knowledge. *Glob. Chang. Biol.* 25, 2779–2792. doi: 10.1111/gcb.14670.

Barausse, A., Michieli, A., Riginella, E., Palmeri, L., and Mazzoldi, C. (2011). Long-term changes in community composition and life history traits in a highly exploited basin (northern Adriatic Sea): The role of environment and anthropogenic pressures. *J. Fish Biol.* 79, 1453–1486. doi: 10.1111/j.1095-8649.2011.03139.x.

Barneche, D. R., White, C. R., and Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science* 645, 642–645.

Bazairi, H., Ben Haj, S., Boero, F., Cebrian, D., De Juan, S., Limam, A., Lleonart, J., Torchia, G., and Rais, C. (2010). *The Mediterranean Sea Biodiversity: state of the ecosystems, pressures, impacts*. Rac/Spa (eds.).

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* 38, 982–983.

Ben Rais Lasram, F., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W., and Mouillot, D. (2010). The Mediterranean Sea as a “cul-de-sac” for endemic fishes facing climate change. *Glob. Chang. Biol.* 16, 3233–3245. doi: 10.1111/j.1365-2486.2010.02224.x.

Bianchi, C. N., and Morri, C. (2000). Marine biodiversity of the Mediterranean Sea: Situation, problems and prospects for future research. *Mar. Pollut. Bull.* 40, 367–376. doi: 10.1016/S0025-326X(00)00027-8.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., et al. (2000). Impact of fishing on size composition and diversity of demersal fish communities. *ICES J. Mar. Sci.* 57, 558–571. doi: 10.1006/jmsc.2000.0727.

Bilgin, S., Bal, H., and Taşçı, B. (2012). Length Based Growth Estimates and Reproduction Biology of Whiting, *Merlangius merlangus euxinus* (Nordman, 1840) in the Southeast Black Sea. *Turkish J. Fish. Aquat. Sci.* 12, 871–881. doi: DOI: 10.4194/1303-2712-v12_4_15.

Bolger, T., and Connolly, P. L. (1989). The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* 34, 171–182. doi: 10.1111/j.1095-8649.1989.tb03300.x.

Bonacci, O., and Vrsalović, A. (2022). Differences in Air and Sea Surface Temperatures in the Northern and Southern Part of the Adriatic Sea. *Atmosphere.* 13, 1158. doi: 10.3390/atmos13071158.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* 59, 197–242. doi: 10.1006/jfbi.2001.1668.

Cardinale, M., Osio, G. C., and Scarcella, G. (2017). Mediterranean Sea: A failure of the European fisheries management system. *Front. Mar. Sci.* 4, 72. doi: 10.3389/fmars.2017.00072.

Casini, M., Bartolino, V., Molinero, J. C., and Kornilovs, G. (2010). Linking fisheries, trophic interactions and climate: Threshold dynamics drive herring C*lupea harengus* growth in the central Baltic Sea. *Mar. Ecol. Prog. Ser.* 413, 241–252. doi: 10.3354/meps08592.

Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., et al. (2016). Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. *R. Soc. Open Sci.* 3, 160416. doi: 10.1098/rsos.160416.

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.* 39, 1208–1210.

Cheung, W. W. L., and Pauly, D. (2016). Impacts and effects of ocean warming on marine fishes. In: Laffoley, D., & Baxter, J.M. (eds.). *Explaining ocean warming: Causes, scale, effects and consequences*. Full report. Gland, Switzerland: IUCN. 239–253.

Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Palomares, M. L. D., et al. (2013a). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat. Clim. Chang.* 3, 254–258. doi: 10.1038/nclimate1691.

Cheung, W. W. L., Watson, R., and Pauly, D. (2013b). Signature of ocean warming in global fisheries catch. *Nature* 497, 365–368. doi: 10.1038/nature12156.

Choat, J. H., and Axe, L. M. (1996). Growth and longevity in acanthurid fishes; an analysis of otolith increments. *Mar. Ecol. Prog. Ser.* 134, 15–26. doi: 10.3354/meps134015.

Choy, S. C. (1985). A rapid method for removing and counting eggs from fresh and preserved decapod crustaceans. *Aquaculture* 48, 369–372. doi: 10.1016/0044-8486(85)90139-5.

Cohen, D. M., Inada, T., Iwamoto, T., and Scialabba, N. (1990). FAO Species Catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date*. FAO Fish. Syn.* 125.

Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W. W. L., Christensen, V., et al. (2012). The Mediterranean Sea under siege: Spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Glob. Ecol. Biogeogr.* 21, 465–480. doi: 10.1111/j.1466-8238.2011.00697.x.

Colloca, F., Scarcella, G., and Libralato, S. (2017). Recent trends and impacts of fisheries exploitation on Mediterranean stocks and ecosystems. *Front. Mar. Sci.* 4, 244. doi: 10.3389/fmars.2017.00244.

Edwards, C. T. T., and Plagányi, É. E. (2011). Protecting old fish through spatial management: Is there a benefit for sustainable exploitation? *J. Appl. Ecol.* 48, 853–863. doi: 10.1111/j.1365-2664.2011.01961.x.

Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Glob. Chang. Biol.* 20, 2473–2483. doi: 10.1111/gcb.12513.

Fablet, R., Pecquerie, L., de Pontual, H., Høie, H., Millner, R., Mosegaard, H., et al. (2011). Shedding light on fish otolith biomineralization using a bioenergetic approach. *PLoS One* 6, e27055. doi: 10.1371/journal.pone.0027055.

Fisher, J. A. D., Frank, K. T., and Leggett, W. C. (2010). Breaking Bergmann's rule: truncation of Northwest Atlantic marine fish body sizes. *Ecology* 91, 2499–2505.

Fonda Umani, S. (1996). Pelagic production and biomass in the Adriatic Sea. *Sci. Mar.* 60, 65–77.

Forster, J., Hirst, A. G., and Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proc. Natl. Acad. Sci. U.S.A.* 109, 19310–19314. doi: 10.1073/pnas.1210460109.

Fortibuoni, T., Giovanardi, O., Pranovi, F., Raicevich, S., Solidoro, C., and Libralato, S. (2017). Analysis of long-term changes in a Mediterranean marine ecosystem based on fishery landings. *Front. Mar. Sci.* 4, 33. doi: 10.3389/FMARS.2017.00033.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science* 365, 979–983. doi: 10.1126/science.aax5721.

Froese, R., and Pauly, D. (2022). FishBase. *World Wide Web Electron. Publ. (Accessed 8 December 2022).* Available at: https://fishbase.mnhn.fr/popdyn/PopGrowthList.php?ID=29&GenusName=Merlangius&SpeciesName=merlangus&fc=183.

García-Monteiro, S., Sobrino, J. A., Julien, Y., Sòria, G., and Skokovic, D. (2022). Surface Temperature trends in the Mediterranean Sea from MODIS data during years 2003–2019. *Reg. Stud. Mar. Sci.* 49, 102086. doi: 10.1016/j.rsma.2021.102086.

Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., Mchugh, M., et al. (2010). Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Glob. Chang. Biol.* 16, 517–527. doi: 10.1111/j.1365-2486.2009.02027.x.

Gerritsen, H. D., Armstrong, M. J., Allen, M., McCurdy, W. J., and Peel, J. A. D. (2003). Variability in maturity and growth in a heavily exploited stock: whiting (*Merlangius merlangus* L.) in the Irish Sea. *J. Sea Res. 49* 49, 69–82. doi: 10.1016/j.icesjms.2003.10.005.

Giovanardi, O., and Rizzoli, M. (1984). Biological data, collected during the Pipeta expeditions, on the whiting, *Merlangius merlangus* (L.) in the Adriatic Sea. *Fao Fish. Reports* 290, 149–153.

Hayward, A., and Gillooly, J. F. (2011). The cost of sex: Quantifying energetic investment in gamete production by males and females. *PLoS One* 6, e16557. doi: 10.1371/journal.pone.0016557.

Hidalgo, M., Olsen, E. M., Ohlberger, J., Saborido-Rey, F., Murua, H., Piñeiro, C., et al. (2014). Contrasting evolutionary demography induced by fishing: The role of adaptive phenotypic plasticity. *Ecol. Appl.* 24, 1101–1114. doi: 10.1890/12-1777.1.

Hidalgo, M., Rouyer, T., Bartolino, V., Cerviño, S., Ciannelli, L., Massutí, E., et al. (2012). Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. *Ecography* 35, 637–649. doi: 10.1111/j.1600-0587.2011.07314.x.

Hopkins, T. S. The structure of Ionian and Levantine Seas. *Reports Meteorol. Oceanogr.* 41, 35–36.

Hunter, J. R., Macewicz, B. J., Chyan-Huei Lo, N., and Kimbrell, C. A. (1992). Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fish. Bull.* 90, 101–128.

Hussy, K., Coad, J. O., Farrell, E. D., Clausen, L. W., and Clarke, M. W. (2012). Sexual dimorphism in size, age, maturation, and growth characteristics of boarfish (*Capros aper*) in the Northeast Atlantic. *ICES J. Mar. Sci.* 69, 1729–1735. doi: doi:10.1093/icesjms/fss156.

ICES (1998). Report of the Workshop on Otolith Ageing of North Sea Whiting. *ICES Expert Gr. Reports* 14, 66. doi: https://doi.org/10.17895/ices.pub.19263203.

ICES (2008). Report of the Workshop on Sexual Maturity Staging of Cod, Whiting, Haddock and Saithe (WKMSCWHS). Available at: https://doi.org/10.17895/ices.pub.19280246.

Ismen, A. (1995). Fecundity of whiting, *Merlangius merlangus euxinus* (L.) on the Turkish Black Sea coast. *Fish. Res.* 22, 309–318. doi: 10.1016/0165-7836(94)00327-S.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., et al. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637. doi: 10.1126/science.1059199.

Kaschner, K., Rius-Barile, J., Kesner-Reyes, K., Garilao, C., Kullander, S. O., Rees, T., et al. (2022). AquaMaps: Predicted range maps for aquatic species. Available at: www.aquamaps.org.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* 77, 765–776.

Kolding, J., Haug, L., and Stefansson, S. (2008). Effect of ambient oxygen on growth and reproduction in Nile tilapia (*Oreochromis niloticus*). *Can. J. Fish. Aquat. Sci.* 65, 1413–1424. doi: 10.1139/F08-059.

Kuparinen, A., and Hutchings, J. A. (2012). Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proc. R. Soc. B Biol. Sci.* 279, 2571–2579. doi: 10.1098/rspb.2012.0120.

Lauerburg, R. A. M., Keyl, F., Kotterba, P., Floeter, J., and Temming, A. (2015). Sex-specific food intake in whiting *Merlangius merlangus*. *J. Fish Biol.* 86, 1729–1753. doi: 10.1111/jfb.12682.

Lindmark, M., Ohlberger, J., and Gårdmark, A. (2022). Optimum growth temperature declines with body size within fish species. *Glob. Chang. Biol.* 28, 2259–2271. doi: 10.1111/gcb.16067.

Lloret, J., Sabatés, A., Muñoz, M., Demestre, M., Solé, I., Font, T., et al. (2015). How a multidisciplinary approach involving ethnoecology, biology and fisheries can help explain the spatio-temporal changes in marine fish abundance resulting from climate change. *Glob. Ecol. Biogeogr.* 24, 448–461. doi: 10.1111/geb.12276.

Lloret, J., Serrat, A., Thordarson, G., Helle, K., Jadaud, A., Bruno, I., et al. (2021). The poor health of deep-water species in the context of fishing activity and a warming climate: will populations of *Molva* species rebuild or collapse? *J. Fish Biol.* 98, 1572–1584. doi: 10.1111/jfb.14347.

Ludwig, W., Dumont, E., Meybeck, M., and Heussner, S. (2009). River discharges of water and nutrients to the Mediterranean and Black Sea: Major drivers for ecosystem changes during past and future decades? *Prog. Oceanogr.* 80, 199–217. doi: 10.1016/j.pocean.2009.02.001.

Macias, D., Garcia-Gorriz, E., Piroddi, C., and Stips, A. (2014). Biogeochemical control of marine productivity in the Mediterranean Sea during the last 50 years. *Global Biogeochem. Cycles* 28, 897–907. doi: 10.1002/2014GB004846.

Mazlum, R. E., and Bilgin, S. (2014). Age, growth, reproduction and diet of the whiting, *Merlangius merlangus euxinus* (Nordmann, 1840), in the southeastern Black Sea. *Cah. Biol. Mar.* 3, 463–474. Available at: https://www.researchgate.net/publication/274248550.

Micheli, F., Halpern, B. S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., et al. (2013). Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: Assessing current pressures and opportunities. *PLoS One* 8, e79889. doi: 10.1371/journal.pone.0079889.

Mir-Arguimbau, J., Balcells, M., Raventós, N., Martín, P., and Sabatés, A. (2020). Growth, reproduction and their interplay in blue whiting (*Micromesistius poutassou*, Risso, 1827) from the NW Mediterranean. *Fish. Res.* 227, 105540. doi: 10.1016/j.fishres.2020.105540.

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Marsaleix, P., Somot, S., et al. (2019). An end-to-end model reveals losers and winners in a warming Mediterranean Sea. *Front. Mar. Sci.* 6, 1–19. doi: 10.3389/fmars.2019.00345.

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P. R., Thorsen, A., and Junquera, S. (2003). Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *J. Northwest Atl. Fish. Sci.* 33, 33–54. doi: 10.2960/J.v33.a3.

Murua, H., and Saborido-Rey, F. (2003). Female reproductive strategies of marine fish species of the North Atlantic. *J. Northwest Atl. Fish. Sci.* 33, 23–31. doi: 10.2960/J.v33.a2.

O'Connor, M. I., Holding, J. M., Kappel, C. V., Duarte, C. M., Brander, K., Brown, C. J., et al. (2015). Strengthening confidence in climate change impact science. *Glob. Ecol. Biogeogr.* 24, 64–76. doi: 10.1111/geb.12218.

Ottersen, G., Hjermann, D. O., and Stenseth, N. C. (2006). Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fish. Oceanogr.* 15, 230–243. doi: 10.1111/j.1365-2419.2006.00404.x.

Panfili, J., de Pontual, H., Troadec, J.-P., and Wright, P. J. (2002). *Manual of Fish Sclerochronology*. Ifremer-IRD, Brest, France. doi: 10.4324/9780080967691-8.

Pauly, D. (1998). Tropical fishes: patterns and propensities. *J. Fish Biol.* 53, 1–17. doi: 10.1006/jfbi.1998.0810.

Pauly, D. (2022). Why do fish reach first maturity when they do? *J. Fish Biol.* 101, 333–341. doi: 10.1111/jfb.14902.

Pauly, D., and Cheung, W. W. L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Glob. Chang. Biol.* 24, e15–e26. doi: 10.1111/gcb.13831.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. *Science* 279, 860–863. doi: 10.1126/science.279.5352.860.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., et al. (2002). Towards sustainability in world fisheries. *Nature* 418, 689–695. doi: 10.1038/nature01017.

Pearson, A. G. E. (1985). *Histochemistry. Theoretical and Applied. Vol. 2: Analytical Technology*. Churchill Livingstone, Edinburgh, UK.

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., et al. (2017). Historical changes of the Mediterranean Sea ecosystem: Modelling the role and impact of primary productivity and fisheries changes over time. *Sci. Rep.* 7, 1–18. doi: 10.1038/srep44491.

Polat, N., and Gümücs, A. (1996). Ageing of whiting (*Merlangius merlangus euxinus*, Nord., 1840) based on broken and burnt otolith. *Fish. Res.* 28, 231–236.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., Molinos, J. G., Halpern, B. S., Hoegh-Guldberg, O., et al. (2016). Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.* 3, 1–21. doi: 10.3389/fmars.2016.00062.

Pörtner, H. O., and Knust, R. (2007). Climate Change Affects Marine Fishes Through the Oxygen Limitation of Thermal Tolerance. *Science* 315, 95–97. doi: 10.1259/0007-1285-53-633-920-b.

Reynolds, J. D., Dulvy, N. K., Goodwin, N. B., and Hutchings, J. A. (2005). Biology of extinction risk in marine fishes. *Proc. R. Soc. B Biol. Sci.* 272, 2337–2344. doi: 10.1098/rspb.2005.3281.

Ross, S. D., and Hüssy, K. (2013). A reliable method for ageing of whiting (*Merlangius merlangus*) for use in stock assessment and management. *J. Appl. Ichthyol.* 29, 825–832. doi: 10.1111/jai.12204.

Russo, A., and Artegiani, A. (1996). Adriatic Sea hydrography. *Sci. Mar.* 60, 33–43.

Russo, A., Carniel, S., Sclavo, M., and Krzelj, M. (2012). 07 Climatology of the Northern-Central Adriatic Sea. *Mod. Climatol. 8, 177-212.* doi: 10.5772/34693.

Saber, S., Macías, D., Ortiz de Urbina, J., and Kjesbu, O. S. (2015). Stereological comparison of oocyte recruitment and batch fecundity estimates from paraffin and resin sections using spawning albacore (*Thunnus alalunga*) ovaries as a case study. *J. Sea Res.* 95, 226–238. doi: 10.1016/j.seares.2014.05.003.

Şalcıoğlu, A., Gubili, C., Krey, G., Sönmez, A. Y., and Bilgin, R. (2020). Phylogeography and population dynamics of the Eastern Mediterranean whiting (*Merlangius merlangus*) from the Black Sea, the Turkish Straits System, and the North Aegean Sea. *Fish. Res.* 229, 1–10. doi: 10.1016/j.fishres.2020.105614.

Santojanni, A., Arneri, E., Bernardini, V., Cingolani, N., Di Marco, M., and Russo, A. (2006). Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. *Clim. Res.* 31, 181–193. doi: 10.3354/cr031181.

Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G., and Gislason, H. (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396. doi: 10.1016/j.icesjms.2005.01.004.

Supić, N., Grbec, B., Vilibić, I., and Ivančić, I. (2004). Long-term changes in hydrographic conditions in northern Adriatic and its relationship to hydrological and atmospheric processes. *Ann. Geophys.* 22, 733–745. doi: 10.5194/angeo-22-733-2004.

Timmerman, C. A., Marchal, P., Denamiel, M., Couvreur, C., and Cresson, P. (2020). Seasonal and ontogenetic variation of whiting diet in the Eastern English Channel and the Southern North Sea. *PLoS One* 15, e0239436. doi: 10.1371/journal.pone.0239436.

Tortonese, E. (1964). The Main Biogeographical Features and Problems of the Mediterranean Fish Fauna. *Copeia* 1964, 98–107.

Tortonese, E. (1970). *Fauna d’Italia*. Edizioni Calderini: Bologna, Italy.

Ungaro, N., Marano, G., and Piccinetti, C. (1995). Adriatic, Black Sea: the whiting doubt. *Cybium* 19, 311–315.

Vallisneri, M., Scapolatempo, M., and Tommasini, S. (2006). Reproductive biology of *Merlangius merlangus* L. (Osteichthyes, Gadidae) in the northern Adriatic Sea. *Acta Adriat.* 47, 159–165.

Vallisneri, M., Vecchi, A., and Manfredi, C. (2004). The biological cycle of *Merlangius merlangus* (Linneus, 1758) (Osteichthyes, Gadidae) in the Northern and Middle Adriatic Sea. *Biol. Mar. Medit.* 11, 652–656.

Vitale, F., Clausen, L. W., and Chonchuir, G. N. (2019). *Handbook of fish age estimation protocols and validation methods.* ICES Cooperative Research Report No. 346. Available at: http://doi.org/10.17895/ices.pub.5221.

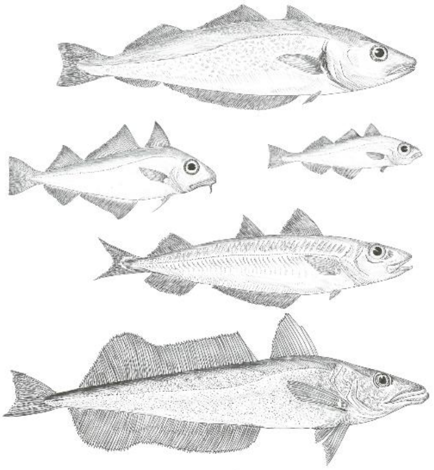
Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T. J. C., et al. (2002). Ecological response to recent climate change. *Nature* 416, 389–395.

Walther, G. R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., et al. (2009). Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.* 24, 686–693. doi: 10.1016/j.tree.2009.06.008.

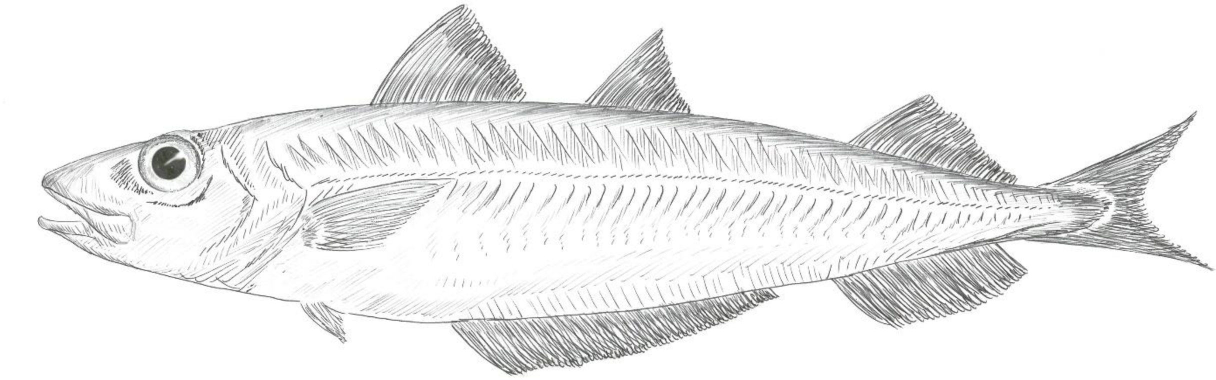
Yemane, D., Field, J. G., and Leslie, R. W. (2008). Indicators of change in the size structure of fish communities: A case study from the south coast of South Africa. *Fish. Res.* 93, 163–172. doi: 10.1016/j.fishres.2008.03.005.

Yildiz, T., and Saadet Karakulak, F. (2019). Age, growth and mortality of whiting (*Merlangius merlangus* Linnaeus, 1758) from the western black sea, turkey. *Turkish J. Fish. Aquat. Sci.* 19, 793–804. doi: 10.4194/1303-2712-v19_9_08.

Yildiz, T., Uzer, U., Yemişken, E., Karakulak, F. S., Kahraman, A. E., and Çanak, Ö. (2021). Conserve immatures and rebound the potential: stock status and reproduction of whiting (*Merlangius merlangus* [Linnaeus, 1758]) in the Western Black Sea. *Mar. Biol. Res.* 17, 815–827. doi: 10.1080/17451000.2021.2019787.



3 Case study II – Blue whiting (*Micromesistius poutassou*)



Life history traits and historical comparison of blue whiting (*Micromesistius poutassou*) growth performance from the western Pomo/Jabuka Pits area (central Adriatic Sea)

Federico Calì[1,2,3,4], Mario La Mesa[4], Fortunata Donato[2], Carlotta Mazzoldi[3], Michela Martinelli[2], Alberto Santojanni[2]

[1]Department of Biological, Geological, and Environmental Sciences (BiGeA), Alma Mater Studiorum - University of Bologna, Italy

[2]National Research Council - Institute for Marine Biological Resources and Biotechnologies (CNR-IRBIM) Ancona, Italy

[3]Department of Biology, University of Padova, Italy

[4]National Research Council - Institute of Polar Sciences (CNR-ISP) Bologna, Italy

Published in *Frontiers in Marine Science* 10:1291173 (November 2023); https://doi.org/10.3389/fmars.2023.1291173

Abstract

Although fishing is considered the primary cause of the decline in fish populations, increasing evidence of the significant role of climate change has been provided recently in the Mediterranean Sea, which shows one of the highest warming trends in the world. In this area, the most important environmental driver is represented by the increase in seawater temperature. Though several studies have addressed the effects of sea warming on thermophilic species, little attention has been paid to cold-water species. Among these, blue whiting (*Micromesistius poutassou*) constitutes one of the most important traditional fisheries resources in the northern part of the basin, particularly in the central Adriatic Sea. This area has experienced intense fishing exploitation by the Italian and Croatian fishing fleets. Since 2015, the Pomo/Jabuka Pits area, the fleets' main fishing ground, has been subject to a series of fishing regulations over time and space.

In the present study, we investigated the age structure and growth performance (by means of otoliths) of blue whiting, comparing samples collected during 1985–86 and 2020–21 in the Pomo/Jabuka Pits. Our results show that the 2020–21 blue whiting specimens had a lower length-at-age compared to 1985–86. The asymptotic length estimate decreased from 29 cm TL in 1985–86 to 25 cm TL in 2020–21. The pattern observed might be related to a modification in the cold and dense water formation dynamics in the northern Adriatic Sea, as a consequence of climate change, resulting in higher temperatures and lower nutrient and oxygen exchange, which may have hampered the optimal growth of the species. Moreover, data on the historical trend of landings from the Adriatic Sea reveals a clear decline in catches starting from 2000 onwards. Although the introduction of a fishing ban in the Pomo/Jabuka Pits was an important milestone, the abundance of this species in the area remains at low levels, highlighting a potentially alarming situation for the stock of blue whiting in the central Adriatic Sea.

Keywords: Adriatic Sea, Pomo Pits, climate change, growth, blue whiting, cold-water species

3.1 Introduction

Knowledge of life history traits and fish population dynamics represents a key issue in understanding how commercially exploited species cope with human-induced stressors, such as climate change and fishing (Hidalgo et al., 2022). This is particularly true for those showing narrow thermal ranges and distributions restricted to small areas, such as the cold-adapted species living in relatively deep waters of the Mediterranean Sea (Lloret et al 2021). Among them, one of the most important fishing resources is blue whiting, *Micromesistius poutassou* (Risso, 1827), whose fishery was the third most important worldwide at the beginning of the twenty-first century (FAO, 2011). This mesopelagic gadoid is broadly distributed along the continental slope of the North Atlantic and the Mediterranean Sea, inhabiting the areas of continental slope and shelf from 150 to more than 1000 m (Bailey, 1982). It is known that this species undergoes seasonal migration in the North Atlantic, moving towards the northern edge of its distribution (Faroes, Iceland, and Norway) during the summer (Cohen, 1990). In the Mediterranean Sea, there are no indications of seasonal migrations, although it has been observed that the species performs diel vertical migrations and is captured more efficiently during daylight when it is closer to the bottom than at night (Martin et al., 2016). The spawning of this species occurs at temperatures between 11−13 °C, which represent the minimum values in the Mediterranean Sea. While in the North Atlantic, the spawning season starts in January showing a wide temporal lag in relation to the latitudinal temperature gradient (Bailey, 1982), in the Mediterranean Sea it is restricted between January and March (Froglia and Gramitto, 1981; Serrat et al., 2019). Despite cold-water species living in deep habitats usually exhibit slow growth and late maturity (Lloret et al., 2021), the Mediterranean blue whiting shows fast growth and early maturity, being sexually mature at the end of the first year of life at around 20 cm TL (Froglia and Gramitto, 1981; Serrat et al., 2019, Mir- Arguimbau et al., 2020).

The blue whiting is the most important commercial species among gadids in the Mediterranean Sea and one of the most important traditional fishery resources in the northern areas of the basin (Gulf of Lions, Catalan, Ligurian, Adriatic, and Aegean Seas). The northern sectors of the Mediterranean Sea are key regions where intermediate and deep-water convection is regularly observed, leading to vertical recirculation, which is essential to sustain the Mediterranean thermohaline circulation (Roether et al., 1996). In particular, these cold areas contribute substantially to the deep-water formation and among them the Adriatic Sea plays a key role, being the area where the eastern Mediterranean Deep Water originates (Pollack, 1951). Here, during winter, low temperatures combined with the strong and dry north-easterly wind (Bora) trigger the formation of cold and dense waters in the northern part, which deepen and move southward carrying oxygen and nutrients to the deep layers, first reaching the middle Adriatic depression (Pomo/Jabuka Pits) and then the Bari Canyon (southern Adriatic) (Marini et al., 2016). Consequently, climate variations occurring in these regions can have huge impacts not only on the local circulation system but also at the Mediterranean scale, with serious consequences for the marine ecosystems, whose health status depends on the functioning of the cold-water generation system. Furthermore, the Adriatic Sea is one of the most exploited basins by trawl fisheries at a global scale (Pitcher et al., 2022) and the combined effect of fishing and climate change could represent a major threat to the long-term maintenance of the locally relevant cold-water species (e.g., whiting - *Merlangius merlangus*, blue whiting – *M. poutassou*, sprat – *Sprattus sprattus*, turbot – *Scophthalmus maximus).* Among these species, the blue whiting underwent the most dramatic decline in landings in the Adriatic Sea, showing an 80–90% decline from the 1980s to 2010s (FAO, 2020). Although the stock status of this species is not routinely assessed, and validated stock assessments are not available for this area, it could be hypothesized that the stock underwent high exploitation rates over the last decades. Indeed, the northern and central Adriatic Sea was identified as the most exploited in the Mediterranean area, showing values of fishing mortality higher than the fishing mortality at Maximum Sustainable Yield for almost all assessed commercial stocks(Colloca et al., 2017, FAO-GFCM 2020). Recent studies recognized the effects of climate change on the productivity potential of several stocks (Free et al., 2019; Moullec et al., 2019), indicating stocks could be negatively affected by increased sea temperatures, although the response is species-specific. In fact, despite the introduction of regulations to reduce the fishing effort (e.g., EU Regulation 1967/2006) among the EU countries through fishing capacity and effort limitations, regulation of mesh size, and spatial/temporal closures, the Mediterranean fisheries resources did not show signs of recovery (Cardinale et al., 2017).

The main fishing ground for blue whiting is located in the Pomo/Jabuka Pits, characterized by muddy seafloors sloping down to 270 m and delimiting one of the largest continental shelves in the Mediterranean and Black Sea (Marini et al., 2016). As one of the most important fishing grounds within the basin, this area has been exploited by both Italian and Croatian fisheries (mainly bottom trawlers) targeting the Norway lobster (*Nephrops norvegicus*) and European hake (*Merluccius merluccius*). Stable bottom temperatures (12−15 °C) and weak bottom currents make this area one of the main nursery grounds of the Mediterranean Sea for many species (Druon et al., 2015) and, thanks to the presence of ideal conditions for fish spawning, feeding and/or growth to maturity, it has been identified as an essential fish habitat (de Juan and Lleonart, 2010). Consequently, after a long discussion about the establishment of a fishing ban in the area, the first partial closure applied toward trawling activities was approved in July 2015, followed by other spatial and temporal regulations (Ministerial Decrees 03/07/2015 and 20/07/2016; Ministerial Decrees 19/10/2016 and 01/06/2017). A Fishery Restricted Area was established in 2018, identifying a fishery-ban zone and two buffer zones where trawling is limited to a small number of authorized vessels with a working-time limit (FAO-GFCM, 2017; MIPAAF, 2017). Although previous studies attempted to investigate the biology of blue whiting in this area (Froglia and Gramitto, 1981), several aspects of the life history of this species are still unknown. Moreover, considering the introduction of management measures, there is a critical need to evaluate the effectiveness of these measures on the species inhabiting the area (Chiarini et al., 2022).

Based on these premises, this study aims at 1) determining whether differences are present in the age structure and growth performance between samples of blue whiting collected in the Pomo/Jabuka Pits area with a time interval of 35 years; 2) updating and providing new insights into the biological cycle of blue whiting in the Adriatic Sea; 3) discussing the potential effects of fishing and climate change on this species.

3.2 Materials and Methods

3.2.1 Sampling

The sampling activity was carried out in the central Adriatic Sea at depths between 100 and 250 m around the western side of the Pomo/Jabuka Pits. Samples were collected in 2020–21 from landings of the San Benedetto Del Tronto and Giulianova fishing fleets (Figure 3.1) (Italian-type bottom otter trawl, 40 mm mesh size at the codend) and in

1985–86 from research cruises on board the research vessel S. Lo Bianco (Italian-type bottom otter trawl, 30 mm mesh size at the codend). The former sampling was carried out in July, October, November, December 1985, and July 1986; the latter in November 2020, February, March, April, July, and December 2021, and aimed to obtain at least 40–60 specimens per sample (representative of the whole size range). Samples were stored in cooling containers and transferred to the laboratory for further processing. In April 2021, an extra sampling activity was performed in the same area onboard the research vessel G. Dallaporta during the "Monitoraggio Pomo 2021" survey (Martinelli et al., 2021) to collect exclusively juveniles coming from the latest reproductive event, the so-called young-of-the-year (YOY), using an experimental bottom otter trawl (12 mm mesh size at the codend).

Total length (TL) to the nearest mm, total weight (TW) to the nearest 0.1 g, and gonad weight (GW, only in 2020–21) to the nearest 0.01 g were recorded for each specimen. The sagittal otoliths were removed, cleaned, and stored dry in vials for aging purposes. Sex was assigned macroscopically in specimens ≥16 cm TL.

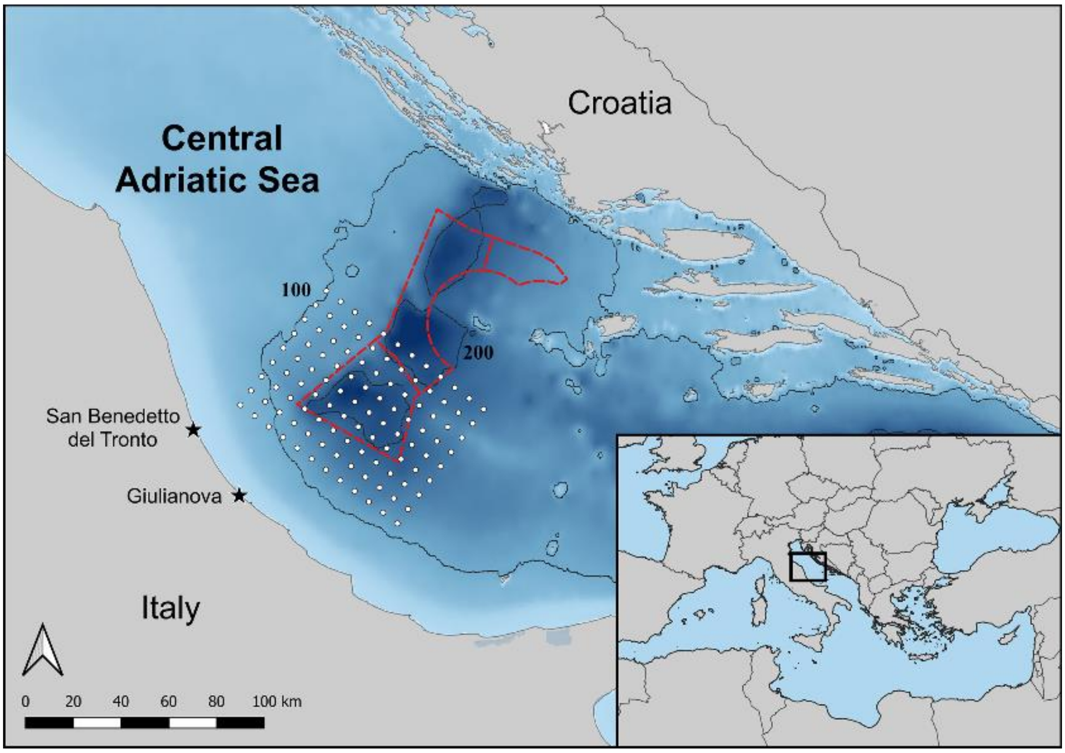


Figure 3.1. Map of the Central Adriatic Sea with bathymetric lines (100 and 200 meters), showing the location of the Pomo/Jabuka Pits Fishery Regulated Area (red dotted line) and blue whiting fishing ground (grey dotted area).

3.2.2 Age estimation

To enhance the contrast between translucent and opaque zones, otoliths were soaked in fresh water for at least 12 hours before reading. Both sagittae of each specimen were analyzed immersed in water over a black surface under reflected light. The *sulcus acusticus* was set facing downwards and the axis from the nucleus to the posterior margin of the otolith was used to count the annual rings. Readings were performed using a stereomicroscope (Leica MZ6) at low magnification (10x) connected to an image analysis system (Leica Flexacam C3 camera and Leica Application Suite software). Since the presence of up to two false rings in the sagittal otoliths within the first year of life was reported in this species (ICES, 2017), the diameter of the first annual ring and the diameter of false inner rings (when present) were measured, using the criterion proposed elsewhere (Mir-Arguimbau et al., 2020) to identify them and considering as true rings the ones between 8.3 and 9.3 mm. Age was estimated as the number of completely formed annuli, consisting of one opaque and one neighboring translucent ring (Figure 3.2). Samples were blindly read twice and in random order by two operators independently, without any indication of the date of capture, sex, or size of the specimens. The age and edge type (translucent or opaque) of each otolith sample were recorded and, in case of disagreement between readers, the sample was excluded. The edge condition (percentage of otoliths with an opaque margin for each month available) was analyzed to determine the periodicity and timing of ring formation, to verify the annual formation of the rings. To evaluate the aging precision (Campana, 2001), the index of average percent error (APE) (Beamish and Fournier, 1981) and the mean coefficient of variation (CV) (Chang, 1982) were calculated by comparing readings between readers. The age was estimated in years, establishing a conventional common birth date (1st February) according to the reproductive period of this species, from December to March (Serrat et al., 2019), and considering the capture date and the edge type. Since we observed only the opaque deposition in fish smaller than 12 cm, they were considered Young of the Year (YOY), and their age was calculated as a year fraction taking into account only the month of capture.

The von Bertalanffy growth function (VBGF) was used to describe the growth of the population:

$TL = L_\infty (1 - e^{-k(t-t0)})$

where TL is the length-at-age t, L_∞ is the asymptotic total length, k is the so-called Brody growth rate coefficient which determines how fast the fish approaches L_∞, and t_0 is the theoretical age at which length is zero. The von Bertalanffy growth function was fitted to the estimated age-length data set and the VBGF parameters were estimated for males, females, and sex combined. Unsexed juveniles smaller than 16 cm TL were included in both female and male growth curves to improve the model fit in the first period of growth. Differences in growth between sampling periods and sexes were tested by applying the Likelihood-ratio test (Kimura, 1980), while mean length-at-age was compared using the Wilcoxon signed-rank test (Wilcoxon, 1945). The Growth Performance Index ($\phi' = \log k + 2\log L_\infty$) was calculated to allow comparison among the growth parameters estimated in different populations of blue whiting and other gadids (Froese and Pauly, 2022). Growth statistical analyses were conducted using R (R Core Team, 2022), RStudio (Posit Team, 2022), and the packages *FSA* and *car* (Fox and Weisberg, 2019; Ogle et al., 2022).

Figure 3.2. *Micromesistius poutassou* sagittal otoliths (distal side up) under reflected light, showing four completely formed annuli (black dots). Female specimen of 26 cm TL captured in April 2021. D = dorsal axis; A = anterior axis; V = ventral axis; P = posterior axis.

3.2.3 Reproductive cycle

Reproductive traits were investigated only from the 2020–21 samples as these data were not available from the 1985–86 samples. The gonad maturity stage was evaluated using the standard ICES six-point scale proposed for whiting (*M. merlangus*) (ICES, 2008): 1) Immature; 2) Maturing; 3) Spawning; 4) Spent; 5) Resting/Skip of spawning; 6) Abnormal. The GW was used to calculate the gonadosomatic index (GSI = GW/TW × 100), to assess the reproductive investment and its temporal trend. The size-at-first sexual maturity L_{50}, i.e. the size at which 50% of individuals are mature, was estimated by considering 173 females and 261 males collected between November (when individuals in early maturation gonadal stages were observed) and March (when still a few spawning individuals were detected among post-spawner ones). Data on size and maturity stage were coupled to fit a predicted proportion of mature individuals (namely at stages 3 and 4) at size using a logistic model using R (R Core Team, 2022), RStudio (Posit Team, 2022), and the package *FSA* (Ogle et al., 2022). The Condition Factor (CF) was calculated using the following relationship, $CF = 10^2 (TW/TL^b)$, where b is 3 or ≠ 3 in the case of isometric or allometric growth, respectively (Bolger and Connolly, 1989). Differences in CF values between sexes and sampling periods were tested by the Mann-Whitney test.

3.3 Results

3.3.1 Fish samples

The size ranges of the samples were between 12–38 cm TL and 6–32 cm TL in 1985–86 and 2020–21, respectively. The total number of specimens analyzed was 193 (83 females, 85 males, 25 unsexed) in 1985–86 and 453 (173 females, 261 males, 19 unsexed) in 2020–21. The length-frequency distributions (LFDs) were different in the two sampling periods (two samples Kolmogorov–Smirnov test, $p < 0.05$), showing a higher proportion of individuals larger than 28 cm TL in 1985–86 (Figure 3.3A). In 2020–21 the modal class was comparable between males and females at around 22 cm TL (Figure 3.3B). Comparing the mean CF calculated for the same size classes (in cm) in both sexes and sampling periods, CF was higher in the 1985–86 sample (mean ± SD = 1.04 ± 0.13) compared to 2020–21 (mean ± SD = 0.98 ± 0.07) (Mann-Whitney test, p < 0.05), while no difference was found between sexes (Mann-Whitney test, p = 0.29) in both samplings.

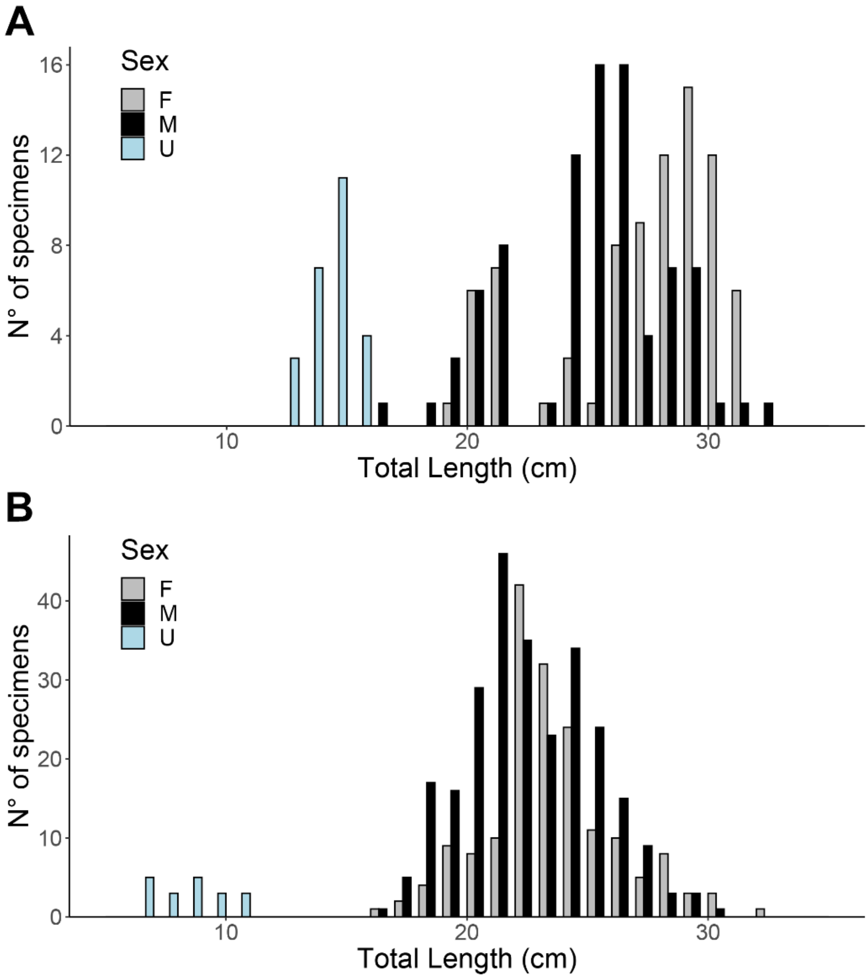


Figure 3.3. Length-frequency distribution (LFD) of *Micromesistius poutassou* from the Pomo/Jabuka Pits. F = females; M = males; U = Unsexed. (A) 1985–86; (B) 2020–21.

3.3.2 Growth and age structure

The otolith edge-zone analysis over the months covered by both sampling periods revealed that the opaque zone was laid during the warmer months, while the hyaline zone was observed during winter and early spring (Supplementary Figure 3.1), confirming the annual deposition of one opaque ring plus one translucent ring. The highest percentage of opaque deposition was observed in July, reaching values above 90% in both samplings (but it should be noticed that there were no samples in May-June and August-September). The average percentage error (APE) and the coefficient of variation (CV) were low, respectively 0.7% and 1.0%, indicating high precision of age readings. The age classes obtained from otolith readings of the selected subsamples were seven and 10 in 1985–86 (age range 0–8) and 2020–21 (age range 0–9), respectively. Significant differences were found in the mean length-at-age calculated for the two populations in both sexes, particularly in ages classes between 0 and 3 years (Wilcoxon signed-rank test; Z = 2.02, $p < 0.1$), with the 1985–86 samples showing higher values than 2020–21 across the groups (Supplementary Figure 3.2). The age-length keys of males, females, and unsexed specimens are reported in Tables 3.1 and 3.2.

Based on the likelihood ratio test on the estimated VBGF parameters, the 1985–86 sample showed higher values of L_∞ and lower values of k compared to 2020–21 (Table 3.3 and Supplementary Table 3.1; Figure 3.4). Males attained lower L_∞ than females in both populations, as expected considering the sexual dimorphism in size, which was barely noticeable in the 2020–21 sample compared to 1985–86 (Table 3.3; Figure 3.4).

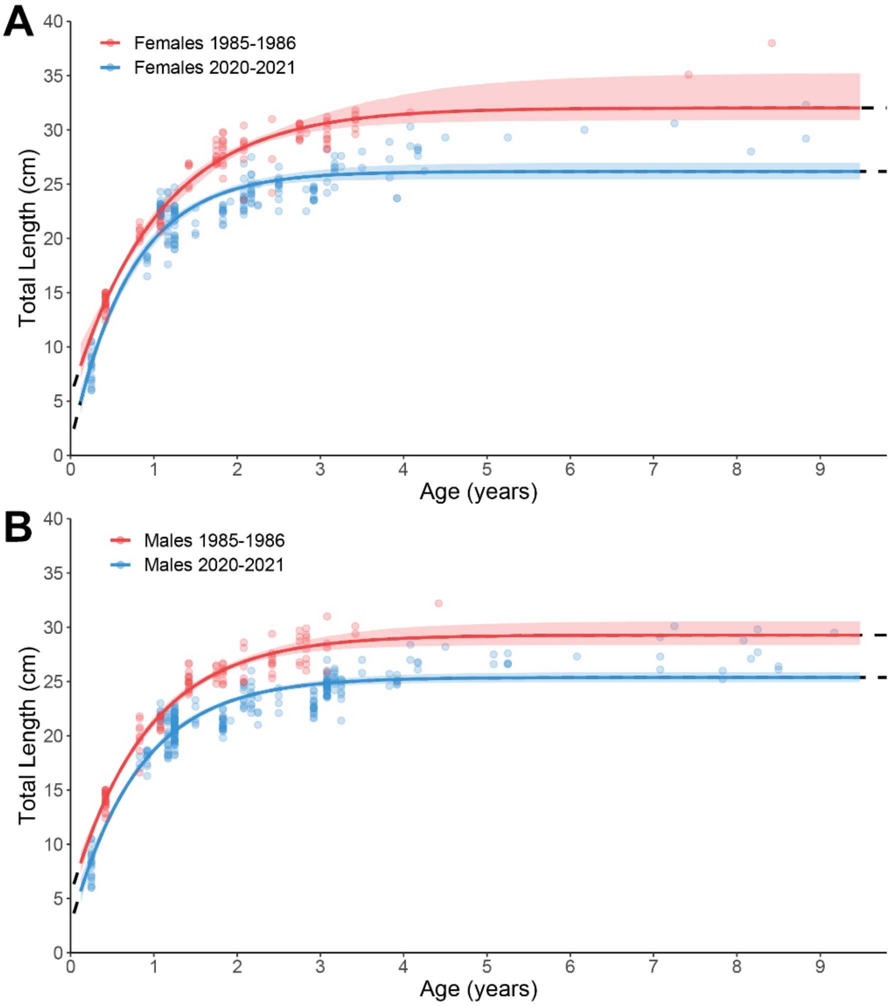


Figure 3.4. Von Bertalanffy growth curves for *Micromesistius poutassou* females (A) and males (B) sampled in 1985–86 (red) and 2020–21 (blue).

Table 3.1. Age-length key for females, males, and unsexed specimens based on otolith readings of *Micromesistius poutassou* sampled in 1985–86 from the Pomo/Jabuka Pits. N = total number; TL = total length; SD = standard deviation.

	Females											Males										
Age (years)	0	1	2	3	4	5	6	7	8	9	N	0	1	2	3	4	5	6	7	8	9	N
Total Length (cm)																						
16											-	1										1
17											-											-
18											-	1										1
19	1										1	3										3
20	5	1									6	2	4									6
21	2	5									7	2	6									8
22											-											-
23			1								1		1									1
24		2	1								3		11	1								12
25		1									1		11	4	1							16
26	1	7									8		8	8								16
27		7	2								9			4								4
28		5	4	3							12			5	2							7
29		5	6	4							15			6	1							7
30			7	5							12				1							1
31			1	4	1						6				1							1
32											-					1						1
33											-											-
34											-											-
35								1			1											-
36											-											-
37											-											-

38									1		1											-
N	9	33	22	16	1	-	-	1	1	-	83	9	41	28	6	1	-	-	-	-	-	85
TL mean (cm)	21.2	26.4	28.9	30.0	31.6	-	-	35.1	38	-		20.2	24.4	27.4	28.8	32.2	-	-	-	-	-	
TL SD	2.2	2.7	1.9	1.1	-	-	-	-	-	-		1.8	2.0	1.5	1.8	-	-	-	-	-	-	

	Unsexed	
Age (years)	0	N
Total Length (cm)		
12	3	3
13	7	7
14	11	11
15	4	4
N	25	25
TL mean (cm)	14.1	
TL SD	0.7	

Table 3.2. Age-length key for females, males, and unsexed specimens based on otolith readings of *Micromesistius poutassou* sampled in 2020–21 from the Pomo/Jabuka Pits. N = total number; TL = total length; SD = standard deviation.

	Females											Males										
Age (years)	0	1	2	3	4	5	6	7	8	9	N	0	1	2	3	4	5	6	7	8	9	N
Total Length (cm)																						
16	1										1	1										1
17	1	1									2	4	1									5
18	4										4	8	9									17
19		9									9		16									16
20		8									8		29									29
21		10									10		42	3	1							46
22		36	6								42		16	19								35
23		12	18	2							32		3	11	9							23
24		4	18	2							24			9	25							34
25			9	2							11			1	22				1			24
26			2	7	1						10			1	3	3	4		2	2		15
27			1	3	1						5				2	1	2	1	1	2		9
28				3	4				1		8					2				1		3
29					1	1			1		3								1	1	1	3
30					1		1	1			3								1			1
31											-											-
32									1		1											-
33											-											-
34											-											-
35											-											-
36											-											-
37											-											-

38											-										-
N	6	80	54	19	8	1	1	1	3	-	173	13	116	44	62	6	6	1	6	6	1	261
TL mean (cm)	17.9	21.9	24.2	26.3	28.3	29.3	30	30.6	29.8	-		17.9	20.8	23.2	24.8	27.2	26.9	27.3	27.3	27.7	29.5	
TL SD	0.7	1.4	1.1	1.5	1.2	-	-	-	2.2	-		0.7	1.2	1.0	0.9	0.9	0.5	-	1.9	1.4	-	

	Unsexed	
Age (years)	0	N
Total Length (cm)		
6	5	5
7	3	3
8	5	5
9	3	3
10	3	3
N	19	19
TL mean (cm)	8.1	
TL SD	1.5	

Table 3.3. Von Bertalanffy growth parameters estimates and their standard errors (SE) of *Micromesistius poutassou* from the Pomo/Jabuka Pits and growth performance index (φ’) for combined sexes, females and males of both sampling periods. The growth rate coefficient (k) and theoretical age at which the average length is zero (t_0) are expressed in years^{-1} and years, respectively. L_∞ = asymptotic total length.

	L_∞ (cm)	SE	k	SE	t_0	SE	φ'
Combined sexes 1985–86	31.11	0.36	0.95	0.05	-0.22	0.03	3.06
Males 1985–86	29.31	0.25	1.08	0.08	-0.18	0.02	2.97
Females 1985–86	32.06	0.28	0.94	0.07	-0.19	0.02	2.98
Combined sexes 2020–21	25.63	0.16	1.31	0.04	-0.06	0.02	2.94
Males 2020–21	25.38	0.17	1.22	0.05	-0.08	0.02	2.89
Females 2020–21	26.16	0.26	1.38	0.08	-0.03	0.02	2.97

3.3.3 Reproductive cycle

Based on the macroscopic observation of gonad maturation and GSI monthly pattern, the spawning season of blue whiting in the study area took place from December to March, with a peak in February. The maximum GSI values were 8% and 3% in females and males, respectively, showing a marked difference in reproductive efforts between the sexes (Figure 3.5). Fitting the logistic model to the proportion of sexually mature specimens, size-at-first maturity (L_{50}) was estimated to be 18.9 ± 0.1 cm TL for males and 19.8 ± 0.3 cm TL for females (Supplementary Figure 3.3).

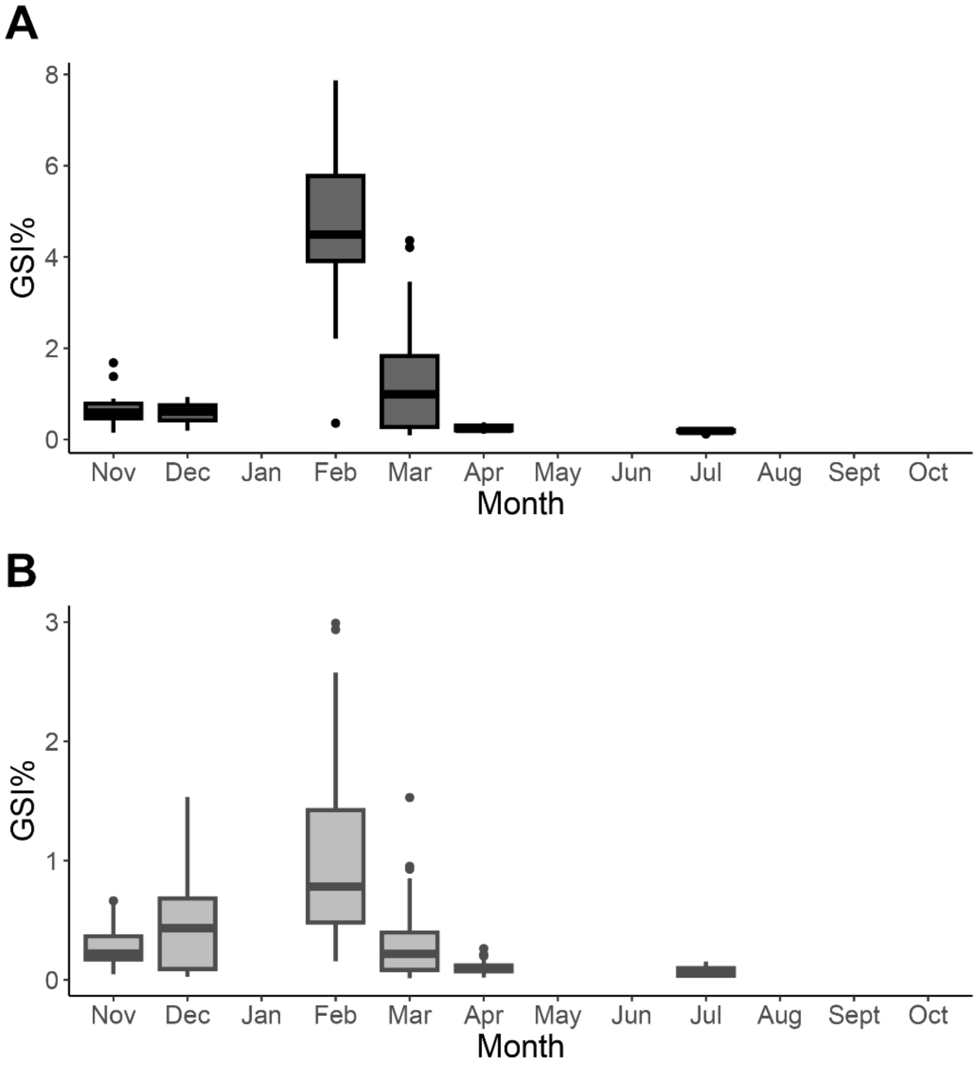


Figure 3.5. Temporal trend of the gonadosomatic index (GSI) for *Micromesistius poutassou* females (A) and males (B**)**. Note the different scales in y-axes.

Table 3.4. Population parameters of *Micromesistius poutassou* from different areas of the Mediterranean Sea and North Atlantic. L_{mat}= size-at-first sexual maturity; Age_{mat} = age-at-first sexual maturity; k = growth rate coefficient; t_0 = theoretical age at which the average length is zero; L_∞ = asymptotic total length.

	Source	Area	TL range (cm)	Age range (years)		L_∞ (cm)		k (years^{-1})		t_0 (years)		L_{50} (cm)		Age_{mat} (years)	
				F	M	F	M	F	M	F	M	F	M	F	M
Mediterranean Sea	Present study 1985–86	Adriatic Sea	12–38	0–8	0–4	32.1	29.3	0.94	1.08	-0.19	-0.18	-	-	-	-
	Present study 2020–21	Adriatic Sea	6–32	0–8	0–9	26.2	25.4	1.38	1.22	-0.03	-0.08	19.8	18.9	1	1
	Froglia and Gramitto, 1981[a]	Adriatic Sea	8–32	0–2*		31.9*		1.03*		-0.11*		21*		1*	
	Mir-Arguimbau et al., 2020	Gulf of Lions	3–39	0–8	0–7	38	33	0.73	0.80	-0.20	-0.30	18	18	1	1
	Orsi-Relini and Peirano, 1985	Ligurian Sea	5–37	0–7	0–5	40.5*		0.23 *		-1.27*		-		2	2
	Serrat et al., 2019	Gulf of Lions	13.4–38	-	-	-	-	-	-	-	-	19	19	-	-
North Atlantic	Silva et al., 1996	off Portugal	14–39	0–10*		-		-		-		19*		2*	
	Post et al., 2019	East Greenland	22–40	0–12*		114.7*		0.02*		-8.18*		-		-	
	Raitt, 1968	West Scotland	16–39	1–10+*		39.9*		0.15*		-3.51*		20*		2–4*	
	Raitt, 1968	Faroe	17–35	1–10+*		33.4*		0.23*		-2.94*		20*		2–4*	
	Raitt, 1968	Iceland	15–36	1–10+*		-		-		-		-		-	

* unsexed; [a] based on length-frequency distributions.

3.4 Discussion

The present study provides a detailed and updated picture of important life history traits of blue whiting in the central Adriatic Sea. Based on growth rates reflected in the samples collected over two sampling periods from the Pomo/Jabuka Pits, we highlight differences between the present and the late 1980s.

3.4.1 Biological parameters

Overall, the size ranges of blue whiting were smaller than previously observed in the same area (Froglia and Gramitto, 1980) and in comparison with other studies carried out in the Mediterranean Sea (Orsi-Relini and Peirano, 1985; Sartor, 1995; Serrat et al., 2019; Mir-Arguimbau et al., 2020) (Table 3.4). The possible explanations for the size reduction are discussed in the next section. As already reported for other gadids, the maximum size in the Mediterranean Sea is much smaller than in the North Atlantic (Mahe et al., 2016; Gonçalves et al., 2017; Mir-Arguimbau et al., 2020) (Table 3.4). To our knowledge, this study provides for the first time the VBGF parameters estimated through otolith readings in the Adriatic Sea. The maximum age estimated in the 2020–21 sample was far higher than that estimated in previous studies in the Adriatic Sea, which used LFDs to estimate VBGF parameters and reported only three age classes (Froglia and Gramitto, 1980). Conversely, our estimates of maximum lifespan were similar to those based on otolith readings reported from other areas of the Mediterranean Sea (Ligurian Sea, Orsi-Relini and Peirano 1985, and Gulf of Lions, Mir-Arguimbau et al., 2020), but smaller than those reported from the North Atlantic (Raitt, 1968; Post et al., 2019) (Table 3.4). The high proportion of opaque otolith margins observed in July of both sampling periods confirms that opaque deposition is associated with the fast-growing season, which occurs during warmer months. Although our samples did not cover the whole year, the analysis of the edge condition agrees with previous studies in the Mediterranean Sea (ICES, 2017; Mir-Arguimbau et al., 2020), allowing us to corroborate the annual ring formation. It is worth noting that the estimated k values were the highest and t_0 the closest to 0 ever reported from the Mediterranean Sea (Maiorano et al., 2010; Mannini and Lanteri, 2017; Mir-Arguimbau et al., 2020) and North Atlantic (Bailey, 1982; Monstad, 1990; Magnussen, 2007; Froese and Pauly, 2022) (Table 3.4). The presence of juveniles caught in early spring-summer allowed a good fitting of the VBGF at the origin and contributed to the estimation of more accurate values of these parameters. Usually, data regarding the length-at-age during the early life stages (when growth is fastest) is not available. A lack of data may lead to an underestimation of k values and could explain the discrepancies in growth parameter estimates between the present and previous studies (Supplementary Figure 3.4).

According to the analysis of samples from 2020–21, sexual maturity is reached within the first year of life in males and females, at 18.9 and 19.8 cm TL, respectively. Our estimates agree with previous observations carried out in the Adriatic Sea (Froglia and Gramitto, 1981) and are slightly higher compared to those of other areas of the Mediterranean Sea (Silva et al., 1996; Serrat et al., 2019; Mir-Arguimbau et al., 2020) (Table 3.4). As expected, they are lower than those estimated in the North Atlantic (Bailey, 1982; ICES, 2004). The difference observed in the comparison of maturity size with other Mediterranean areas could be related to a bias in the sampling strategy, as we were not able to collect samples during the spawning peak in January and we also had a limited number of specimens < 20 cm TL. Macroscopic observations on gonads and GSI trends indicated clearly that spawning took place in winter, in agreement with the pattern observed in general in the Mediterranean Sea (Froglia and Gramitto, 1981; Serrat et al., 2019; Mir-Arguimbau et al., 2020). The highest mean values of GSI were reached in February, 5% for females and 1% for males, confirming the different reproductive efforts between sexes (Serrat et al., 2019).

3.4.2 Historical comparison

The historical comparison highlighted some differences in the growth performance and age structure between the 1985–86 and 2020–21 samples. In particular, the 2020–21 sample was characterized by specimens with a lower mean length-at-age across the age classes (Figure 3.5), and a higher proportion of older age classes (9% was 4 or more years old), compared to 1985–86. Comparing the age-length key, a stronger slowdown in growth seemed to occur after the Year Class four in 2020–21. The lack of old specimens in the 1985–86 sampling prevented us from making robust assumptions for the comparison over the entire lifespan of this species. However, the length-at-age data of the only two specimens older than four years from the 1985–86 sample allows us to hypothesize a possible decrease in the growth potential of blue whiting over the total investigated period. It is worth noting that the age readings of both sampling periods were performed by the same expert readers, making data comparison reliable and maximizing the reduction of methodological biases. The decrease in growth efficiency is further supported by comparing the CF between the sampling periods, indicating a higher energetic investment in body growth in 1985–86. A growing body of knowledge has linked a wide range of biological responses of marine organisms to climate change/environmental anomalies and fishing (Engelhard et al., 2014; Poloczanska et al., 2016; Diaz Pauli and Sih, 2017; Charbonneau et al., 2019) and it is well-known in literature that they played a primary role in the recent interdecadal dynamics of the Adriatic resources (Coll et al., 2009; Conversi et al., 2009; Barausse et al., 2011; Lotze et al., 2011; Fortibuoni et al., 2015, 2017; Sguotti et al., 2022). Body condition in harvested fish is known to be affected by the combined effects of environmental features, population density and fishing impact, with a species-specific and ontogenetic variation (Rueda et al., 2015). Similarly, the growth potential of a population may be strongly influenced by environmental factors, such as food supply and temperature (Magnussen et al., 2007), and/or by fishing exploitation (e.g., through the removal of larger/older individuals or the selection of fast-growing and early maturing specimens) (Bianchi et al., 2000; Shin et al., 2005; Hidalgo et al., 2012). Although the historical comparison is limited just to two sampling periods, our findings nevertheless raise intriguing questions regarding the nature of the changes in growth patterns observed, as they could be explained by one or a combination of the above-mentioned factors.

Given the positive correlation between primary productivity and forage fish abundance in the Adriatic Sea (Santojanni et al., 2006), as well as the gradual decrease in nutrient inputs over the last four decades (Marini and Grilli, 2023), a possible explanation for the decrease in growth performance could be related to a decrease in prey availability for blue whiting, which feeds on zooplankton and small planktivorous fish (Sartor et al., 1995). Another environmental change driver is represented by the rise in sea temperature in the Adriatic Sea (Supplementary Figure 3.5), which could have had direct negative effects by creating unfavorable thermal conditions that interfere with the metabolic functions of this cold-water species, as reported by Trenkel et al. (2015). This mechanism has recently been linked to a decrease in landings and abundance of blue whiting in other Mediterranean areas (Sbrana et al., 2019). Finally, the possible effect of fishing activity must be considered when explaining the reduction of length-at-age and specimens larger than 28 cm TL across our study-period (Supplementary Figures 3.2 and Figure 3.3), taking into account the long history of exploitation of the area as a fishing ground for the European hake and Norway lobster (Chiarini et al., 2022). Fishing is a size-selective process, determining higher mortality rates for the larger/older specimens and modifying the size structure of fish assemblages (Bianchi et al., 2000; Shin et al., 2005). As a result, it can determine evolutionary responses in harvested populations towards favoring a smaller maximum size and size/age at maturity, and therefore a higher probability of reproducing before being caught (Trippel, 1995).

As stated, these data must be interpreted with caution because we used two punctual sampling periods, that are not representative of a real trend over the last decades. Indeed, the adaptive phenotypic plasticity may determine changes in population life history traits even on a short-term scale, depending on the environmental context (Hidalgo et al., 2014). Such natural oscillations occur not only in biological parameters but also in abundance as a result of environmental variations and fishing exploitation (Martin et al., 2016; Mir-Arguimbau et al., 2022). Another limitation of this study is represented by the small sample size of the 1985–86 sample (not fully representative of the population) and the different methodologies used in the two periods. The different selectivity of the net due to different mesh sizes represents a limit to properly compare the LFDs and size structure of the samples, even if we can assume a comparable selectivity on adult specimens since it was reported that juveniles smaller than 20 cm TL account for a large proportion of catches in otter bottom trawler deploying a 40 mm mesh size at the codend (Mir-Arguimbau et al., 2022).

Despite the noted constraints, the decrease of length-at-age and asymptotic length together with the decline observed in the landing trend in the Adriatic Sea (Supplementary Figure 3.6) support the idea of a poor health status for the blue whiting population in the Adriatic Sea, which is likely due to fishing exploitation and/or environmental constraints and is worthy of closer attention. Despite the restrictive measures established in 2015 in the Pomo/Jabuka Pits, there has been no evidence of a positive effect on the abundance of blue whiting (Chiarini et al., 2022). It could be possible that unfavorable environmental factors hamper the recovery of the stock and could threaten its long-term maintenance. Nevertheless, the presence in the 2020–21 sample of specimens close to the known maximum age for Mediterranean Sea populations (Fiorentino et al., 2003; Tsikliras and Stergiou, 2015) could represent an early signal of a recovery process made very slow by unfavorable environmental conditions, but further studies are needed to confirm or dismiss this hypothesis.

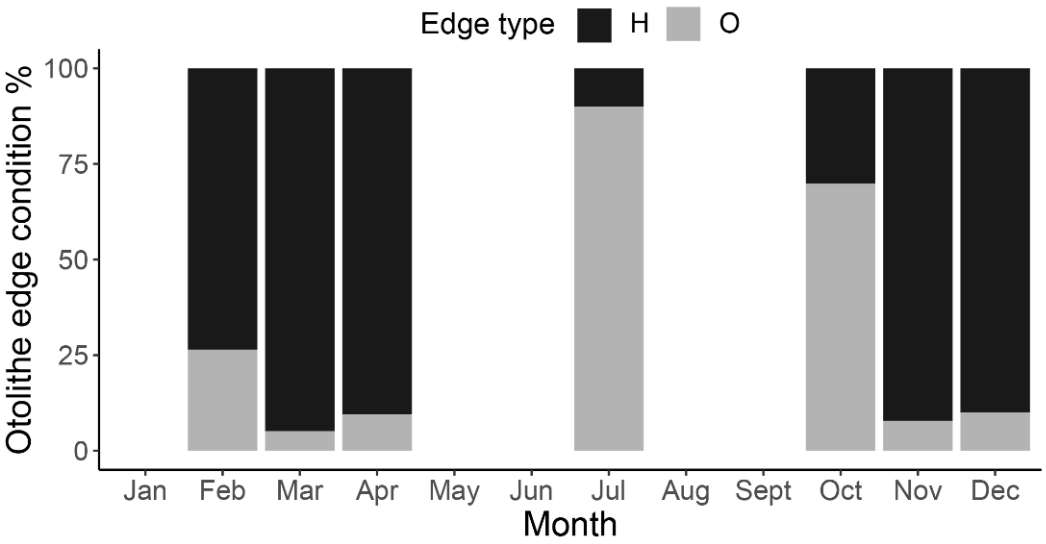
Acknowledgments

We thank all of the staff of the National Research Council (CNR) and the Hydrobiological Station Umberto D'Ancona (University of Padova), as well as the fishers involved for their essential contribution to the data collection and interpretation. We wish also to thank Dr. Carlo Froglia for his work in collecting data and otoliths that made the historical comparison possible and Jennifer Pytka for the English editing. We especially thank Aluizio Junior Gomes Filho and Luca Giaccaglia (EcoTechSystems), for kindly providing precious support in collecting the samples at landing sites. The research leading to these results was conceived under the International Ph.D. program "Innovative Technologies and Sustainable Use of Mediterranean Sea Fishery and Biological Resources" (www.FishMed-PhD.org, accessed July 10, 2023). This study represents partial fulfillment of the requirements for the Ph.D. thesis of Federico Calì.

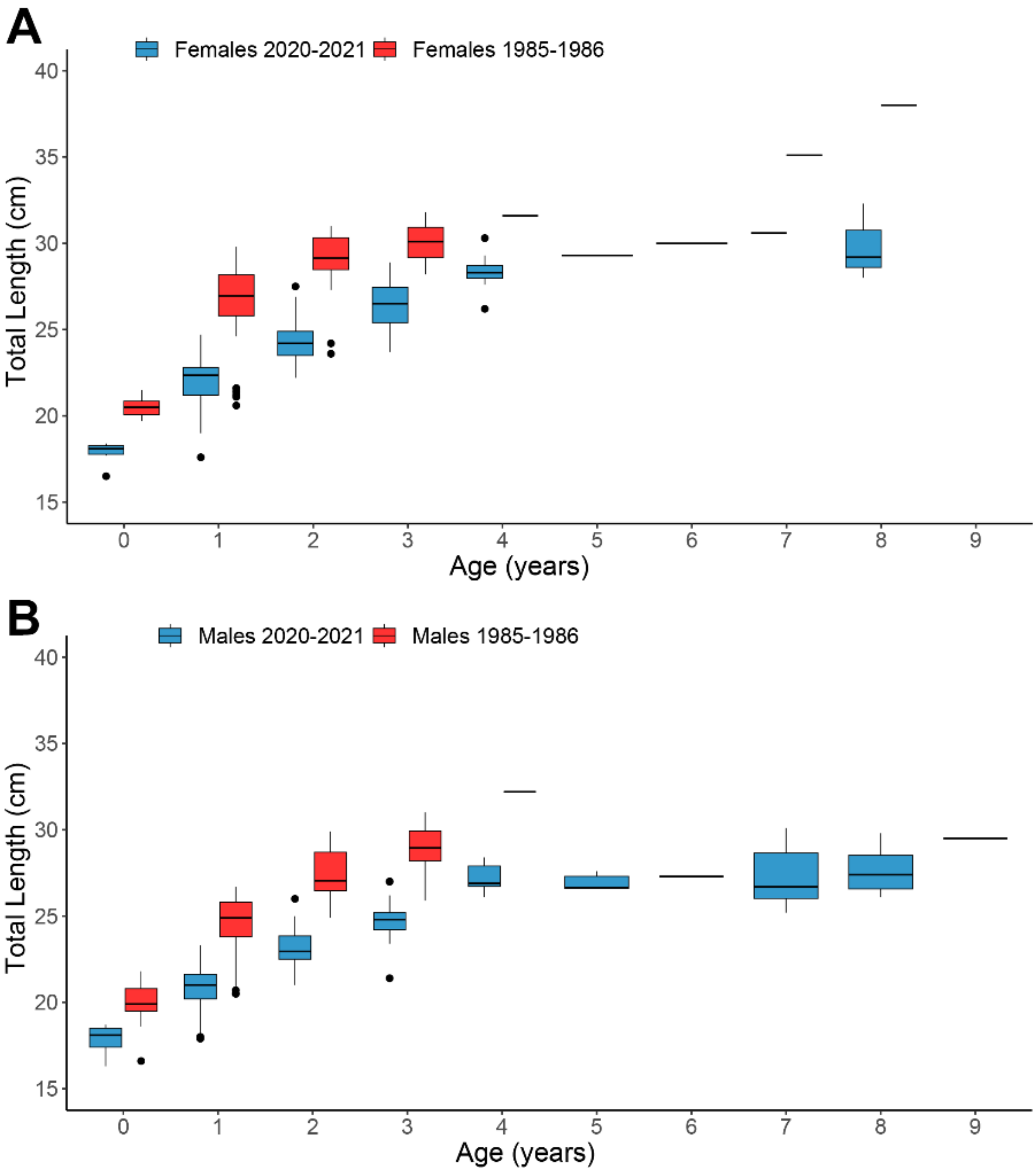
Supplementary material

Supplementary Table 3.1. Likelihood ratio test comparing the von Bertalanffy growth parameters estimated for sexes and sampling periods of *Micromesistius poutassou* from the Pomo/Jabuka Pits. Statistics are based on four null hypotheses, assuming that each parameter or a combination of them do not differ between sexes or sampling years. K = growth rate coefficient; t_0= theoretical age at which the average length is zero; L_∞ = asymptotic total length; df = degrees of freedom; * significant at α = 0.05; ** significant at α = 0.01; ns = not significant.

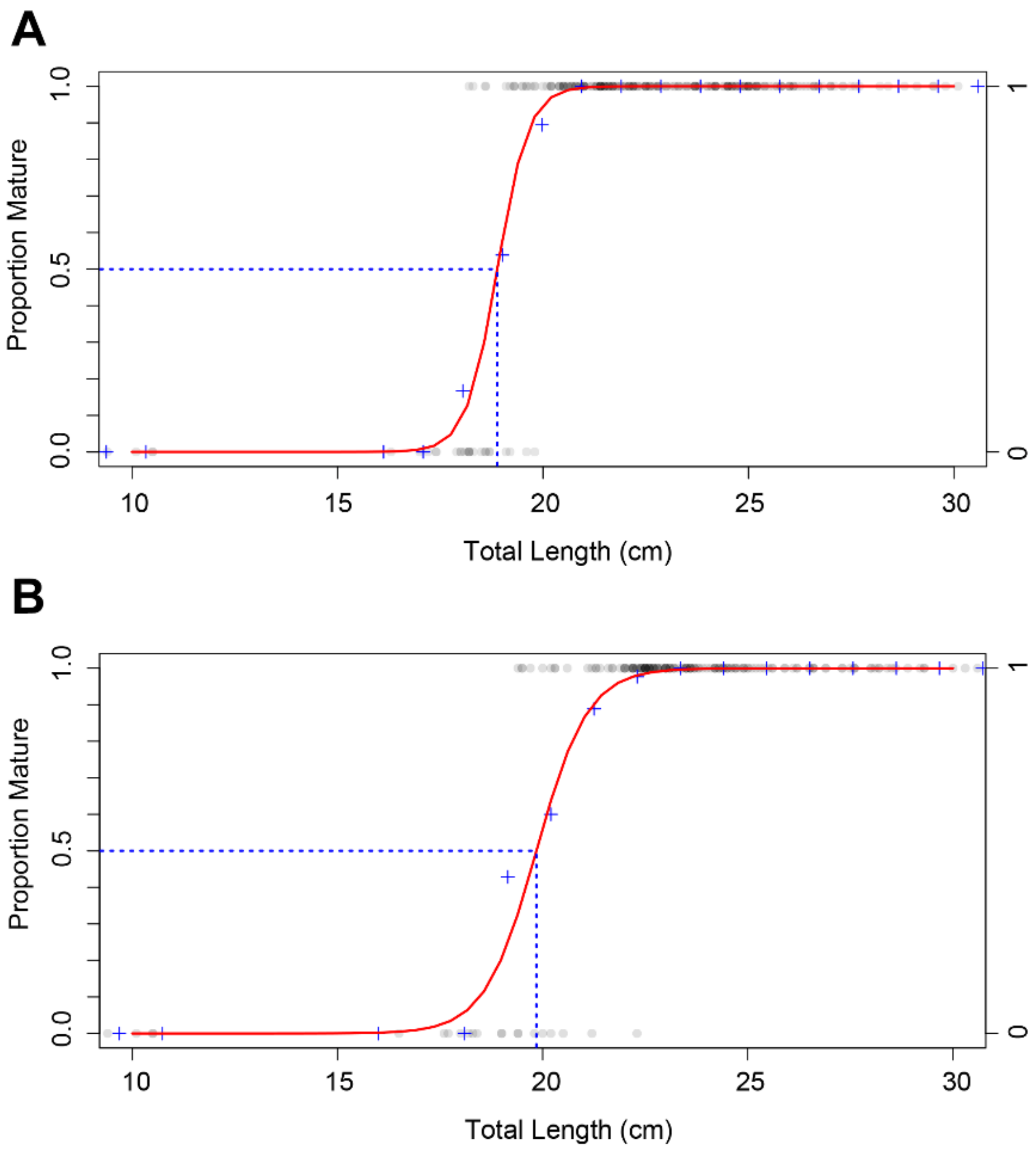
	Parameter	χ^2	df	p-value
Females vs males 1985-86	all	51.5	3	**
	L_∞	15.9	1	**
	k	1.6	1	ns
	t_0	0.02	1	ns
Females vs males 2020-21	all	46.2	3	**
	L_∞	5.6	1	*
	k	2.6	1	ns
	t_0	2	1	ns
Females 1985-86 vs 2020-21	all	201.9	3	**
	L_∞	97.6	1	**
	k	11.5	1	**
	t_0	8.6	1	**
Males 1985-86 vs 2020-21	all	247.9	3	**
	L_∞	82.1	1	**
	k	1.5	1	ns
	t_0	3.7	1	ns



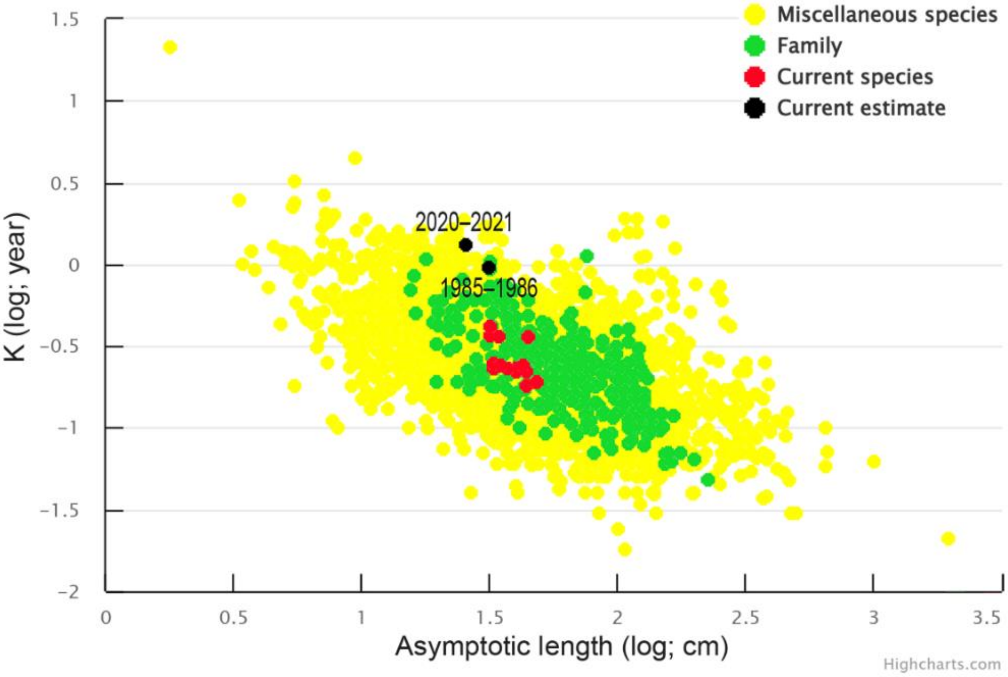
Supplementary Figure 3.1. Monthly proportion of *Micromesistius poutassou* individuals showing otoliths with opaque (O; grey) or hyaline margin (H; black).



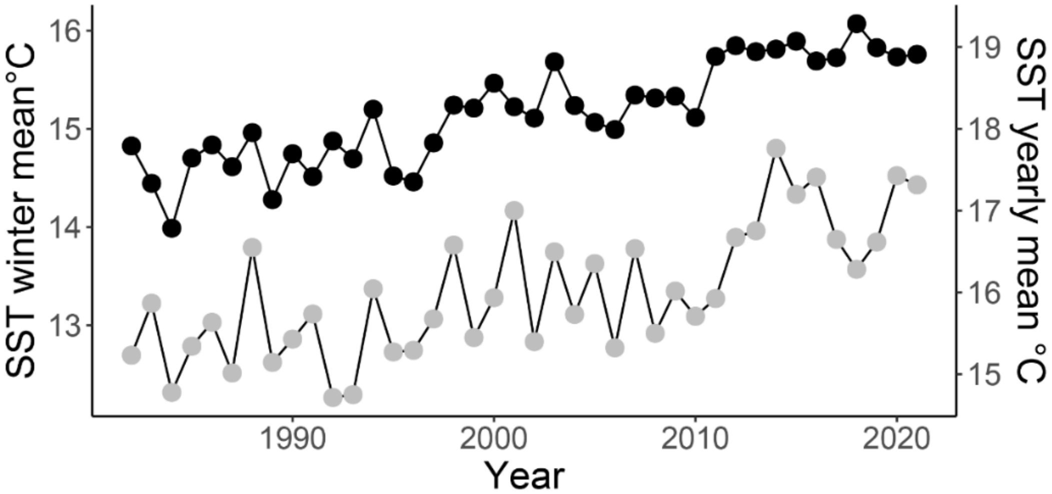
Supplementary Figure 3.2. Boxplots of length-at-age of *Micromesistius poutassou* females (A) and males (B) sampled in 1985–86 (red) and 2020–21 (blue).



Supplementary Figure 3.3. Sexual maturity ogives of males (A) and females (B) of *Micromesistius poutassou.* The dotted vertical blue line intercepting the x-axis indicates the size at which 50% of individuals are mature (L_{50}).

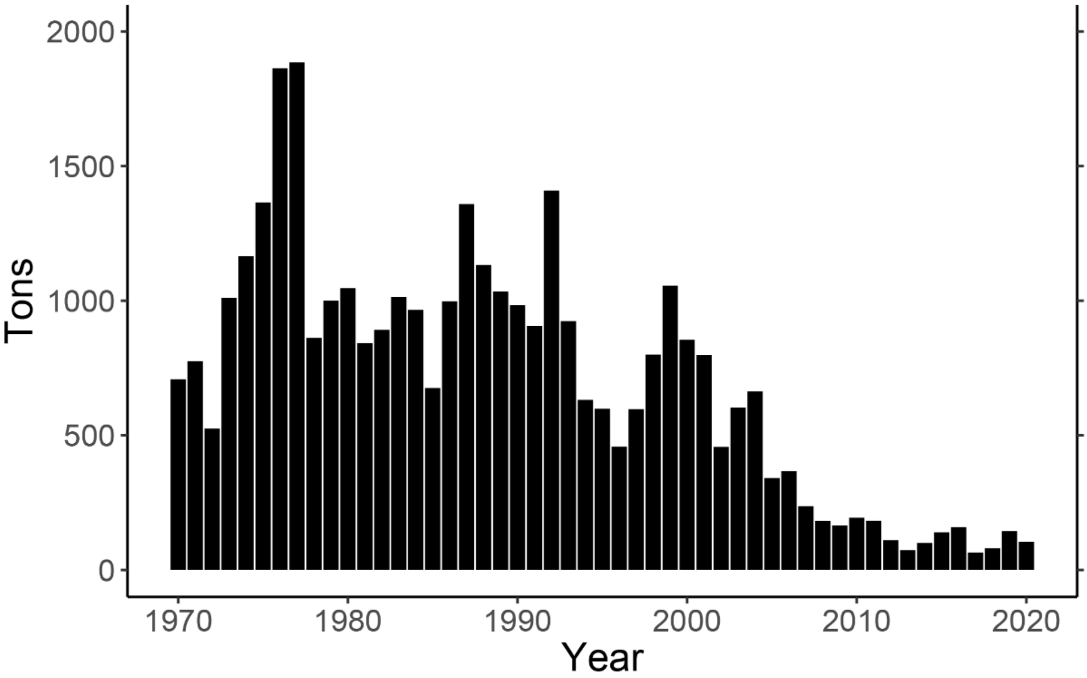


Supplementary Figure 3.4. Auximetric plot for *Micromesistius poutassou* allowing to compare the asymptotic length (L∞) and growth rate coefficient (k) parameters estimated in this study (black) with other estimates obtained for the same species (red), other gadids (green), and other bony fish (yellow). Modified from Froese and Pauly, 2022.



Supplementary Figure 3.5. Temporal trend of the mean annual (black) and winter (grey; between January and March) values of surface temperature (SST) in the Pomo/Jabuka Pits area from 1982 to 2021. Satellite data from Copernicus Marine

Service, Mediterranean Sea - High Resolution L4 Sea Surface Temperature Reprocessed. https://doi.org/10.48670/moi-00173.



Supplementary Figure 3.6. Landing temporal trend of *Micromesistius poutassou* from the Adriatic Sea, obtained from FAO official landings (FAO, 2020).

References

Bailey, R. S. (1982). The population biology of blue whiting in the North Atlantic. *Adv. Mar. Biol.* 19, 257–355. doi: 10.1016/S0065-2881(08)60089-9.

Barausse, A., Michieli, A., Riginella, E., Palmeri, L., and Mazzoldi, C. (2011). Long-term changes in community composition and life history traits in a highly exploited basin (northern Adriatic Sea): The role of environment and anthropogenic pressures. *J. Fish Biol.* 79, 1453–1486. doi: 10.1111/j.1095-8649.2011.03139.x.

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* 38, 982–983.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., et al. (2000). Impact of fishing on size composition and diversity of demersal fish communities. *ICES J. Mar. Sci.* 57, 558–571. doi: 10.1006/jmsc.2000.0727.

Bolger, T., and Connolly, P. L. (1989). The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* 34, 171–182. doi: 10.1111/j.1095-8649.1989.tb03300.x.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* 59, 197–242. doi: 10.1006/jfbi.2001.1668.

Cardinale, M., Osio, G. C., and Scarcella, G. (2017). Mediterranean Sea: A failure of the European fisheries management system. *Front. Mar. Sci.* 4, 72. doi: 10.3389/fmars.2017.00072.

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.* 39, 1208–1210.

Charbonneau, J. A., Keith, D. M., and Hutchings, J. A. (2019). Trends in the size and age structure of marine fishes. *ICES J. Mar. Sci.* 76, 938–945. doi: 10.1093/icesjms/fsy180.

Chiarini, M., Guicciardi, S., Zacchetti, L., Domenichetti, F., Canduci, G., Angelini, S., et al. (2022). Looking for a simple assessment tool for a complex task: Short-term evaluation of changes in fisheries management measures in the Pomo/Jabuka Pits area (Central Adriatic Sea). *Sustain.* 14, 7742. doi: 10.3390/su14137742.

Cohen, D. M., Inada, T., Iwamoto, T., and Scialabba, N. (1990). FAO Species Catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date*. FAO Fish. Syn.* 125.

Coll, M., Santojanni, A., Palomera, I., and Arneri, E. (2009). Food-web changes in the Adriatic Sea over the last three decades. *Mar. Ecol. Prog. Ser.* 381, 17–37. doi: 10.3354/meps07944.

Colloca, F., Scarcella, G., and Libralato, S. (2017). Recent trends and impacts of fisheries exploitation on Mediterranean stocks and ecosystems. *Front. Mar. Sci.* 4, 244. doi: 10.3389/fmars.2017.00244.

Conversi, A., Peluso, T., and Fonda-Umani, S. (2009). Gulf of Trieste: A changing ecosystem. *J. Geophys. Res. Ocean.* 114, 1–10. doi: 10.1029/2008JC004763.

de Juan, S., and Lleonart, J. (2010). A conceptual framework for the protection of vulnerable habitats impacted by fishing activities in the Mediterranean high seas. *Ocean Coast. Manag.* 53, 717–723. doi: 10.1016/j.ocecoaman.2010.10.005.

Diaz Pauli, B., and Sih, A. (2017). Behavioural responses to human-induced change: Why fishing should not be ignored. *Evol. Appl.* 10, 231–240. doi: 10.1111/eva.12456.

Druon, J. N., Fiorentino, F., Murenu, M., Knittweis, L., Colloca, F., Osio, C., et al. (2015). Modelling of European hake nurseries in the Mediterranean Sea: An ecological niche approach. *Prog. Oceanogr.* 130, 188–204. doi: 10.1016/j.pocean.2014.11.005.

Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Glob. Chang. Biol.* 20, 2473–2483. doi: 10.1111/gcb.12513.

EU (2006). Council Regulation (EC) No 1967/2006 of 21 December 2006 Concerning Management Measures for the Sustainable Exploitation of Fishery Resources in the Mediterranean Sea, Amending Regulation (EEC) No 2847/93 and Repealing Regulation (EC) No 1626/94, EU.

FAO-GFCM (2020). The State of Mediterranean and Black Sea Fisheries 2020. General Fisheries Commission for the Mediterranean. Rome, Italy.

https://doi.org/10.4060/cb2429en.

FAO-GFCM (2017). Recommendation GFCM/41/2017/3 on the establishment of a fisheries restricted area in the Jabuka/Pomo Pit in the Adriatic Sea. Available at: https://www.fao.org/gfcm/decisions/en/.

FAO (2020). FishStatJ - Universal software for fishery statistical time series. Available at: https://www.fao.org/fishery/en/topic/166235/en.

FAO (2011). Review of the State of World Marine Fishery Resources. FAO Fisheries and Aquaculture Technical Paper No. 569, Rome, Italy.

Fiorentino, F., Gancitano, S., Giusto, G. B., and Rizzo P (2003). Stima della longevità in gadiformi dello stretto di sicilia sulla base della lettura di otoliti. *Biol. Mar. Mediterr.* 10, 814–818.

Fortibuoni, T., Aldighieri, F., Giovanardi, O., Pranovi, F., and Zucchetta, M. (2015). Climate impact on Italian fisheries (Mediterranean Sea). *Reg. Environ. Chang.* 15, 931–937. doi: 10.1007/s10113-015-0781-6.

Fortibuoni, T., Giovanardi, O., Pranovi, F., Raicevich, S., Solidoro, C., and Libralato, S. (2017). Analysis of long-term changes in a Mediterranean marine ecosystem based on fishery landings. *Front. Mar. Sci.* 4. doi: 10.3389/FMARS.2017.00033.

Fox, J., and Weisberg, S. (2019). *An R Companion to Applied Regression*. Available at: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science* 365, 979–983. doi: 10.1126/science.aax5721.

Froese, R., and Pauly, D. (2022). FishBase. *World Wide Web Electron. Publ. (Accessed 9 December 2022).* Available at: https://fishbase.mnhn.fr/popdyn/PopGrowthList.php?ID=29&Genus-Name=Micromesistius&SpeciesName=poutassou&fc=183.

Froglia, C., and Gramitto, M. E. (1981). Summary of biological parameters on *Micromesistius poutassou* (Risso) in the Adriatic. *Fao Fish. Reports* 253, 93–94.

Froglia, C., and Gramitto, M. E. (1980). Observations on growth of *Micromesistius poutassou* (Risso) (Pisces, Gadidae) in the central Adriatic Sea. in *XXVIIe*

Congres - Assemblee pleniere CIESM, Comite Vertebres marins et Cephalopodes (Cagliari, Italy).

Gonçalves, P., Ávila De Melo, A., Murta, A. G., and Cabral, H. N. (2017). Blue whiting (*Micromesistius poutassou*) sex ratio, size distribution and condition patterns off Portugal. *Aquat. Living Resour.* 30, 24. doi: 10.1051/alr/2017019.

Hidalgo, M., El-Haweet, A. E., Tsikliras, A. C., Tirasin, E. M., Fortibuoni, T., Ronchi, F., et al. (2022). Risks and adaptation options for the Mediterranean fisheries in the face of multiple climate change drivers and impacts. *ICES J. Mar. Sci.* 79, 2473–2488. doi: 10.1093/icesjms/fsac185.

Hidalgo, M., Olsen, E. M., Ohlberger, J., Saborido-Rey, F., Murua, H., Piñeiro, C., et al. (2014). Contrasting evolutionary demography induced by fishing: The role of adaptive phenotypic plasticity. *Ecol. Appl.* 24, 1101–1114. doi: 10.1890/12-1777.1.

Hidalgo, M., Rouyer, T., Bartolino, V., Cerviño, S., Ciannelli, L., Massutí, E., et al. (2012). Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. *Ecography* 35, 637–649. doi: 10.1111/j.1600-0587.2011.07314.x.

ICES (2004). Report of the Northern Pelagic and Blue Whiting Fisheries Working Group (WGNPBW). *ICES Expert Gr. Reports (until 2018)*, 241pp. Available at: https://doi.org/10.17895/ices.pub.19266569.v1%0A%0A.

ICES (2008). Report of the Workshop on Sexual Maturity Staging of Cod, Whiting, Haddock and Saithe (WKMSCWHS). Available at: https://doi.org/10.17895/ices.pub.19280246.

ICES (2017). Workshop on Age estimation of Blue Whiting (*Micromesistius poutassou*) WKARBLUE2, 6-9 June 2017, Lisbon, Portugal. *Ices C. 2017/Ssgieom22*, 60.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* 77, 765–776.

Lloret, J., Serrat, A., Thordarson, G., Helle, K., Jadaud, A., Bruno, I., et al. (2021). The poor health of deep-water species in the context of fishing activity and a warming climate: will populations of *Molva* species rebuild or collapse? *J. Fish Biol.* 98, 1572–1584. doi: 10.1111/jfb.14347.

Lotze, H. K., Coll, M., and Dunne, J. A. (2011). Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14, 198–222. doi: 10.1007/s10021-010-9404-8.

Magnussen, E. (2007). Interpopulation comparison of growth patterns of 14 fish species on Faroe Bank: Are all fishes on the bank fast-growing? *J. Fish Biol.* 71, 453–475. doi: 10.1111/j.1095-8649.2007.01502.x.

Martin, P., Maynou, F., Recasens, L., and Sabatés, A. (2016). Cyclic fluctuations of blue whiting (*Micromesistius poutassou*) linked to open-sea convection processes in the northwestern Mediterranean. Fish. Oceanogr. 25, 229–240. https://doi.org/10.1111/fog.12147.

Mahe, K., Oudard, C., Mille, T., Keating, J., Gonçalves, P., Clausen, L. W., et al. (2016). Identifying blue whiting (*Micromesistius poutassou*) stock structure in the Northeast Atlantic by otolith shape analysis. *Can. J. Fish. Aquat. Sci.* 73, 1363–1371. doi: 10.1139/cjfas-2015-0332.

Maiorano, P., Sion, L., Carlucci, R., Capezzuto, F., Giove, A., Costantino, G., et al. (2010). The demersal faunal assemblage of the north-western Ionian Sea (central Mediterranean): Current knowledge and perspectives. *Chem. Ecol.* 26, 219–240. doi: 10.1080/02757541003693987.

Mannini, A., and Lanteri, L. (2017). "*Micromesistius poutassou*," in *Sintesi delle conoscenze di biologia, ecologia e pesca delle specie ittiche dei mari italiani / Synthesis of the knowledge on biology, ecology and fishery of the halieutic resources of the Italian seas*, eds. P. Sartor, A. Mannini, R. Carlucci, E. Massaro, S. Queirolo, A. Sabatini, et al., 304-310 (Suppl. 1).

Marini, M., and Grilli, F. (2023). The Role of Nitrogen and Phosphorus in Eutrophication of the Northern Adriatic Sea : History and Future Scenarios. *Appl. Sci.* 13, 9267. Available at: https://doi.org/10.3390/app13169267.

Marini, M., Maselli, V., Campanelli, A., Foglini, F., and Grilli, F. (2016). Role of the Mid-Adriatic deep in dense water interception and modification. *Mar. Geol.* 375, 5–14. doi: 10.1016/j.margeo.2015.08.015.

Martinelli, M., Angelini, S., Belardinelli, A., Canduci, G., Chiarini, M., Domenichetti, F., et al. (2021). Accordo tra MIPAAF e CNR-IRBIM Ancona in merito alla proposta progettuale relativa alle attività di monitoraggio periodico delle fosse di Pomo e all’attuazione di misure che, nel rispetto dei piani di gestione, comportino il mantenimento delle condizioni ambientali idonee alla vita e all’accrescimento dei molluschi bivalvi, ponendo in essere misure supplementari tese a proteggere le diverse fasi del ciclo biologico delle specie interessate (CUP J41F19000080001). Parte Monitoraggio Fosse di Pomo periodo 2019-2020, esteso 2021. Report finale, Ottobre 2021.

MIPAAF (2017). Misure per la pesca nella Fossa di Pomo. D.M. 01/06/2017.

Mir-Arguimbau, J., Martín, P., Balcells, M., Sala-Coromina, J., and Sabatés, A. (2022). Fishery dynamics of blue whiting, *Micromesistius poutassou*, a highly discarded bycatch species in the NW Mediterranean Sea. *Sci. Mar.* 86, 1–12. doi: 10.3989/scimar.05240.025.

Mir-Arguimbau, J., Balcells, M., Raventós, N., Martín, P., and Sabatés, A. (2020). Growth, reproduction and their interplay in blue whiting (*Micromesistius poutassou*, Risso, 1827) from the NW Mediterranean. *Fish. Res.* 227, 105540. doi: 10.1016/j.fishres.2020.105540.

Monstad, T. (1990). Distribution and growth of blue whiting in the North-East Atlantic 1980-1988. *PINRO-IMR Symp.*, 227–267.

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Marsaleix, P., Somot, S., et al. (2019). An end-to-end model reveals losers and winners in a warming Mediterranean Sea. *Front. Mar. Sci.* 6, 1–19. doi: 10.3389/fmars.2019.00345.

Ogle, D. H., Doll, J. C., Wheeler, A. P., and Dinno, A. (2022). *FSA: Simple Fisheries Stock Assessment Methods*. Available at: https://cran.r-project.org/package=FSA.

Orsi-Relini, L., and Peirano, A. (1985). Biological notes on the blue whiting, *Micromesistius poutassou* (Risso) of the Ligurian Sea. *FAO Fish. Rep.* 336, 113–117.

Pitcher, C. R., Hiddink, J. G., Jennings, S., Collie, J., Parma, A. M., Amoroso, R., et al. (2022). Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. *Proc. Natl. Acad. Sci. USA* 119, e2109449119. doi: 10.1073/pnas.2109449119.

Pollack, M. J. (1951). The sources of the deep water of the eastern Mediterranean

Sea. *J. Mar. Res.* 10, 128–152.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., Molinos, J. G., Halpern, B. S., Hoegh-Guldberg, O., et al. (2016). Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.* 3, 1–21. doi: 10.3389/fmars.2016.00062.

Posit Team (2022). RStudio: Integrated Development Environment for R. Available at: http://www.posit.co/.

Post, S., Fock, H. O., and Jansen, T. (2019). Blue whiting distribution and migration in Greenland waters. *Fish. Res.* 212, 123–135. doi: 10.1016/j.fishres.2018.12.007.

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available at: https://www.r-project.org/.

Raitt, D. F. S. (1968). Synopsis of biological data on the blue whiting *Micromesistius poutassou* (Risso, 1810). *Fao Fish. Syn.* 54, 1–39.

Roether, W., Manca, B. B., Klein, B., Bregant, D., Georgopoulos, D., Beitzel, V., et al. (1996). Recent Changes in Eastern Mediterranean Deep Waters. *Science* 271, 333–335. doi:10.1126/science.271.5247.333.

Rueda, L., Massutí, E. M., Alvarez-Berastegu, D., and Hidalgo, M. (2015). Effect of intra-specific competition, surface chlorophyll and fishing on spatial variation of gadoid’s body condition. *Ecosphere* 6, 175. doi: 10.1890/ES15-00087.1.

Santojanni, A., Arneri, E., Bernardini, V., Cingolani, N., Di Marco, M., and Russo, A. (2006). Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. *Clim. Res.* 31, 181–193. doi: 10.3354/cr031181.

Sartor, P. (1995). Regime alimentare di osteitti gadiformi nel mar Tirreno Settentrionale. *Atti Soc. Tosc. Sci. Nat., Mem., Ser. B* 102, 59–67.

Sbrana, M., Fiorentino, F., Musumeci, C., Garofalo, G., Lanteri, L., Ligas, A., et al. (2019). Climate change, fishery and resources: the case of cold water species *Micromesistius poutassou* (Risso, 1827) (Pisces, Gadidae). In *50° Congresso della Società Italiana di Biologia Marina Livorno, 10-14 giugno 2019*. Livorno, Italy.

Serrat, A., Lloret, J., Frigola-Tepe, X., and Muñoz, M. (2019). Trade-offs between life history traits in a coldwater fish in the Mediterranean Sea: the case of blue whiting *Micromesistius poutassou*. *J. Fish Biol.* 95, 428–443. doi: 10.1111/jfb.13993.

Sguotti, C., Bischoff, A., Conversi, A., Mazzoldi, C., Möllmann, C., and Barausse, A. (2022). Stable landings mask irreversible community reorganizations in an overexploited Mediterranean ecosystem. *J. Anim. Ecol.* 91, 2465–2479. doi: 10.1111/1365-2656.13831.

Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G., and Gislason, H. (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396. doi: 10.1016/j.icesjms.2005.01.004.

Silva, A., Pestana, G., Dias, C., and Godinho, S. (1996). Preliminary results on the distribution and spawning of blue whiting, *Micromesistius poutassou*, off the Portuguese coast. *ICES C.* 1996/H:16, 1–22. Available at: https://www.ices.dk/sites/pub/CM%20Doccuments/1996/H/1996_H16.pdf.

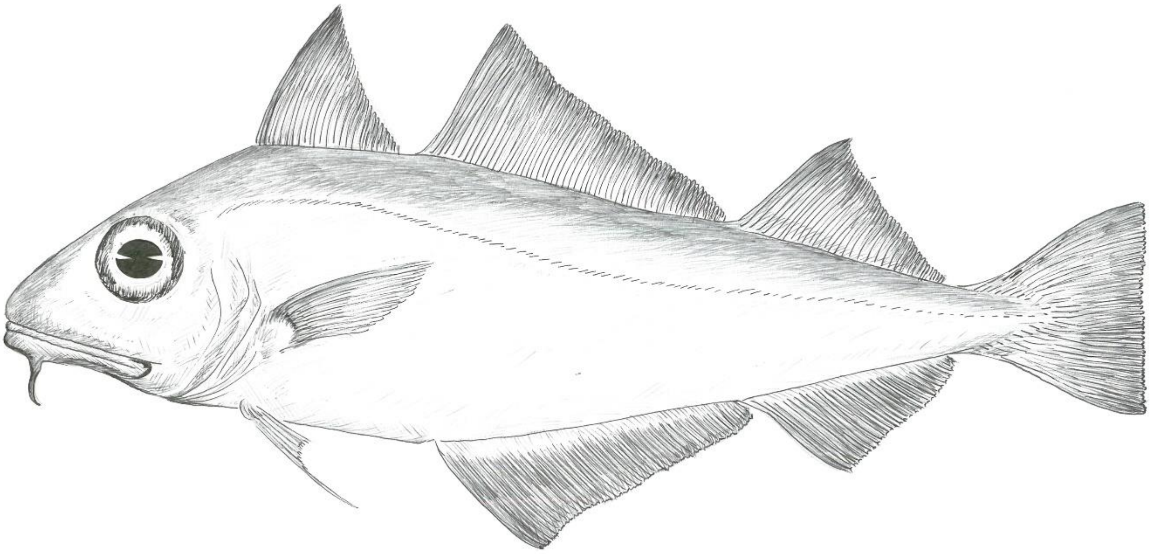
Trenkel, V. M., Lorance, P., Fässler, S. M. M., and Høines, A. S. (2015). Effects of density dependence, zooplankton and temperature on blue whiting *Micromesistius poutassou* growth. *J. Fish Biol.* 87, 1019–1030. doi: 10.1111/jfb.12775.

Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *BioScience*, 45: 759e771.

Tsikliras, A. C., and Stergiou, K. I. (2015). Age at maturity of Mediterranean marine fishes. *Mediterr. Mar. Sci.* 16, 5–20. doi: 10.12681/mms.659.

Wilcoxon, F. (1945). Individual Comparisons by Ranking Methods. *Biometrics Bulletin* 1(6), 80–83. https://doi.org/10.2307/3001968.

4 Case study III – Poor cod (*Trisopterus capelanus*)



Growth, reproduction and factors involved in body size reduction of the poor cod (*Trisopterus capelanus*) in the northern Adriatic Sea

Federico Calì[1,2,3,4], Mario La Mesa[4], Fortunata Donato[2], Mattia Panin[3], Carlotta Mazzoldi[3], Alberto Santojanni[2]

[1]Department of Biological, Geological, and Environmental Sciences (BiGeA), Alma Mater Studiorum - University of Bologna, Italy

[2]National Research Council - Institute for Marine Biological Resources and Biotechnologies (CNR-IRBIM) Ancona, Italy

[3]Department of Biology, University of Padova, Italy

[4]National Research Council - Institute of Polar Sciences (CNR-ISP) Bologna, Italy

Manuscript submitted to *Fisheries Research*

Abstract

The poor cod (*Trisopterus capelanus*) is a gadoid endemic species of the Mediterranean and Black Seas showing fast growth and early sexual maturity. It accounted for 3 to 10% of the total catch biomass of the Italian trawling fleet until the 21st century. However, its abundance has decreased significantly over the past two decades, with most of the landings occurring in the Adriatic Sea. The aims of the present study are to update information about the biological parameters of poor cod in the northern Adriatic Sea, to compare the size/age structure and growth performance of populations sampled with an interval of 34 years, to discuss the outcomes of the comparison taking into account the potential effects of fishing pressure and climate change. Fish samples were collected monthly from commercial bottom trawlers of the northern Adriatic Sea in 2020–2021 and the growth performance of this population was compared with data coming from a previous sampling carried out in a comparable area in 1986–1987. Age estimations were performed using data from age readings of thin otolith sections. The size at first sexual maturity (assessed in the recent samples) was achieved within the first year of life, at around 12 cm TL for males and 13 cm TL for females. The growth and age structure of the poor cod from the northern Adriatic Sea revealed some differences in the growth trajectories between the sampling periods, showing a reduction in the asymptotic length in both sexes. We hypothesize that the decreased growth performance might be related to a metabolic constraint, possibly related to the increased temperature and its consequences, but it could be also explained as a response to the high levels of fishing exploitation or as a combination of both stressors.

Keywords: Adriatic Sea, age and growth, poor cod, sea warming, fishing exploitation

4.1 Introduction

The poor cod, *Trisopterus capelanus* (Lacepède 1800), is a gadoid species widespread throughout the Mediterranean and along the western coasts of the Black Sea. It is more abundant in the western basin, in the northern-central Adriatic, and along the northern coast of the Aegean Sea (Sbrana, 2017). The benthopelagic behaviour of the poor cod is characterised by a close association with the sea bottom, particularly for trophic purposes (Gramitto, 1999). Stomach content analyses revealed that its diet is mainly composed of small benthic crustaceans (Peracarida, Decapoda, and Brachyura) and teleosts (Gobidae), showing a generalistic feeding strategy, with different prey items depending on the local availability (Sartor, 1995; Gramitto, 1999; Morte et al., 2001). From a depth of 20 m to over 400 m, the species lives on muddy and sandy bottoms forming small shoals, with greater abundances between 40 and 120 m. Likewise many other gadiform species, the poor cod shows a peak of spawning during the winter, although it exhibits an extended residual spawning activity with a variable duration of five to seven months after the peak (Politou and Papaconstantinou, 1991; Vallisneri et al., 2003). The poor cod shows fast growth and early sexual maturity, being mature at the end of the first year of life at around 13 cm total length (TL) (Froglia, 1981; Politou and Papaconstantinou, 1991; Vallisneri et al., 2003). With the availability of new genetic data on the family Gadidae, numerous specific studies have been devoted to the taxonomy of this family since the beginning of the 21st century, stimulating the scientific debate about the evolution of this important bony fish group (Gaemers, 2016). In the past, the poor cod was known as *Trisopterus minutus capelanus* and considered as a subspecies of the Atlantic species *Trisopterus minutus.* The taxonomic revision of the genus, based on morphological and molecular analyses, recognised that Mediterranean specimens belong to a distinct species, *T. capelanus* (Delling et al., 2011). Moreover, Mattiangeli et al. (2003), using allozymes and minisatellites, found a high degree of genetic differentiation between individuals sampled in the western Mediterranean Sea (Gulf of Lion and Ligurian Sea) and those from the eastern part (Aegean Sea). Consequently, these findings suggest the existence of a minimum of two reproductively isolated populations in the Mediterranean Sea.

Although not significant in terms of commercial value, the poor cod is a common endemic fish species that frequently appears in the northern Mediterranean fish markets (Cohen et al., 1990). Until the beginning of the 21st century, this species accounted for 3 to 10% of the total catch biomass of the Italian trawling fleet (Biagi et al., 1992), representing in some seasons more than one-third of commercial catches of the Adriatic bottom trawlers (Froglia, 1981). With over 65% of the total landings of poor cod in Italy occurring in the Adriatic Sea, this region has a great share in terms of landings at the Mediterranean scale (Sbrana, 2017). This is due to the high productivity of the Adriatic Sea and a favourable bottom type for the poor cod (and for the trawling activities). Despite its relevancy at a local scale for several Adriatic fisheries, there is little information about the state of exploitation of this resource, and the scanty information available suggests that the abundance of this species has decreased significantly over the past two decades. By analysing the historical data series of the GRUND survey (1982–2003) and the MEDITS survey (1994-2009) carried out in the Adriatic Sea, it has been observed a decreasing trend of the density and abundance indexes, which remained at extremely low levels after the year 2000 (Ciavaglia et al., 2006). The same negative trend is noticeable from the historical landing data series of one of the most important Italian trawling fleets, located in the northern Adriatic Sea (Mazzoldi et al., 2014). The poor cod landings of the Chioggia trawling fleet declined at the end of the 20th century (from 70 tons in 1996 to 5 tons in 2002), maintaining consistently low values (less than 5 tons) until now. Unfortunately, official landing data for the entire Adriatic area are available only from 2005 onward (FAO, 2022), not allowing us to track back the exploitation history of this resource. The few attempts to investigate the state of its exploitation indicated that the resource was overfished in several Mediterranean areas (Politou and Papaconstantinou, 1991; Metin et al., 2008; Sbrana, 2017). Yet, Froglia (1981) reported that between the 70s and 80s, during the late spring, the Italian Adriatic trawlers used to catch great quantities of poor cod juveniles, which were frequently discarded on board because of their low size and commercial value.

Several aspects of the biology of the Adriatic population of poor cod have been investigated by various authors (Froglia, 1981; Tangerini and Arneri, 1983; Giannetti and Gramitto, 1993; Gramitto, 1999; Vallisneri et al., 2003); nonetheless, little attention has been paid to the study of this species over the last two decades and the only data available come from the Croatian area (Šantić et al., 2010, 2015). In addition, considering the serious decline of the poor cod population and that data on this species have not been collected consistently in the past years within fishery data collection programs (i.e., EU - Data Collection Framework), urgent attention is required to shed light on its population dynamics. Moreover, as the poor cod shows an affinity for relatively cold waters (as its congeneric species), it could also have been affected negatively by the severe sea warming trend occurring in the area (García-Monteiro et al., 2022; Sguotti et al., 2022). Drawing from these premises, the present study aims to

i) update the information about the biological parameters of poor cod in the northern Adriatic Sea;

ii) compare the size/age structure and growth performance of poor cod Adriatic populations sampled with a time interval of 34 years;

iii) discuss the outcomes of the historical comparison taking into account the potential effects of fishing pressure and climate change.

4.2 Materials and Methods

4.2.1 Study area

The study area encompasses the western side of the northern Adriatic Sea, which is situated in the central Mediterranean Sea. This semi-enclosed basin is one of the most productive and heavily fished areas in the Mediterranean Sea (Russo et al., 2015). The basin has distinct morphological variations, with the western section characterised by a predominantly uniform and sandy composition, with a gentle slope. In contrast, the eastern coastline displays an uneven topography, characterised by numerous islands and a steeply sloping bathymetry composed of rocky formations (Artegiani et al., 1997). The northern sub-basin extends from its northernmost point to a depth of 100 m and is distinguished by a notably shallow average depth of approximately 30 m (Figure 4.1). Additionally, it is marked by the presence of strong river runoffs. According to Hopkins (1992) and Ludwig et al. (2009), it is widely thought that Po and other rivers in northern Italy contribute approximately 20% of the overall Mediterranean river runoff. The temperature of the sea bottom exhibits a pronounced seasonal pattern, with coastal waters experiencing a range of 7 °C (winter) to 27 °C (summer), while deeper waters exhibit a range of 10 °C (winter) to 18 °C (summer) (Russo et al., 2012). The physical properties and dynamics of this subarea are significantly impacted by atmospheric forces and river discharges, resulting in considerable temporal and spatial fluctuations (Russo and Artegiani, 1996; Supić et al., 2004). Optimal conditions for fishing activities are generated by the combination of shallow waters, sandy-muddy seafloors and high nutrient inputs, which contribute to high productivity and suitability for trawling purposes. Indeed, recent studies employing AIS technology have identified the northern-central Adriatic Sea as the most heavily fished in the Mediterranean Sea (Amoroso et al., 2018; Ferrà et al., 2018; Merino et al., 2019).

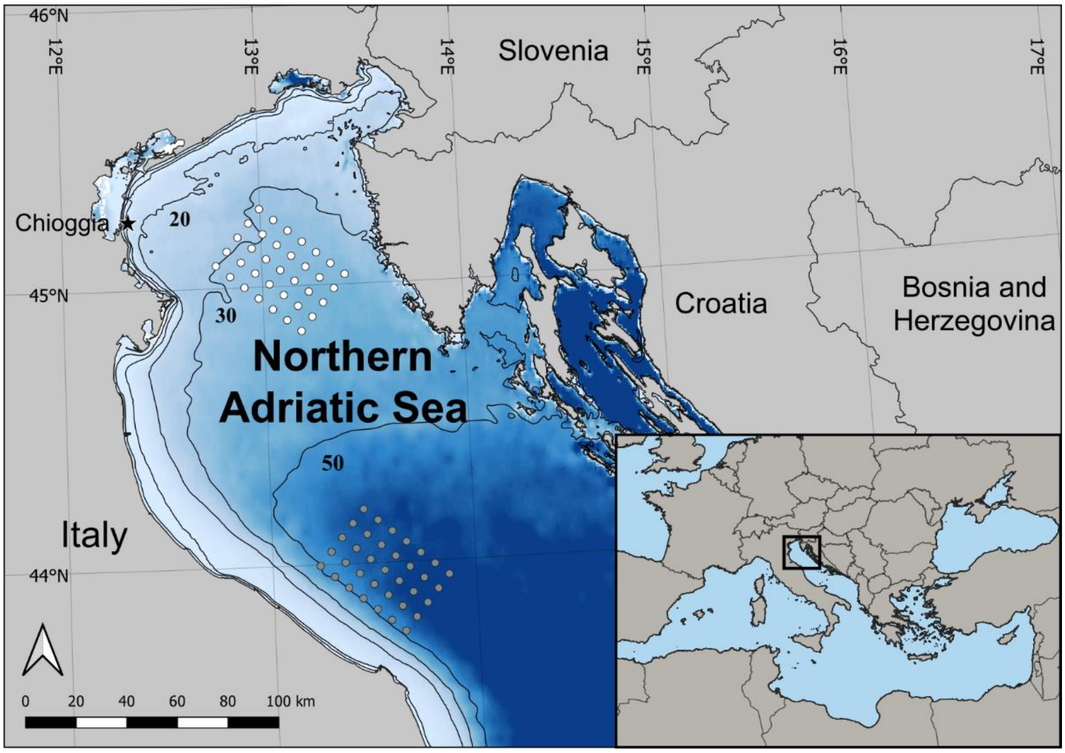


Figure 4.1. The northern-central Adriatic Sea and location of the Chioggia harbour (★). The white dotted area indicates the sampling area of the current study, while the grey dotted area indicates the sampling area of the 1986–1987 samples (Giannetti and Gramitto, 1993), whose raw data were used in this study for comparative purposes.

4.2.2 Sampling 2020–2021

Monthly fish samples were obtained from trawlers of the Chioggia fleet operating in the fishing ground off the mouth of the Po River from October 2020 to December 2021. No samples were collected in August, as a result of the annual summer trawl fishing ban. Fish specimens were captured utilising an Italian-type otter trawl net, known as a *tartana*, towed at depths ranging from 20 to 40 m (mesh size of 40 mm at the cod-end).

Furthermore, in cases where sampling on board was not feasible, samples of poor cod were obtained from the landing sites of the Chioggia trawling fleet. These samples were collected from local fishers who were operating in the same fishing grounds. The length frequency distributions (LFD) of each sample were obtained by measuring all the sampled individuals to the nearest half cm (total length, TL). A monthly subsample consisting of 40-60 specimens, which were chosen randomly in order to represent the entire size range, was selected to undergo biological examinations. The measurements included TL to the nearest mm, total weight (TW) to the nearest 0.1 g, and gonad weight (GW) to the nearest 0.01 g. Sex was determined by macroscopic examination of gonads in specimens larger than 10 cm TL and the maturity stage of the gonads was assessed using the standard ICES (2008) six-point scale: 1) Immature; 2) Maturing; 3) Spawning; 4) Spent; 5) Resting/Skip of spawning; 6) Abnormal. Individuals smaller than 10 cm TL were considered unsexed juveniles because the sex could not be determined macroscopically. The sagittal otoliths were extracted, cleaned, and preserved dry in vials for age determination. The gonadosomatic index (GSI = GW/TW × 100) was calculated to evaluate the reproductive investment in gonads. Gonad subsamples of all the specimens whose macroscopic evaluation of maturity stage was doubtful were preserved in Dietrich solution (900 ml of distilled water, 450 ml of 95% ethanol, 150 ml of 40% formaldehyde, and 30 ml of acetic acid). This preservation method was employed in order to facilitate subsequent histological analyses used to validate the macroscopic assessment of gonadal maturity (Follesa and Carbonara, 2019). The condition factor (Kn) was obtained as the ratio of the corresponding predicted TW (expressed as $a*L^b$) for a fish of the same length (Le Cren, 1951):

$$Kn = TW / a * L^b,$$

where a and b are coefficients estimated from a linear regression logTL/logTW of the specimens collected in 2020–2021.

4.2.3 Sampling 1986–1987

To perform a historical comparison of growth parameters, data collected from the 2020–2021 sampling were integrated with the data from a previous sampling carried out in 1986–1987, whose research outcomes were partially published in Giannetti and Gramitto (1993). The old samples were collected in April, June, December 1986, and

June, October 1987 from a coastal area north of Ancona, which is approximately 100 km from the sampling area of 2020–2021 (Figure 4.1). Fish specimens were captured during trawl fishing utilising an Italian-type otter trawl net, towed at depths around 50 metres (mesh size of 35 mm at the cod-end). Having obtained access to the unprocessed data from the previous sampling, we subsequently applied a standardised methodology to both samples to conduct statistical analysis, with the aim of mitigating methodological bias.

4.2.4 Growth

A representative subsample was chosen from the entire samples, with specimens grouped into 1 cm total length (TL) classes. Age readings were conducted on an equal number of males and females (when available) within each length class in every monthly sample, in order to comprehensively capture the entire range of population sizes. To obtain comparable age readings between the 2020–2021 and the 1986–1987 samples, we used the same preparation technique described in Giannetti and Gramitto (1993), consisting in obtaining thin cross-sections of the otoliths. Indeed, determining the age of poor cod from the whole sagittal otoliths is challenging due to the thickness and the presence of bumps (Figure 4.2A). In order to obtain thin sections (0.25-0.40 mm thickness), otoliths were embedded in resin (Crystalbond 509 Amber, Aremo products Inc.), ground from both sides using an abrasive paper and polished on a lapping film with 0.05 µm alumina powder. Particular attention was paid to obtaining a final reading plane passing across the nucleus, using the shape of *sulcus acusticus* as a reference. The otolith sections were fixed onto glass slides using resin and subsequently immersed in fresh water against a dark background to increase the contrast between translucent and opaque zones. Otolith readings were performed under reflected light, and the rings were counted from the nucleus to the distal margin of the section (Figure 4.2B). The sections were observed under a stereomicroscope (Leica MZ6) at low magnification (10x). The age of the specimen was determined by counting the number of fully developed annuli, which are composed of an opaque ring and an adjacent translucent ring. The samples were read twice by two operators using a blind and randomised approach. The operators independently conducted the readings without any knowledge of the date of capture, sex, or size of the fish. The age and edge type (translucent or opaque) of each otolith sample were assigned and, in case of discrepancy between readers, the sample was excluded from the analysis. By analysing the edge condition (the monthly percentage of otoliths with an opaque margin), the periodicity and timing of ring formation were determined, enabling confirmation of the annual formation of the rings. To evaluate the ageing precision (Campana, 2001) the index of average percent error (APE; Beamish and Fournier, 1981) and the mean coefficient of variation (CV; Chang, 1982) were calculated by comparing readings within and between readers. The estimation of age was conducted in years, by establishing a conventional common birth date (1st January) based on the reproductive period of this species, which takes place from December to March (Froglia, 1981), and taking into account the capture date and edge type. Given that in fish smaller than 10 cm we only observed a single deposition (opaque), they were classified as Young of the Year (YOY), and their age was calculated as a year fraction using only the month of capture and the birthdate. The von Bertalanffy growth function (VBGF) was used to describe the growth of the population:

$TL = L_\infty (1 - e^{-k(t-t_0)})$,

where TL is the length at age t, L_∞ is the asymptotic total length, k is the Brody growth rate coefficient which determines how fast the fish approaches L_∞, and t_0 is the theoretical age at which the average length is zero. The observed length at age data pairs was fitted with the VBGF. The VBGF parameters were calculated in each sampling for males and females separately. Unsexed juveniles smaller than 10 cm TL sampled in spring were included in both female and male growth curves to improve the model fit in the first period of fast growth. Differences between periods and sexes were tested by applying the Likelihood-ratio test (Kimura, 1980) for the growth parameters, while mean length-at-age was compared using the Wilcoxon signed-rank test (Wilcoxon, 1945). The Growth Performance Index ($\phi' = \log k + 2\log L_\infty$) was calculated to allow comparison among the growth parameters estimated in different populations of poor cod and other gadids (Froese and Pauly, 2022).

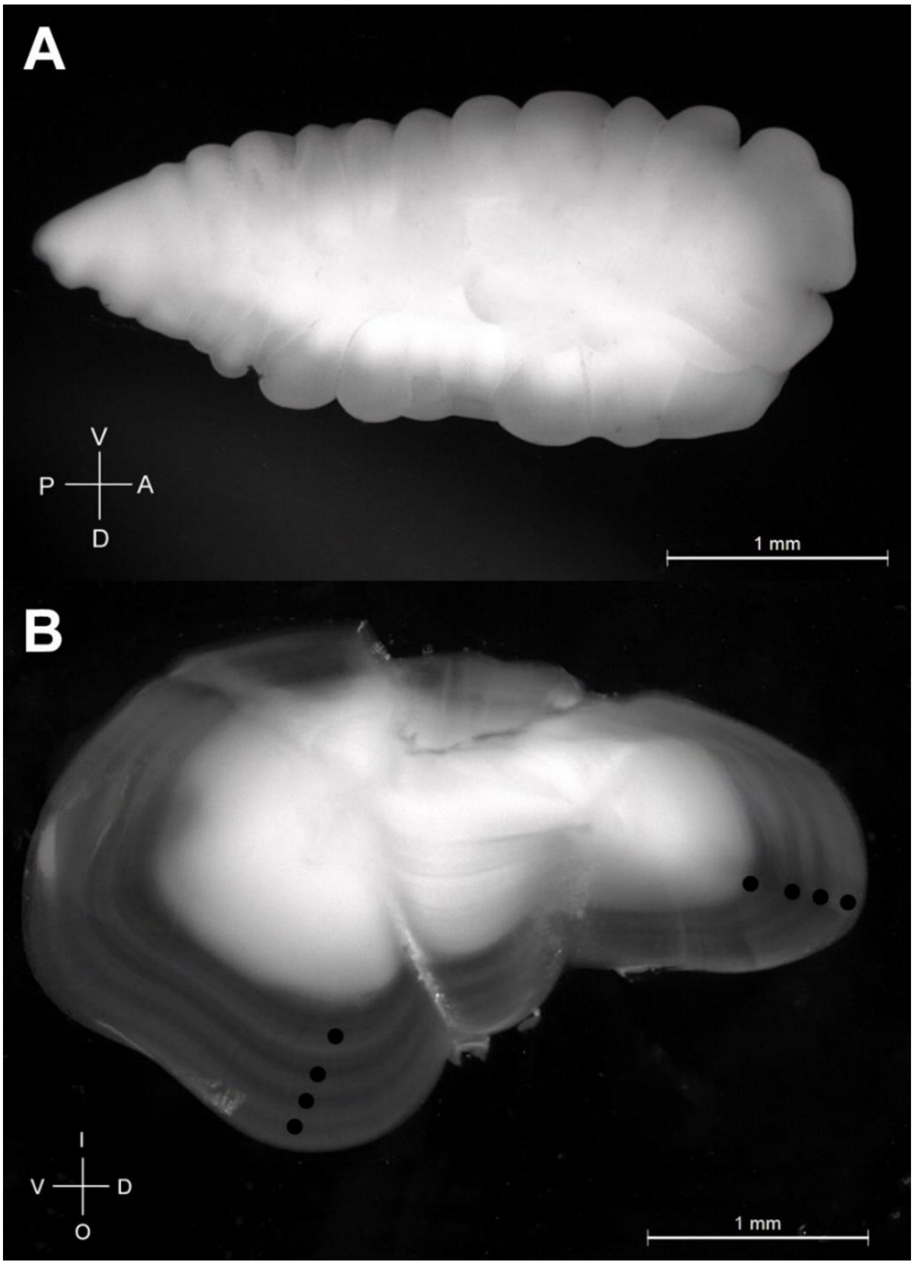


Figure 4.2. Left otolith of a female specimen of poor cod (18.6 cm TL), whole (A, distal side view) and after thin-sectioning (B). Four completely formed annuli visible in the thin section are marked with black dots (reflected light). D = dorsal axis; V = ventral axis; A = anterior axis; P = posterior axis; I = inner axis (proximal); O = outer axis (distal).

4.2.5 Reproductive traits 2020–2021

Reproductive traits were investigated only from the 2020–2021 samples as these data were not available from the 1986–1987 samples. The size-at-first sexual maturity L_{50}, i.e., the size at which 50% of individuals are mature, was estimated based on 203 females and 157 males, collected between December (when individuals in early maturation gonadal stages were observed) and May (when still a few spawning individuals were detected among post-spawner ones). Data on size and maturity stage were coupled to fit a predicted proportion of mature individuals (namely at stages 3 and 4) at size using a logistic model. To estimate accurately the L_{50}, histological analyses of gonads were carried out on the specimens whose macroscopic maturity stage was doubtful and on males < 13 cm TL during the spawning season. Indeed, since males showed gonads of smaller size compared to females, the macroscopic evaluation of male gonads could not be effective in identifying small mature specimens. Gonad samples preserved in Dietrich solution for at least 20 days were dehydrated, embedded in Paraplast, cut into a series of transverse Sections (7 µm) and mounted on slides. The slides were then stained with Mayer's haematoxylin and eosin (Pearse, 1985). The histological sections were then examined under a light microscope (Leica DM LB) and imaged using a digital camera (Leica DFC 420). The following criteria were employed to ascertain the maturity of a specimen: presence of spermatids and spermatozoa in the testis lobules for males; presence of vitellogenic oocytes in different stages within the ovarian lamellae for females (although the later stages of development are clearly visible macroscopically). We used as a reference for the histological examinations of gonads the study of Brown-Peterson et al. (2011). Statistical analyses were conducted using R (R Core Team, 2022), RStudio (Posit Team, 2022), and the packages FSA and car (Fox and Weisberg, 2019; Ogle et al., 2022).

4.3 Results

4.3.1 Population parameters 2020–2021

A total of 580 specimens were collected, including 228 males, 341 females, and 11 undetermined sex specimens. Males ranged in size from 7.9 to 19.6 cm TL, females from 6.6 to 24.8 cm TL, and undetermined from 6.3 to 10 cm TL. The LFDs were different between sexes (two samples Kolmogorov–Smirnov test, $p < 0.05$), showing a higher proportion of females above the size of 16 cm TL (Figure 4.3). Looking at the LFDs of the total catches of the poor cod of the Chioggia trawling fleet is clear that YOYs (modal size 7.5 cm TL) were recruited to the fishery in May. As a consequence, it was possible to observe throughout the warm season a bimodal distribution in the LFD of the total catch, which became almost unimodal in September, indicating a rapid increase in size during the summer months (Supplementary Figure 4.1).

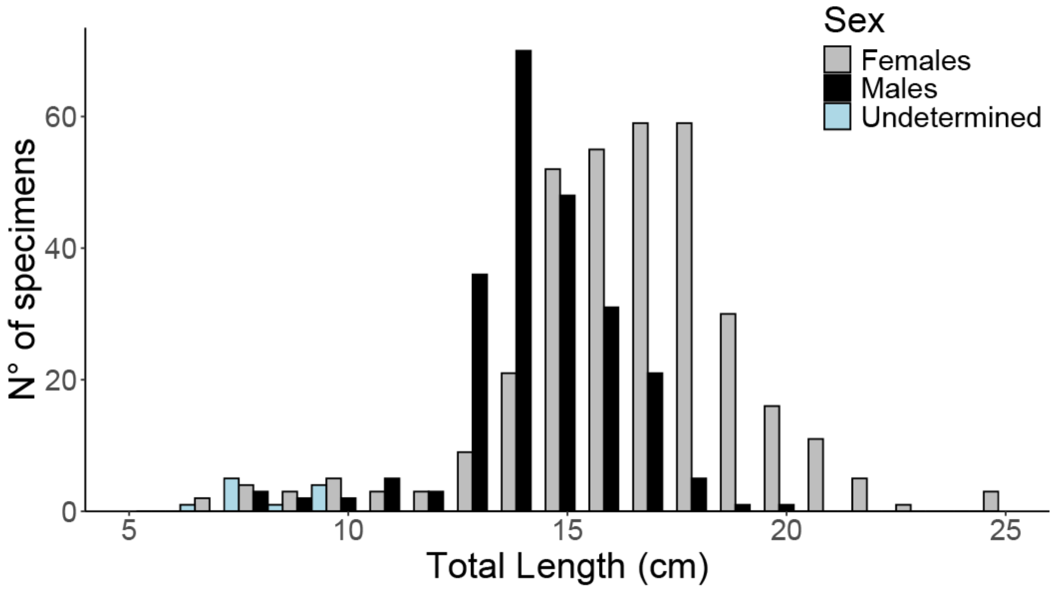


Figure 4.3. Length-frequency distribution (LFD) of poor cod sampled from trawling fishery of the northern Adriatic Sea during 2020–2021, by sex.

4.3.2 Growth and age structure 2020–2021

Age readings by means of otolith thin sections were carried out on 454 (189 males and 265 females) specimens out of 580 specimens. The maximum age was 3 years for males and 4 years for females, respectively. Approximately 90% of aged specimens were within the 0+ and 2+ age class, with a modal age of 1 year (40% of the population). The annual periodicity of annulus deposition was confirmed by the edge-zone analysis, suggesting that translucent and opaque zones are generated annually. The hyaline zone was laid mainly from the end of the summer to the mid-winter, specifically from August to January. In contrast, the opaque zone underwent deposition for nearly the entire year, exhibiting an unequivocal predominance from February to July (Figure 4.4).

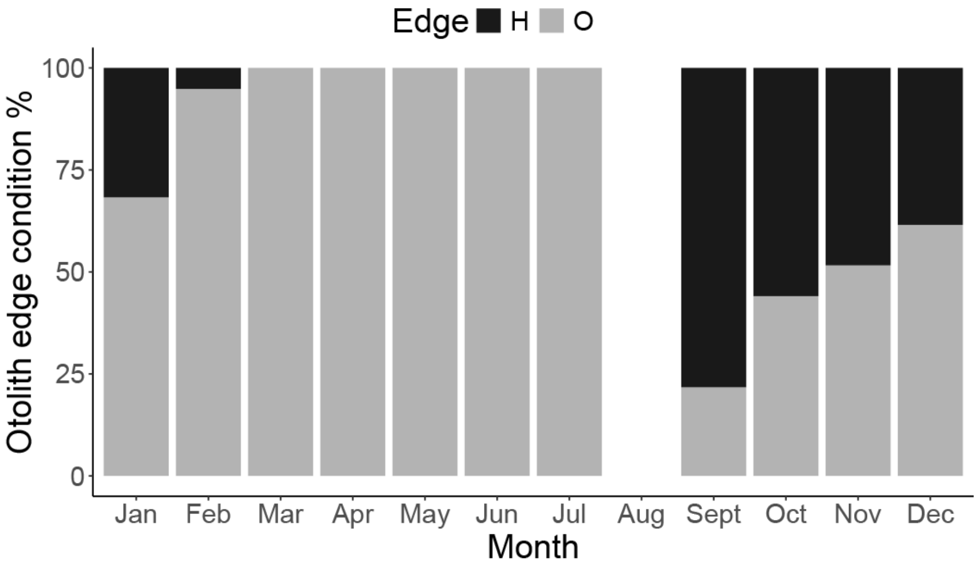


Figure 4.4. Monthly edge composition (%), indicating the proportion of the poor cod specimens with hyaline (black) or opaque (grey) margins in the otolith edge.

Age readings between readers were precise, supporting the reliability of otolith sections for ageing poor cod. The average percentage error (APE) and the coefficient of variation (CV) were low (6.4% and 9.1%, respectively), with a percent agreement between readers of 92%. When examining the age-length keys of both sexes, females exhibited not only greater size but also older age than males (Table 4.1).

4.3.3 Comparison samples 2020–2021 vs 1986–1987

The comparison of the age-length keys between the periods highlighted a higher proportion of large-sized (> 20 cm TL) and old specimens in 1986–1987 compared to 2020–2021 (Tables 4.1 and 4.2). Although no significant differences were found in the mean length-at-age between sexes and samplings (Wilcoxon signed-rank test; Z = 1.281, p > 0.01), the 2020–2021 specimens showed a higher mean size during the first two years of life compared to 1986–1987. However, the growth rate of the 2020–*2021* specimens decreased afterwards, and the trend was reversed in older age groups (Figure 4.5). The comparison of the von Bertalanffy growth curves confirmed the differences in growth patterns, highlighting different growth trajectories between individuals from the different sampling periods (Figure 4.6). Based on the results of the Kimura likelihood ratio test (Supplementary Table 4.1), the estimated VBGF parameters indicated that the 1986–1987 samples exhibited greater values of $L\infty$ and lower values of k in comparison to the 2020–2021 ones (Figure 4.6). Males showed a significantly lower L_∞ compared to females only in 2020–2021 (as expected, considering the sexual dimorphism in size), a difference not found in the 1986–1987 samples, even if the male L_∞ was lower compared to the female one (Table 4.3).

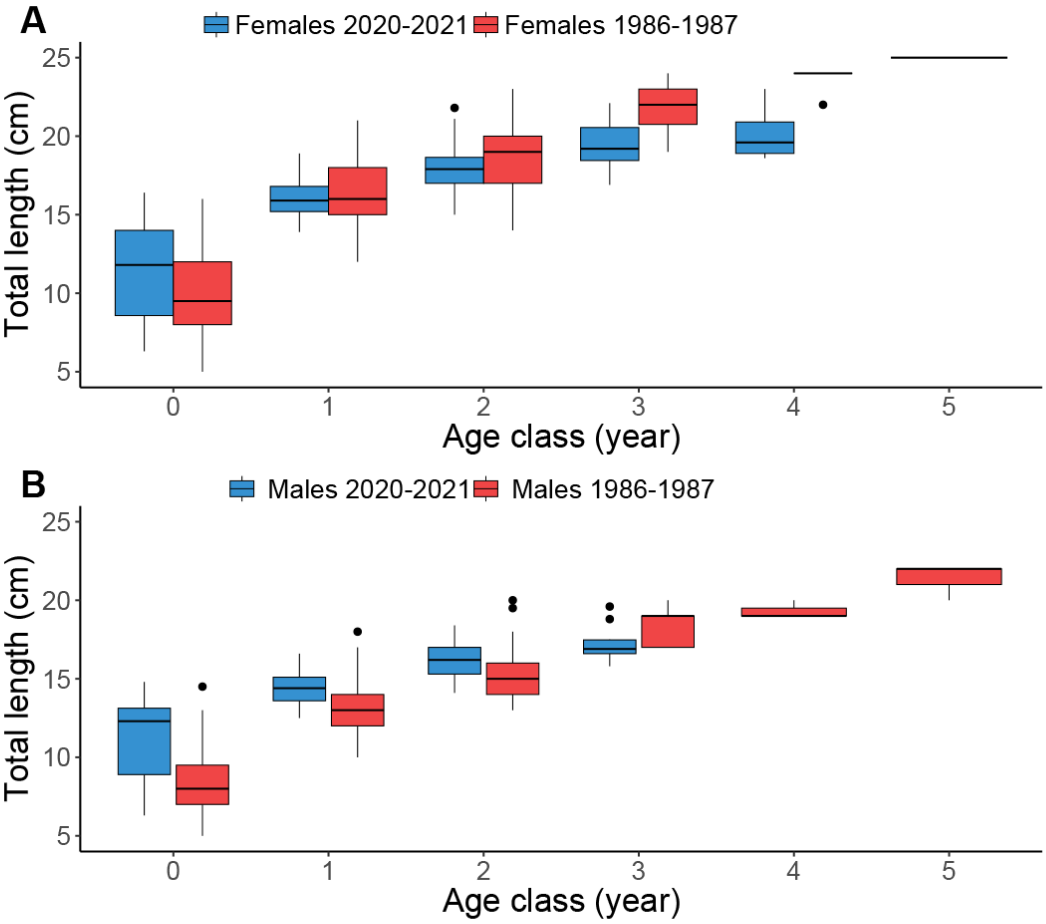


Figure 4.5. Boxplots of length-at-age of poor cod females (A) and males (B) sampled in 1986–1987 (elaborated from raw data of Giannetti and Gramitto, 1993) and in 2020–2021 (present study). Horizontal lines identify the mean value of each age class.

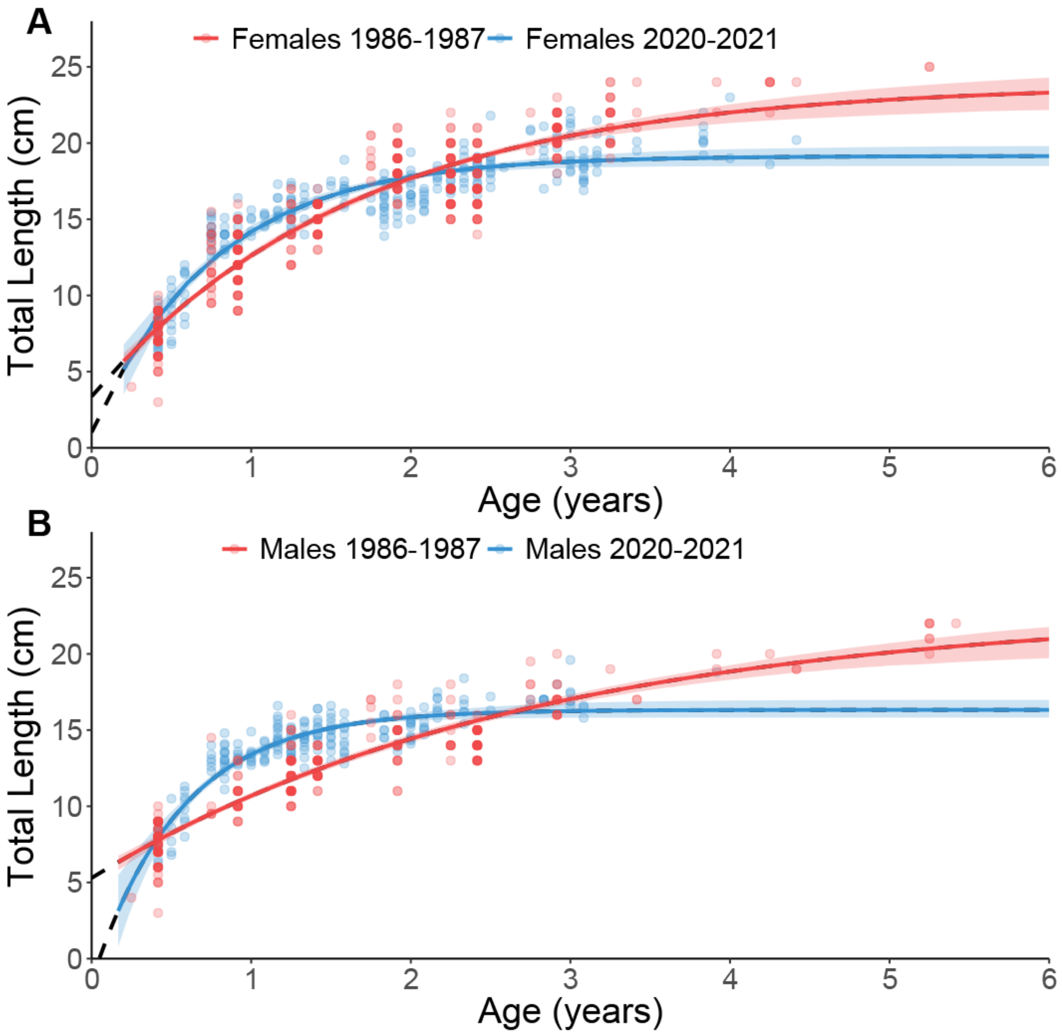


Figure 4.6. Von Bertalanffy growth curves for poor cod females (A) and males (B) sampled in 1986–1987 (elaborated from raw data of Giannetti and Gramitto, 1993) and in 2020–2021 (present study).

Table 4.1. Age-length key for females and males based on otolith readings of poor cod sampled in 2020–2021 (present study) in the northern-central Adriatic Sea. N = total number; SD = standard deviation; TL = total length.

	Females						Males					
Age class (years)	0+	1+	2+	3+	4+	N	0+	1+	2+	3+	4+	N
TL class (cm)												
6	5					5	3					3
7	5					5	4					4
8	7					7	5					5
9	6					6	4					4
10	3					3	3					3
11	4					4	4					4
12	4					4	8	5				13
13	7	2				9	12	31				43
14	12	9				21	5	30	6			41
15	6	28	4			38		25	11	1		37
16	1	20	13	1		35		8	10	5		23
17		15	23	4		42			10	2		12
18		3	22	11	1	37			2	1		3
19			9	7	1	17				1		1
20			6	9	1	16						-
21			2	5		7						-
22				2		2						-
23					1	1						-
24												
25												
N	60	77	79	39	4	259	48	99	39	10	-	196

TL mean (cm)	11.4	16.0	18.0	19.5	20.2	11.2	14.4	16.1	17.3	-
TL SD	3.0	1.1	1.4	1.4	2.0	2.5	1.0	1.1	1.1	-

Table 4.2. Age-length key for females and males based on otolith readings of poor cod sampled in 1986–1987 (elaborated from raw data of Giannetti and Gramitto 1993) in the northern-central Adriatic Sea. N = total number; SD = standard deviation; TL = total length.

	Females							Males						
Age class (years)	0+	1+	2+	3+	4+	5	N	0+	1+	2+	3+	4+	5	N
TL class (cm)														
6														
7														
8														
9	1						1							
10	4						4	5	4					9
11	14						14	7	21					28
12	17	4					21	2	20					22
13	15	4					19	3	28	9				40
14	14	13	1				28	1	15	20				36
15	6	15	9				30		12	14				26
16	1	21	17				39		4	8				12
17		12	24				36		3	8	2			13
18		14	17				31		1	5				6
19		11	22	1			34			1	2	2		5
20		8	20	5			33			1	1	1	1	4
21		2	17	3			22						2	2
22			9	8	1		18						4	4
23			1	3			4							
24				4	5		9							
25						2	2							
N	72	104	137	24	6	2	345	18	108	66	5	3	7	207
TL mean (cm)	12.6	16.5	18.5	21.8	23.7	25.0		11.3	12.9	15.2	18.4	19.3	21.4	

TL SD	1.5	2.2	2.1	1.5	0.8	0.0		1.3	1.7	1.7	1.3	0.6	0.8

Table 4.3. Von Bertalanffy growth parameters estimates and their standard errors (SE) of poor cod from the northern-central Adriatic Sea and growth performance index (φ') for combined sexes, females and males of both sampling periods. The growth rate coefficient (k) and theoretical age at which the average length is zero (t_0) are expressed in years^{-1} and years, respectively. L_∞ = asymptotic total length.

	L_∞ (cm)	SE	k	SE	t_0	SE	φ'
Females 1986–1987	24.08	0.28	0.58	0.07	-0.28	0.02	2.53
Males 1986–1987	23.46	0.25	0.34	0.08	-0.76	0.02	2.27
Females 2020–2021	19.15	0.26	1.29	0.08	-0.04	0.02	2.67
Males 2020–2021	16.32	0.17	1.8	0.05	0.04	0.02	2.68

4.3.4 Reproductive cycle 2020–2021

The spawning season occurred from December to June, with increased activity at the onset of winter, as supported by macroscopic observations of gonad maturation and the GSI monthly pattern (Figure 4.7 A, B). The GSI mean value for females during the spawning peak in December was 8% (maximum 11%), while for males it was 0.7% (maximum 1.6%), indicating a substantial difference in reproductive effort between sexes. The peak in GSI was followed by a slow decrease to minimum values of reproductive activity from July onwards. Kn values started to decrease at the spawning period onset, showing higher values before and at the end of the spawning season (Figure 4.7 C, D). Outside the spawning period, low average values of Kn were observed in September and October in males and females, respectively.

During the spawning period, sexually mature specimens were clearly recognizable through microscopic observation of histological samples, from the presence of active vitellogenesis and spermatogenesis processes in females and males, respectively. In active spawning females ovaries showed a high proportion of oocytes in advanced developmental stages, although all the oocyte stages were present (Supplementary Figure 4.2 A). In active spawning males, the testes exhibited large lobule lumina filled with spermatozoa, with the other cellular types restricted to the lobule walls (Supplementary Figure 4.2 B). Based on the logistic model fitted to the proportion of sexually mature specimens, size-at-first maturity L_{50} was estimated at 13.2 ± 0.4 cm TL for females and 12.6 ± 0.1 cm TL for males (Figure 4.8).

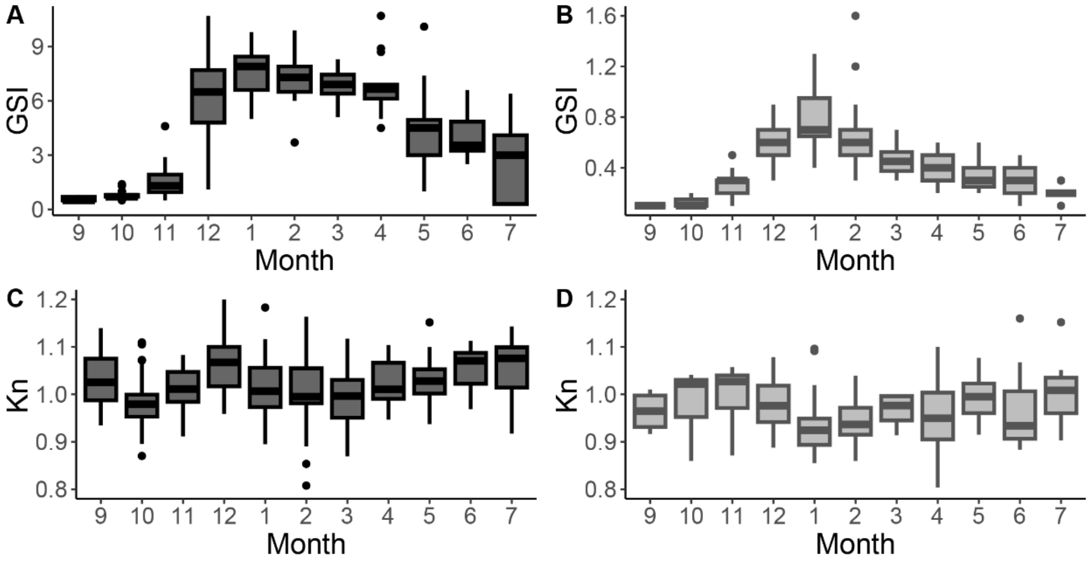


Figure 4.7. Monthly variation, along with their corresponding standard error bars, of the mean Gonadosomatic Index (GSI) and Le Cren Condition Factor (Kn) for females (dark grey; A, C) and males (light grey; B, D) poor cod. Note that GSI values are expressed in different scales. Horizontal bold lines identify the monthly mean value.

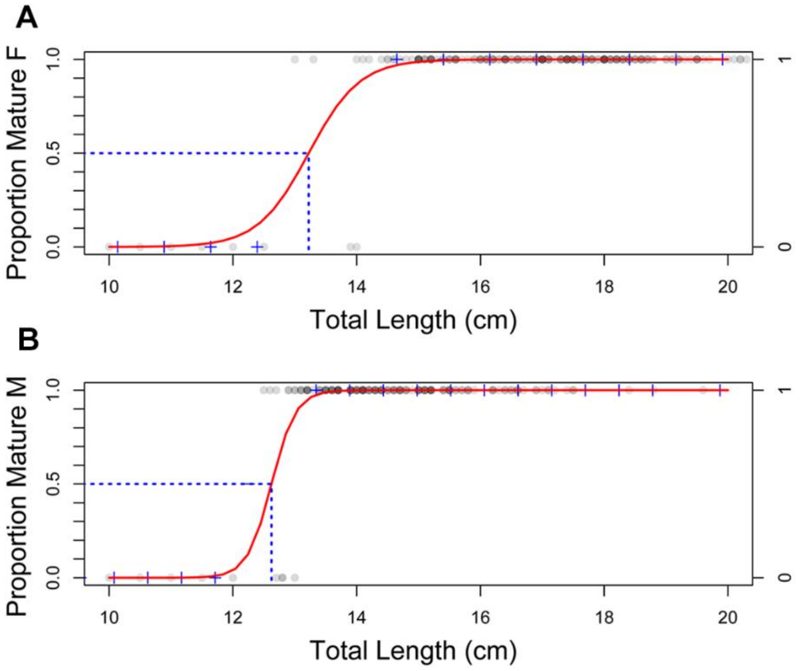


Figure 4.8. Sexual maturity ogives of females (A) and males (B) poor cod. The dotted vertical blue line intercepting the x-axis indicates the size at which 50% of individuals are mature (13.2 ± 0.4 cm TL and 12.6 ± 0.1 cm TL for females and males, respectively).

4.4 Discussion

The current investigation offers an updated insight into some relevant life history traits of poor cod from the northern Adriatic Sea. Moreover, by analysing the growth rates exhibited in samples obtained from the northern Adriatic Sea with a time shift of 34 years, we detected some differences in growth and size/age structures between the current and the late 1980s population.

4.4.1 Sampling 2020–2021

The size range of the poor cod was smaller than previously observed in the same area (Froglia, 1981; Tangerini and Arneri, 1983; Giannetti and Gramitto, 1993; Gramitto, 1999; Vallisneri et al., 2003) and in comparison, with other studies carried out in the Mediterranean Sea (Politou and Papaconstantinou, 1991; Sartor, 1995; Morte et al., 2001; Metin and Ilkyaz, 2008; Šantić et al., 2015). Likewise, the age range we found was smaller than the observed one in previous studies (based on age readings from otolith thin-sectioning) in the Adriatic Sea (Giannetti and Gramitto, 1993; Šantić et al., 2015) and comparable with those reported in the Mediterranean Sea (Politou and Papaconstantinou, 1991; Righini et al., 1995; Metin and Ilkyaz, 2008). Comparing the results obtained in studies with the application of the thin-sectioning technique with those that used only LFD trend data or age readings on the whole otoliths (Froglia, 1981; Tangerini and Arneri, 1983), there is a clear difference in the age range found, always greater applying the thin-sectioning technique. It is evident that the other two methodologies do not allow the identification of the older age classes and then obtaining accurate information on the population age structure (Polat and Gümücs, 1996). In fact, using the progression of LFDs throughout the year it is possible to follow only the modal classes numerically abundant (namely 0+ and 1+ age class), making assumptions on the growth of only a part of the life cycle (Froglia, 1981) (Fig. A.1). On the other hand, as already mentioned in section 2.4, the age reading of the whole otolith is not feasible because of their thickness and irregular surface, leading to a misinterpretation of the annual pattern.

It is noteworthy to mention that the estimated values of k and t_0 were the highest and the closest to 0, respectively, ever reported in the Mediterranean Sea (Politou and Papaconstantinou, 1991; Giannetti and Gramitto, 1993; Metin and Ilkyaz, 2008; Šantić et al., 2015; Sbrana, 2017). The sampling of juveniles during the spring allowed us to properly fit the VBGF at the initial growing stages, thereby aiding in the estimation of more accurate values for these parameters. Typically, information concerning the length-at-age during the early stages of life, when growth occurs at its peak, is difficult to obtain. The insufficiency of data (i.e., juveniles sampled only once during the spring) may result in an underestimation of k values, which could account for the inconsistencies observed in the estimates of growth parameters between the current study and prior research. The same results in terms of differences with the available literature on gadid species were highlighted in recent growth studies in which a good number of small specimens was included in the sample collection to fit the VBGF (Mir-Arguimbau et al., 2020; Calì et al., 2023a, 2023b). However, it is not possible to exclude that the differences we observed are attributable to the different environmental conditions in the investigated areas, which could strongly affect the growth rate (ICES, 2017; Kutsyn, 2024). The high proportion of opaque otolith margins observed from February to July confirms that opaque deposition is associated with the fast-growing season, which occurs during the period of increasing water temperatures. The analysis of the edge condition agrees with previous studies in the Adriatic Sea (Giannetti and Gramitto, 1993), allowing us to corroborate the annual ring formation.

The analysis of reproductive traits in 2020–2021 samples indicates that both males and females attain sexual maturity at the end of the first year of life (at 12.6 and 13.2 cm TL, respectively), in agreement with previous studies in the Adriatic (Froglia, 1981; Tangerini and Arneri, 1983) and the Mediterranean Seas (Politou and Papaconstantinou, 1991; Sbrana, 2017). Our estimates are slightly lower compared to the maturity size reported in the same area by Vallisneri et al. (2003) (14–15 cm TL), which used only macroscopic examination of gonads. The use of histological techniques to validate the macroscopic examination allowed us to perform a more accurate evaluation of the gonadal development, reducing misinterpretation occurring using only macroscopic observations (Follesa and Carbonara, 2019). Macroscopic observations on gonads and GSI trends indicated clearly that the peak of spawning takes place in winter and continues through the spring until June, in agreement with the general pattern observed in the Mediterranean Sea (Froglia, 1981; Tangerini and Arneri, 1983; Politou and Papaconstantinou, 1991; Šantić et al., 2010; Sbrana, 2017). The highest monthly mean values of GSI were reached in January, 8% for females and 0.7% for males, confirming the highly different reproductive efforts between sexes already observed in other gadid species (Vallisneri et al., 2006; Serrat et al., 2019; Calì et al., 2023a, 2023b). The monthly trend of Kn values can be used as an indicator of food energy fluctuations and, consequently, the overall health of the fish. Seasonal variation in the Kn of poor cod may be associated with gonadal fluctuations (Serrat et al., 2019). The decline in Kn in correspondence with the spawning peak suggests that this fish had a high reproduction cost, as already reported by Politou and Papaconstantinou (1991). In fact, the protracted spawning period of the poor cod, which is characterised by several reproductive events (Ragonese and Bianchini, 1998), likely results in the depletion of energy reserves in muscle and mesenteric fat and could explain the lower Kn values observed during the extended spawning period (Lloret et al., 2013). Interestingly, we found a different trend of Kn between sexes during the pre-spawning period (October and November), with females showing a decline in Kn values, which was not observed in males. This finding could be related to the fact that females, having a higher energetic cost in gonadal development, undergo stronger oscillation in consumption of energy reserves and therefore could be more sensitive to environmental and prey availability variations.

4.4.2 Historical comparison

The comparison of population structures and growth trajectories between 1986–1987 and 2020–2021 samples revealed some interesting differences. As highlighted by comparing the age-length keys, the 1986–1987 sample was composed of a higher number of large-sized specimens (> 20 cm TL), showing also one age class more (5+) compared to 2020–2021. Moreover, the comparison of VBGF models and mean length-at-age suggests the possible occurrence of a shift in the poor cod growth trajectory over the last decades, with a consistent pattern observed in both sexes. In fact, our results indicate that 2020–2021 specimens grew faster during the first two years of life (age classes 0+, 1+) but then stopped the somatic growth, attaining a smaller maximum size. Although the present results must be interpreted with caution because of several limitations (discussed below), they are significant in at least two major respects. Firstly, the reduction in body size could represent an example of one of the most common adaptative responses to sea warming, reported worldwide and supported by both theoretical and empirical studies (Cheung et al., 2013; Baudron et al., 2014). Indeed, as expected by the Gill-Oxygen Limitation Theory (Pauly and Cheung, 2018), body growth is limited by the gills' capability to provide oxygen through their surface and the lower oxygen available due to the increase in temperature triggers (through phenotypic plasticity) a reduction of body size to maintain the scope for aerobic activity. Another interesting result to be linked with environmental changes (i.e., sea warming) is evinced by comparing the temporal window of opaque deposition between 1986–1987 and 2020–2021. In the recent sampling, it seems to start and end before compared to what was observed by Giannetti and Gramitto (1993), which reported a high proportion of opaque depositions between April and November. This difference could be explained by the inherent difficulties in evaluating the edge type in thin sections since these evaluations were made by different operators using different instrumentations (i.e., light and stereomicroscopes). However, since Calì et al. (2023b) reported similar differences in the edge deposition pattern between whiting specimens collected in the northern Adriatic Sea with a comparable time shift and evaluated by the same expert operators, it is possible to consider this discrepancy another adaptative response to the sea warming occurred between the two samplings. Secondly, the potential impact of fishing pressure must be taken into account when attempting to elucidate the variations observed. Considering that the northern Adriatic Sea has undergone high levels of fishing exploitation over the last decades (Barausse et al., 2014; Sguotti et al., 2022), it is possible to consider these differences attributable to fishing activity. The reduction in size and age structure is the most common effect in fish stocks that have been subjected to overexploitation (Bianchi et al., 2000; Shin et al., 2005; Hidalgo et al., 2012), giving a possible explanation for the reduced age range resulted from the historical comparison. Moreover, being the fishing harvest a size-selective process that determines higher mortality rates for the larger/older specimens, it may determine evolutionary responses favouring specimens with higher growth rate and earlier sexual maturity (having higher probabilities of reproducing before being caught) (Trippel, 1995). Therefore, the difference in growth trajectories between 1986–1987 and 2020–2021 could be explained as an adaptive response to the fishing pressure exerted on poor cod, whose adaptive response has led the specimens to grow faster and mature earlier at the expense of long-term somatic growth. Unfortunately, no data about the reproductive traits was available from the 1986–1987 samples and information from previous work is not enough detailed to validate this hypothesis. However, additional support to the hypothesis that fishing exploitation could have triggered adaptative responses in poor cod is given by the increased sexual dimorphism in size (ΔL_∞ 1986–1987 = 0.9 cm; ΔL_∞2020–2021 = 2.8 cm). This more pronounced difference in size may indicate a sex-dependent response to the size-selectivity of fishing related to the different energetic investments in gamete production and to the stronger influence of body size on the reproductive potential of females (Hayward and Gillooly, 2011). Indeed, it could be hypothesized that in females (having a much higher reproductive effort than males in gadids) the adaptative value of a size reduction induced by fishing would be lower because of the reduction in the reproductive output (fecundity increases exponentially with body size) and thus the fitness of the population (Barneche et al., 2018). Lastly, it is not possible to exclude that both sea warming and fishing exploitation have contributed to the pattern of change observed, acting either synergistically or in parallel. When this happens, the outcomes can show a wide range of variation depending on the local ecological context and disentangling their effects is often difficult (Genner et al., 2010; Hidalgo et al., 2012; Engelhard et al., 2014; O'Connor et al., 2015), besides being outside the scope of this study.

Yet, our approach has some limitations and the results of the historical comparison should be interpreted with caution. Firstly, because our hypotheses are based on two punctual sampling periods that are not representative of the actual trend over the past decades. As a matter of fact, changes in population life history traits may be determined even on a short-term scale by adaptive phenotypic plasticity, contingent upon the environmental context (Hidalgo et al., 2014). Secondly, we compared slightly different sampling areas, which are at a distance of about 100 km and present different bathymetric features. However, Tangerini and Arneri (1983), analysing the age and size structure of poor cod samples collected in the whole northern and central Adriatic Sea, did not find any difference between the areas, supporting the hypothesis of the existence of a single population widely distributed in the area. The only difference regarding the size of specimens was found in areas characterized by depth values higher than 100 m, which were not considered in this study. Although the specimens compared were caught using a net with a slightly different selectivity (mesh size 5 mm smaller in 1986–1987), we believe that this difference does not affect the validity of the comparison because juvenile specimens of 7 cm TL are fully caught using a codend with a mesh size of 35 mm (Froglia, 1981). Consequently, any difference in selectivity would affect only the proportion of young specimens, which are not relevant in the comparison.

4.4.3 Conclusions

In conclusion, the present study provides updated and detailed information on some important life history traits of poor cod in the northern Adriatic Sea, cautiously advancing the hypothesis that the differences observed by comparing samples with a time shift of 34 years could be related to the effect of sea warming and/or fishing pressure occurred in the Adriatic Sea during the last decades. Indeed, recent studies on other commercial gadid species from the Adriatic Sea, using the same methodological approach, reported similar results and a general trend of reduction in the maximum size, giving support to the results of the present study. Moreover, considering these findings altogether and the different environmental niches of gadid species in the Adriatic area (Sbrana, 2017), it could be hypothesised that some adaptative processes (e.g., through phenotypic plasticity) occurred and are still ongoing in this cold-water family as a result of external stressors. Despite these promising results, several questions remain unanswered at present about the drivers of the trend observed, posing the need for additional research to elucidate the underlying mechanisms.

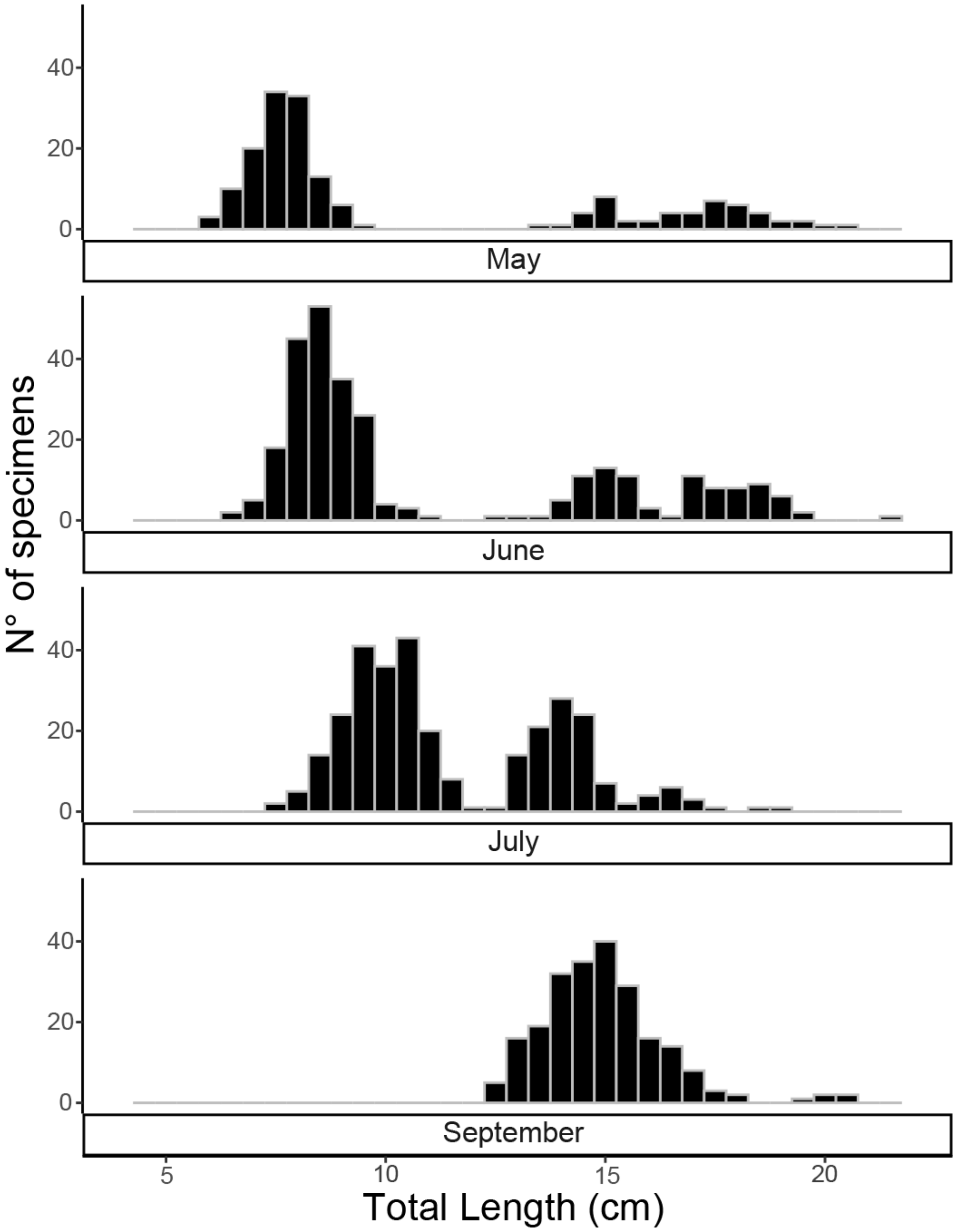
Acknowledgments

We thank all of the staff of the National Research Council (CNR) and the Hydrobiological Station Umberto D’Ancona (University of Padova), as well as the fishers involved for their essential contribution to the samples and data collection. We wish also to thank Dr. Carlo Froglia for his work in preserving the original data and otoliths that made the historical comparison possible. The research leading to these results was conceived under the International Ph.D. program “Innovative Technologies and Sustainable Use of Mediterranean Sea Fishery and Biological Resources” (www.FishMed-PhD.org, accessed July 10, 2023). This study represents partial fulfillment of the requirements for the Ph.D. thesis of Federico Calì.

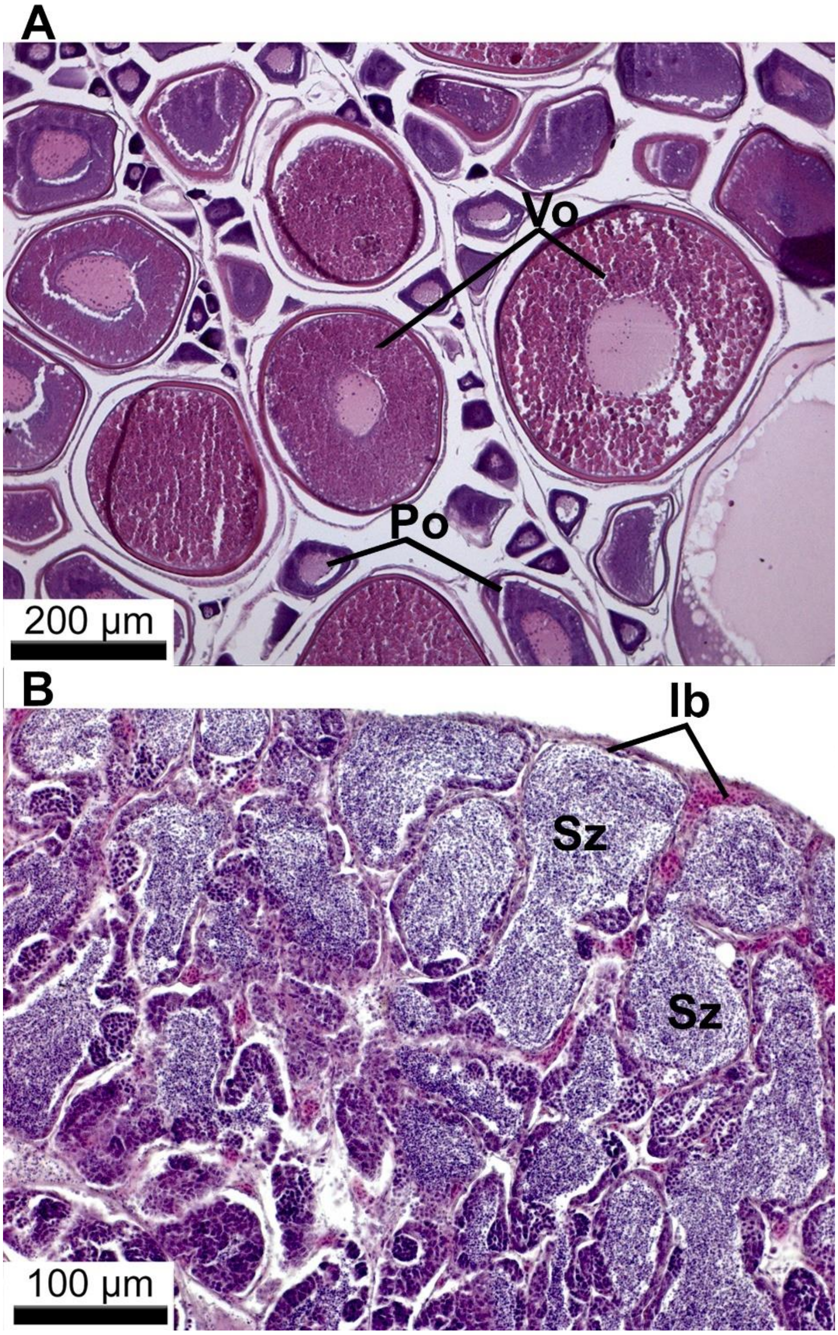
Supplementary material

Supplementary Table 4.1. Likelihood ratio test comparing the von Bertalanffy growth parameters estimated for sexes and sampling periods of poor cod from the northern-central Adriatic Sea. Statistics are based on four null hypotheses, assuming that each parameter or a combination of them do not differ between sexes or sampling years. K = Brody growth rate coefficient; t_0 = theoretical age at which the average length is zero; L_∞ = asymptotic total length; df = degrees of freedom; * significant at α = 0.05; ** significant at α = 0.01; ns = not significant.

	Parameter	χ^2	df	p-value
Females vs males 1986–1987	all	352.7	3	**
	L_∞	0.4	1	*
	k	10.6	1	ns
	t_0	21.7	1	**
Females vs males 2020–2021	all	137	3	**
	L_∞	36.3	1	**
	k	4.9	1	*
	t_0	1.4	1	ns
Females 1986–1987 vs 2020–2021	all	86.5	3	**
	L_∞	43.5	1	**
	k	26.5	1	*
	t_0	5.8	1	**
Males 1986–1987 vs 2020–2021	all	215.5	3	**
	L_∞	58.0	1	**
	k	63.3	1	**
	t_0	37.5	1	**



Supplementary Figure 4.1. Length-frequency distribution of poor cod captured from bottom trawlers of the Chioggia fleet between spring and early autumn 2021. The bimodal distribution is due to the joining of the young-of-the-year in the sampled population in spring, which disappears in September when they join the adult population. No samples were collected in August, as a result of the annual summer trawl fishing ban.



Supplementary Figure 4.2. Histological sections of gonads (stained with haematoxylin and eosin) showing microscopical features and of poor cod mature specimens with doubtful macroscopic stage assignment. (A) Ovary section of a female specimen (17.5 cm TL) caught in February showing oocytes in different developmental stages (active vitellogenesis); (B) testis section of a male specimen (11.8 cm TL) caught in November showing active spermatogenesis and testis lobules filled with spermatozoa. Magnification: ovaries = 100x; testicles = 200x. Abbreviations: Po = previtellogenic oocyte, Vo = vitellogenic oocyte (early and late stages), lb = lobule, Sz = spermatozoa.

References

Amoroso, R. O., Pitcher, C. R., Rijnsdorp, A. D., McConnaughey, R. A., Parma, A. M., Suuronen, P., et al. (2018). Bottom trawl fishing footprints on the world’s continental shelves. *Proc. Natl. Acad. Sci. U. S. A.* 115, E10275–E10282. doi: 10.1073/pnas.1802379115.

Artegiani, A., Paschini, E., Russo, A., Bregant, D., Raicich, F., and Pinardi, N. (1997). The Adriatic Sea General Circulation . Part I : Air – Sea Interactions and Water Mass Structure. *J. Phys. Oceanogr.* 27, 1492–1514.

Barausse, A., Correale, V., Curkovic, A., Finotto, L., Riginella, E., Visentin, E., and Mazzoldi, C. (2014). The role of fisheries and the environment in driving the decline of elasmobranchs in the northern Adriatic Sea. *ICES J. Mar. Sci. 71*, 1593–1603.

Barneche, D. R., White, C. R., and Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science (80-.).* 645, 642–645.

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., and Tara Marshall, C. (2014). Warming temperatures and smaller body sizes : synchronous changes in growth of North Sea fishes. *Glob. Chang. Biol.* 20, 1023–1031. doi: 10.1111/gcb.12514.

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* 38, 982–983.

Biagi, F., De Ranieri, S., and Viva, C. (1992). Recruitment, length at first maturity and feeding of poor-cod, *Trisopterus minutus capelanus*, in the Northern Tyrrhenian Sea. *Bolletino di Zool.* 59, 87–93. doi: 10.1080/11250009209386653.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., et al. (2000). Impact of fishing on size composition and diversity of demersal fish communities. *ICES J. Mar. Sci.* 57, 558–571. doi: 10.1006/jmsc.2000.0727.

Brown-Peterson, N. J., Wyanski, D. M., Saborido-Rey, F., Macewicz, B. J., Lowerre-Barbieri, S. K., Brown-peterson, N. J., et al. (2011). A Standardized Terminology for Describing Reproductive Development in Fishes. *Mar. Coast. Fish. Dyn. Manag. Ecosyst. Sci.* 3, 52–70. doi: 10.1080/19425120.2011.555724.

Calì, F., Mesa, M. La, Donato, F., Mazzoldi, C., Martinelli, M., and Santojanni, A.

(2023a). Life history traits and historical comparison of blue whiting (*Micromesistius poutassou*) growth performance from the western Pomo / Jabuka Pits area (central Adriatic Sea). doi: 10.3389/fmars.2023.1291173.

Calì, F., Stranci, F., Mesa, M. La, Mazzoldi, C., Arneri, E., and Santojanni, A. (2023b). Whiting (*Merlangius merlangus*) Grows Slower and Smaller in the Adriatic Sea : New Insights from a Comparison of Two Populations with a Time Interval of 30 Years. *Fishes* 8, 341. Available at: https://doi.org/10.3390/fishes8070341.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* 59, 197–242. doi: 10.1006/jfbi.2001.1668.

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.* 39, 1208–1210.

Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Palomares, M. L. D., et al. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat. Clim. Chang.* 3, 254–258. doi: 10.1038/nclimate1691.

Ciavaglia, E., Manfredi, C., Di Silverio, M. C., and Piccinetti, C. (2006). Serie storiche e biologia di *Trisopterus minutus capelanus* (Lacepede, 1800) in Alto e Medio Adriatico. *Biol. Mar. Medit.* 13, 210–214.

Cohen, D. M., Inada, T., Iwamoto, T., and Scialabba, N. (1990). Fao Species Catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date*. FAO Fish. Syn. 125.*

Delling, B., Noren, M., Kullander, S. O., and González, J. A. (2011). Taxonomic review of the genus *Trisopterus* (Teleostei: Gadidae) with recognition of the capelan *Trisopterus capelanus* as a valid species. *J. Fish Biol.* 79, 1236–1260. doi: 10.1111/j.1095-8649.2011.03107.x.

Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Glob. Chang. Biol.* 20, 2473–2483. doi: 10.1111/gcb.12513.

FAO (2022). FishStatJ - Universal software for fishery statistical time series. Available at: https://www.fao.org/fishery/en/topic/166235/en.

Ferrà, C., Tassetti, A. N., Grati, F., Pellini, G., Polidori, P., Scarcella, G., et al. (2018). Mapping change in bottom trawling activity in the Mediterranean Sea through AIS data. *Mar. Policy* 94, 275–281. doi: 10.1016/j.marpol.2017.12.013.

Follesa, M. C., and Carbonara, P. (2019). Atlas of the maturity stages of Mediterranean fishery resources. *Studies and Reviews n. 99.* Rome: FAO. Available at: https://policycommons.net/artifacts/1526159/atlas-of-the-maturity-stages-of-mediterranean-fishery-resources/2214270/.

Fox, J., and Weisberg, S. (2019). An R Companion to Applied Regression. Available at: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Froese, R., and Pauly, D. (2022). FishBase. *World Wide Web Electron. Publ. (Accessed 8 December 2022).* Available at: https://fishbase.mnhn.fr/popdyn/PopGrowthList.php?ID=29&GenusName=Merlangius&SpeciesName=merlangus&fc=183.

Froglia, C. (1981). Summary of biological parameters on *Trisopterus minutus capelanus* (Risso) in the Adriatic. *Fao Fish. Reports* 253, 97–100.

Gaemers, P. A. M. (2016). Taxonomy, distribution and evolution of trisopterine gadidae by means of otoliths and other characteristics. *Fishes* 1, 18–52. doi: 10.3390/fishes1010018.

García-Monteiro, S., Sobrino, J. A., Julien, Y., Sòria, G., and Skokovic, D. (2022). Surface Temperature trends in the Mediterranean Sea from MODIS data during years 2003–2019. *Reg. Stud. Mar. Sci.* 49, 102086. doi: 10.1016/j.rsma.2021.102086.

Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., Mchugh, M., et al. (2010). Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Glob. Chang. Biol.* 16, 517–527. doi: 10.1111/j.1365-2486.2009.02027.x.

Giannetti, G., and Gramitto, M. E. (1993). Growth and age determination of poor cod *Trisopterus minutus capelanus* (Lacepède) (Pisces, Gadidae) in the central

Adriatic Sea by thin sectioned otoliths. *Quad. Ist. Ric. Pesca Mar .* 5, 119–128.

Gramitto, M. E. (1999). Feeding habits and estimation of daily ration of poor cod *Trisopterus minutus capelanus* (gadidae) in the Adriatic Sea. *Cybium* 23, 115–130.

Hayward, A., and Gillooly, J. F. (2011). The cost of sex: Quantifying energetic investment in gamete production by males and females. *PLoS One* 6. doi: 10.1371/journal.pone.0016557.

Hidalgo, M., Olsen, E. M., Ohlberger, J., Saborido-Rey, F., Murua, H., Piñeiro, C., et al. (2014). Contrasting evolutionary demography induced by fishing: The role of adaptive phenotypic plasticity. *Ecol. Appl.* 24, 1101–1114. doi: 10.1890/12-1777.1.

Hidalgo, M., Rouyer, T., Bartolino, V., Cerviño, S., Ciannelli, L., Massutí, E., et al. (2012). Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. *Ecography (Cop.).* 35, 637–649. doi: 10.1111/j.1600-0587.2011.07314.x.

Hopkins, T. S. (1992). The structure of Ionian and Levantine Seas. *Reports Meteorol. Oceanogr.* 41, 35–36.

ICES (2008). Report of the Workshop on Sexual Maturity Staging of Cod, Whiting, Haddock and Saithe (WKMSCWHS). Available at: https://doi.org/10.17895/ices.pub.19280246.

ICES (2017). Workshop on Age estimation of Blue Whiting (*Micromesistius poutassou*) WKARBLUE2, 6-9 June 2017, Lisbon, Portugal. *Ices C. 2017/Ssgieom22*, 60.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* 77, 765–776.

Kutsyn, D. (2024). Life history traits of the Black Sea whiting *Merlangius merlangus* (Gadidae): compliance with the temperature-size rule. *Environ. Biol. Fishes*, *107*, 91–105.

Le Cren, E. D. (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.*, 201–219.

Lloret, J., Shulman, G., and Love, R. M. (2013). *Condition and health indicators of exploited marine fishes*. John Wiley & Sons, Chichester, UK.

Ludwig, W., Dumont, E., Meybeck, M., and Heussner, S. (2009). River discharges of water and nutrients to the Mediterranean and Black Sea: Major drivers for ecosystem changes during past and future decades? *Prog. Oceanogr.* 80, 199–217. doi: 10.1016/j.pocean.2009.02.001.

Mattiangeli, V., Ryan, A. W., Galvin, P., Mork, J., and Cross, T. F. (2003). Eastern and Western poor cod (*Trisopterus minutus capelanus*) populations in the Mediterranean Sea: Evidence from allozyme and minisatellite loci. *Mar. Ecol.* 24, 247–258. doi: 10.1046/j.0173-9565.2003.00795.x.

Mazzoldi, C., Sambo, A., and Riginella, E. (2014). The Clodia database : a long time series of fishery data from the Adriatic Sea. *Sci. data* 1, 1–8. doi: 10.1038/sdata.2014.18.

Merino, G., Coll, M., Granado, I., Gee, J., Kroodsma, D., Miller, N. A., et al. (2019). “FAO Area 37 - AIS-based fishing activity in the Mediterranean and Black Sea,” in *Global Atlas of AIS-based fishing activity - Challenges and opportunities*, eds. M. Taconet, D. Kroodsma, and J. A. Fernandes (Rome: FAO). Available at: www.fao.org/documents/card/en/c/ca7012en.

Metin, G., and Ilkyaz, A. T. (2008). Use of otolith length and weight in age determination of poor cod (*Trisopterus minutus* Linn., 1758). *Turkish J. Zool.* 32, 293–297.

Metin, G., Ilkyaz, A. T., and Kinacigil, H. T. (2008). Growth, mortality, and reproduction of poor cod (*Trisopterus minutus* Linn., 1758) in the central Aegean sea. *Turkish J. Zool.* 32, 43–51.

Mir-Arguimbau, J., Balcells, M., Raventós, N., Martín, P., and Sabatés, A. (2020). Growth, reproduction and their interplay in blue whiting (*Micromesistius poutassou*, Risso, 1827) from the NW Mediterranean. *Fish. Res.* 227, 105540. doi: 10.1016/j.fishres.2020.105540.

Morte, M. S., Redón, M. J., and Sanz-Brau, A. (2001). Feeding habits of *Trisopterus minutus capelanus* (Gadidae) off the Eastern Coast of Spain (Western Mediterranean). *Mar. Ecol.* 22, 215–229. doi: 10.1046/j.1439-0485.2001.01731.x.

O'Connor, M. I., Holding, J. M., Kappel, C. V., Duarte, C. M., Brander, K., Brown, C. J., et al. (2015). Strengthening confidence in climate change impact science. *Glob. Ecol. Biogeogr.* 24, 64–76. doi: 10.1111/geb.12218.

Ogle, D. H., Doll, J. C., Wheeler, A. P., and Dinno, A. (2022). FSA: Simple Fisheries Stock Assessment Methods. Available at: https://cran.r-project.org/package=FSA.

Pauly, D., and Cheung, W. W. L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Glob. Chang. Biol.* 24, e15–e26. doi: 10.1111/gcb.13831.

Pearse, A. G. E. (1985) *Histochemistry, theoretical and applied analytical technology*. Churchill Livingstone, Edinburgh, UK.

Polat, N., and Gümücs, A. (1996). Ageing of whiting (*Merlangius merlangus euxinus*, Nord ., 1840) based on broken and burnt otolith. *Fish. Res.* 28, 231–236.

Politou, C.-Y., and Papaconstantinou, C. (1991). Population biology of poor cod (*Trisopterus minutus capelanus*) in the eastern coast of Greece.

Posit Team (2022). RStudio: Integrated Development Environment for R. Available at: http://www.posit.co/.

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available at: https://www.r-project.org/.

Ragonese, S., and Bianchini, M. . (1998). Growth , mortality and yield-per-recruit of the poor cod , *Trisopterus minutus capelanus* , from the Strait of Sicily. *Naga, ICLARM Q.* 21, 61–70. Available at: http://hdl.handle.net/1834/26069.

Righini, P., Silvestri, R., and Abella, A. (1995). Brief note on biological parameters of *Trisopterus minutus capelanus* (Risso) in the Northern Tyrrenian Sea. in *Rapports du Congress de la CIESM (No. 34)*.

Russo, A., and Artegiani, A. (1996). Adriatic Sea hydrography. *Sci. Mar.* 60, 33–43.

Russo, A., Carniel, S., Sclavo, M., and Krzelj, M. (2012). Climatology of the Northern-Central Adriatic Sea. *Mod. Climatol.* doi: 10.5772/34693.

Russo, T., Pulcinella, J., Parisi, A., Martinelli, M., Belardinelli, A., Santojanni, A., et al. (2015). Modelling the strategy of mid-water trawlers targeting small pelagic fish in the Adriatic Sea and its drivers. *Ecol. Modell.* 300, 102–113. doi: 10.1016/j.ecolmodel.2014.12.001.

Šantić, M., Pallaoro, A., Mikulandra, I., Rada, B., and Jardas, I. (2015). Age, growth and mortality of poor cod (*Trisopterus minutus* L.) from the eastern Adriatic Sea. *Arch. Biol. Sci.* 67, 921–927. doi: 10.2298/ABS141106053S.

Šantić, M., Pallaoro, A., Stagličić, N., Mikulandra, I., and Jardas, I. (2010). Co-variation of gonadosomatic index, condition factor and length-weight relationships of poor cod, *Trisopterus minutus* (Gadidae), in the Eastern Adriatic Sea. *Cybium* 34, 279–284.

Sartor, P. (1995). Regime alimentare di osteitti gadiformi nel mar Tirreno Settentrionale. *Atti Soc. Tosc. Sci. Nat., Mem., Ser. B* 102, 59–67.

Sbrana, M. (2017). "*Trisopterus capelanus*," in *Sintesi delle conoscenze di biologia, ecologia e pesca delle specie ittiche dei mari italiani / Synthesis of the knowledge on biology, ecology and fishery of the halieutic resources of the Italian seas*, eds. P. Sartor, A. Mannini, R. Carlucci, E. Massaro, and S. Queirolo (Biol. Mar. Mediterr.), 467-478 (Suppl. 1).

Serrat, A., Lloret, J., Frigola-Tepe, X., and Muñoz, M. (2019). Trade-offs between life history traits in a coldwater fish in the Mediterranean Sea: the case of blue whiting *Micromesistius poutassou*. *J. Fish Biol.* 95, 428–443. doi: 10.1111/jfb.13993.

Sguotti, C., Bischoff, A., Conversi, A., Mazzoldi, C., Möllmann, C., and Barausse, A. (2022). Stable landings mask irreversible community reorganizations in an overexploited Mediterranean ecosystem. *J. Anim. Ecol.* 91, 2465–2479. doi: 10.1111/1365-2656.13831.

Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G., and Gislason, H. (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396. doi: 10.1016/j.icesjms.2005.01.004.

Supić, N., Grbec, B., Vilibić, I., and Ivančić, I. (2004). Long-term changes in hydrographic conditions in northern Adriatic and its relationship to hydrological and atmospheric processes. *Ann. Geophys.* 22, 733–745. doi: 10.5194/angeo-22-733-2004.

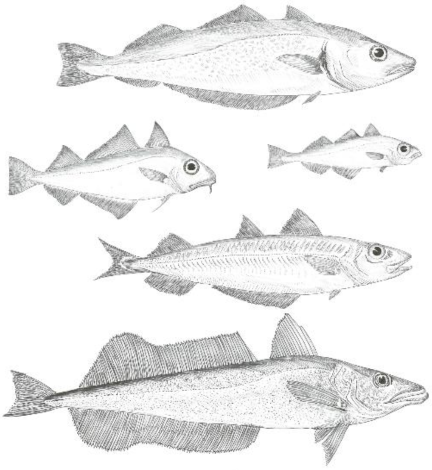
Tangerini, P., and Arneri, E. (1983). Biological data collected during the Pipeta expeditions, on the poor ccd, *Trisopterus minutus capelanus* (Risso), in the Adriatic Sea. *Fao Fish. Reports* 290, 155–159.

Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *Bioscience* 45, 759–771.

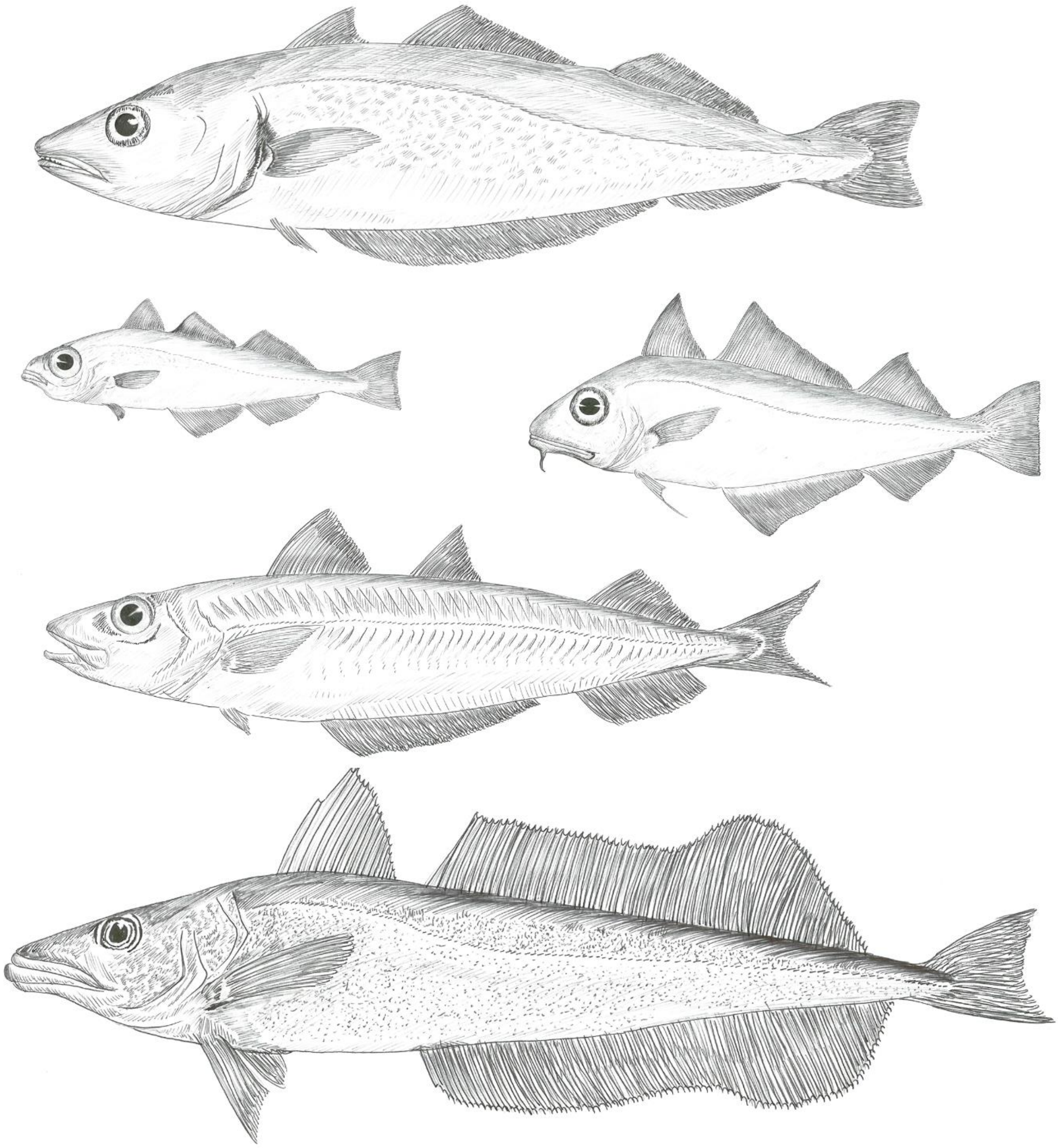
Vallisneri, M., Manfrin Piccinetti, G., and Piccinetti, C. (2003). Biologia riproduttiva di *Trisopterus minutus capelanus* (Lacepede, 1800) nel Mar Adriatico - Reproductive biology of *Trisopterus minutus capelanus* (Lacepede, 1800) in the Adriatic Sea. *Biol. Mar. Medit.* 10, 296–299.

Vallisneri, M., Scapolatempo, M., and Tommasini, S. (2006). Reproductive biology of *Merlangius merlangus* L. (Osteichthyes, Gadidae) in the northern Adriatic Sea. *Acta Adriat.* 47, 159–165.

Wilcoxon, F. (1945). Individual comparisons by ranking methods. *Biometrics Bull.* 1, 80–83. Available at: https://doi.org/10.2307/3001968.



5 Case study IV – Multispecies model Adriatic Gadiformes



Increase in thermal sensitivity in the last cold refugium of the Mediterranean Sea: a spatio-temporal modelling of the Adriatic Sea gadiform community

Federico Calì[1,2,3,4], Federico Maioli[1], Manuel Hidalgo[5], Patricia Puerta[5], Mario La Mesa[4], Carlotta Mazzoldi[3], Chiara Manfredi[1], Michele Casini[1], Alberto Santojanni[2]

[1]Department of Biological, Geological, and Environmental Sciences (BiGeA), Alma Mater Studiorum - University of Bologna, Italy

[2]National Research Council - Institute for Marine Biological Resources and Biotechnologies (CNR-IRBIM) Ancona, Italy

[3]Department of Biology, University of Padova, Italy

[4]National Research Council - Institute of Polar Sciences (CNR-ISP) Bologna, Italy

[5]Spanish Institute of Oceanography (IEO, CSIC), Balearic Oceanographic Center (COB), Ecosystem Oceanography Group (GRECO), Moll de Ponent s/n, 07015 Palma, Spain

Manuscript in preparation for *Progress in Oceanography*

Abstract

Overfishing is a major factor affecting marine ecosystems, reducing the natural capacities of fish populations to cope with short- and long-term environmental variability. On top of these impacts, climate change has diverse ecological effects, including changes in the production, phenology, and distribution of living marine resources. The species inhabiting in semi-enclosed seas are among the most vulnerable, due to limited migratory options and high levels of cumulative anthropogenic impacts such as pollution, habitat degradation, and overfishing with complex interactions. This is the general case of the Mediterranean area, but even more pressing in the Adriatic Sea, one of the last cold refugia due to its unique combination of hydrographic and environmental features, resulting in a higher abundance of cold-water species such as Gadiformes. This study aims to estimate spatial and temporal changes of five gadiform fish, namely European hake, whiting, blue whiting, poor cod, and silvery pout, in the Adriatic Sea using a multispecies hierarchical model applied to fisheries-independent trawl survey data. We compare two known thermal regimes, 1998–2010 vs 2011–2020, in order to assess a potential differential effect of depth, chlorophyll, and temperature between periods on both the occurrence and the abundance patterns of gadiform species.

Depth was the main factor influencing the occurrence pattern of gadiform species in the whole period considered, while the abundance models revealed species-specific and between-periods varying effects from all the environmental covariates. In particular, we show a significative increase in the influence of the thermal covariates in the most recent period, suggesting an increased sensitivity to temperature. Almost all the species showed a negative impact of increasing temperature, except for European hake, which showed the opposite pattern. Considering that the Adriatic Sea shows the highest warming trend in the Mediterranean area, our results underline a worrying situation for almost all the cold-water species analysed, evidencing the need to further understand how … investigation to understand these dynamics and set up proper adaptive management measures on time to ensure the long-term persistence of these populations.

Keywords: cold-water species, Adriatic Sea, joint species distribution models, sea warming, Gadiformes

5.1 Introduction

Although overfishing is widely acknowledged as the principal factor affecting marine ecosystems (Pauly et al., 1998; Barausse et al., 2011; Kuparinen and Hutchings, 2012; Fortibuoni et al., 2017), there is mounting evidence in recent decades that environmental modifications play an increasingly significant role in affecting the dynamics of fish populations. The ecological effects of climate change include changes in the production, phenology, and distribution of living marine resources (Poloczanska et al., 2016; Pinsky et al., 2018; Free et al., 2019). Among the most vulnerable ecosystems, it is possible to identify not only the cold regions (i.e., polar areas) but also the semi-enclosed seas (Hidalgo et al., 2022). This vulnerability is mainly due to the limited migratory options available to species, but also to the contemporary presence of high levels of anthropogenic impacts such as pollution, habitat degradation, and overfishing. These stressors can interact synergistically with climate change, amplifying its negative effect on the ecosystem (Hoegh-Guldberg et al., 2014). Temperate species generally exhibit a low sensitivity to temperature fluctuations, but the magnitude of the response can vary considerably depending on the location within their distribution range. Multiple studies have demonstrated that temperature-sensible species have shifted their distribution towards higher latitudes and deeper waters in response to ocean warming in order to maintain physiological homeostasis (Engelhard et al., 2014; Poloczanska et al., 2016). Nevertheless, migration towards higher latitudes can be hindered by geographical limitations, as is the case with enclosed seas. The Mediterranean Sea is the largest and deepest enclosed sea on earth, hosting a high percentage of endemic species and being defined as a “hotspot” for global marine biodiversity (Coll et al., 2010). Temporal trends indicate that overexploitation and habitat loss are the main human drivers of historical changes (Lotze et al., 2011) and recently, climate change is threatening the Mediterranean biodiversity (Costello et al., 2010; Hidalgo et al., 2022). Within this context, the northern sectors are the ones undergoing the highest warming trend (García-Monteiro et al., 2022), giving the possibility to investigate in advance the ecological consequences on a more local scale. In these areas (Gulf of Lion, Adriatic Sea, and Aegean Sea), the formation of cold and dense water is consistently observed during the winter and plays a key role in facilitating vertical recirculation, which is essential for the maintenance of the Mediterranean thermohaline circulation (Roether et al., 1996; Schroeder et al., 2017).

In particular, the Adriatic Sea, being the major source of the Eastern Mediterranean Deep Water (Orlic et al., 1992), provides the most representative example of this phenomenon. In this sub-basin, the winter season is characterised by the convergence of low temperatures and the presence of a strong and dry north-easterly wind known as “Bora”. These climatic conditions, together with significant freshwater inputs accounting for one-third of the total Mediterranean inflow (Vodopivec et al., 2022), trigger strong evaporation and cooling of surface waters. Hence, water masses, becoming colder and denser, sink in the lower layers and subsequently migrate southwards following the distinctive bathymetric latitudinal gradient. During the southward cold and dense water migration, essential elements such as oxygen and nutrients are transferred to the deeper strata. These elements are then delivered to the middle Adriatic depression (known as Pomo/Jabuka Pits), before progressing further to the Bari Canyon located in the southern Adriatic Sea (Orlic et al., 1992; Marini et al., 2016). Waters outflowing from the Adriatic finally arrive at the bottom layers of the Ionian Sea, from where they spread south- and eastward, supplying the Mediterranean thermohaline circulation system (Roether et al., 1996). The dynamic circulation patterns and hydrographic characteristics of the Adriatic Sea influence not only its role in the Mediterranean thermohaline circulation system but also its biota.

The Adriatic Sea can be considered a cold refugium due to its unique combination of hydrographic and environmental features (Ben Rais Lasram et al., 2010), which determines a slightly different species composition compared to the other Mediterranean areas (Lipej et al., 2022), showing a higher abundance of the so-called cold-water species (Tortonese, 1964; Pranovi et al., 2013). A paradigmatic example is provided by the order Gadiformes, whose members are mostly widespread in temperate and cold regions of the world (e.g., the North Atlantic). Currently, there are 21 species of gadiform fish that are known to exist in the Adriatic Sea (Lipej et al., 2022). However, only a few of these species are commercially valuable and have been traditionally exploited by fishing activities. (genera *Merluccius*, *Merlangius*, *Micromesistius*, *Trisopterus*, and *Gadiculus*). Several studies have reported examples of the effects of sea warming on cold-water Mediterranean species (Debes et al., 2008; Ben Rais Lasram et al., 2010; Genner et al., 2010; Lloret et al., 2015; Serrat and

Muñoz, 2022), but little attention has been paid to the cold-water species inhabiting the Adriatic Sea. Recently, Sguotti et al. (2022) reported that the northern Adriatic Sea demersal community has undergone several regime shifts over the last 40 years under the interactive effects of fishing pressure and sea warming. Furthermore, a decline in growth performance and size has been observed in two gadid species inhabiting distinct areas of the Adriatic Sea. This change has been attributed to the warming trend and climate-induced environmental modifications that have occurred in recent decades (Calì et al., 2023a, 2023b). However, there is still a lack of knowledge regarding the effects of temperature on the spatio-temporal dynamics of gadiform species in the Adriatic Sea. Given the recent rapid warming of the Adriatic sea surface temperature (García-Monteiro et al., 2022) and the predicted general decrease of species richness in the area (Albouy et al., 2013), there is an urgent need to understand how gadiform species respond to climate change and if they could be considered as early warning indicators of impending climate change effects on the entire ecosystem.

In this study, we estimate spatial and temporal changes in the occurrence and abundance pattern of five gadiform species in the northern-central Adriatic Sea (FAO Geographical Sub Area-GSA 17) using a multispecies distribution model and fisheries-independent trawl survey data from 1998 to 2020. This model is employed to evaluate how some environmental variables affect the spatial distribution and the temporal variation of gadiform species. In particular, two different means of sea bottom temperature were included as covariates to investigate the potential effects of climate change. We applied a Hierarchical model of species communities (HMSC; Ovaskainen et al., 2017; Ovaskainen and Abrego, 2020), which is a Bayesian joint species distribution model that has been recently developed to be applied for the study of different communities in a variety of contexts, such as studying phenological changes, community assembly processes, and the effects of life history traits on spatio-temporal dynamics (Weigel et al., 2021; Maioli et al., 2023; Montanyès et al., 2023). The hierarchical structure of this model allows for highlighting environmental response patterns both at the species and at the community level, improving the detection of such relationships in rare species (Ovaskainen and Soininen, 2011; Norberg et al., 2019; Poggiato et al., 2021). Thus, considering the peculiar environmental conditions making the northern-central Adriatic Sea a cold refugium, and the recent shift in the thermal conditions, we selected five species of gadiform as a study model in order to address the following questions:

1) What are the primary environmental factors influencing the distribution and abundance patterns of gadiform species in the northern-central Adriatic Sea?

2) Are the species' responses to temperature different in magnitude and direction?

3) Is it possible to identify a shift in the temporal trend of temperature and consequently in species' response to the thermal covariates?

5.2 Materials and Methods

5.2.1 Study area

The study area is the western part of the central and northern Adriatic Sea (GSA 17; Figure 5.1), whose continental shelf, which is one of the largest of the Mediterranean and Black Seas (Marini et al., 2016), gently slopes down southward and eastward. The seabed is characterised by sandy-muddy bottoms and low values of depth on average. Nevertheless, the central and northern Adriatic Sea show different bathymetric features, having an average depth of 140 m and 35 m, respectively. Moreover, the central Adriatic Sea is characterised by the presence of mid-Adriatic depressions collectively called Pomo/Jabuka Pits, spanning across the West-East axis and reaching a depth of 260 m (Santelli et al., 2017). These depressions constitute the only deep-water habitat in this area, whose stable bottom temperatures (12−15°C) and low bottom currents make this spot one of the main nursery areas of the Mediterranean Sea (Druon et al., 2015). This area, which is also profitable for fish spawning and feeding, has been identified as an essential fish habitat (de Juan and Lleonart, 2010). Primary productivity shows high values in the Adriatic area, mainly on the north-western side, thanks to the presence of abundant river runoffs, which are thought to be around 20% of the whole Mediterranean freshwater input (Hopkins, 1992). The combination of nutrient inputs and shallow waters favours short trophic chains and high efficiencies of energy transfer between trophic levels (Fanelli et al., 2023), determining high biological productivity and creating optimal conditions for fishing activities. As a matter of fact, recent AIS-based studies have recognised this area as the most trawled in the entire Mediterranean Sea (Ferrà et al., 2018; Merino et al., 2019) and possibly in the world (Pitcher et al., 2022). Sea bottom temperature shows a strong seasonal cycle, ranging from 7 °C (winter) to 27 °C (summer) in coastal waters and from 10 °C (winter) to 18 °C (summer) in deeper areas (Russo et al., 2012). The physical properties and dynamics of the area are strongly influenced by atmospheric forces and river discharges, displaying marked temporal and spatial variations (Russo and Artegiani, 1996; Supić et al., 2004).

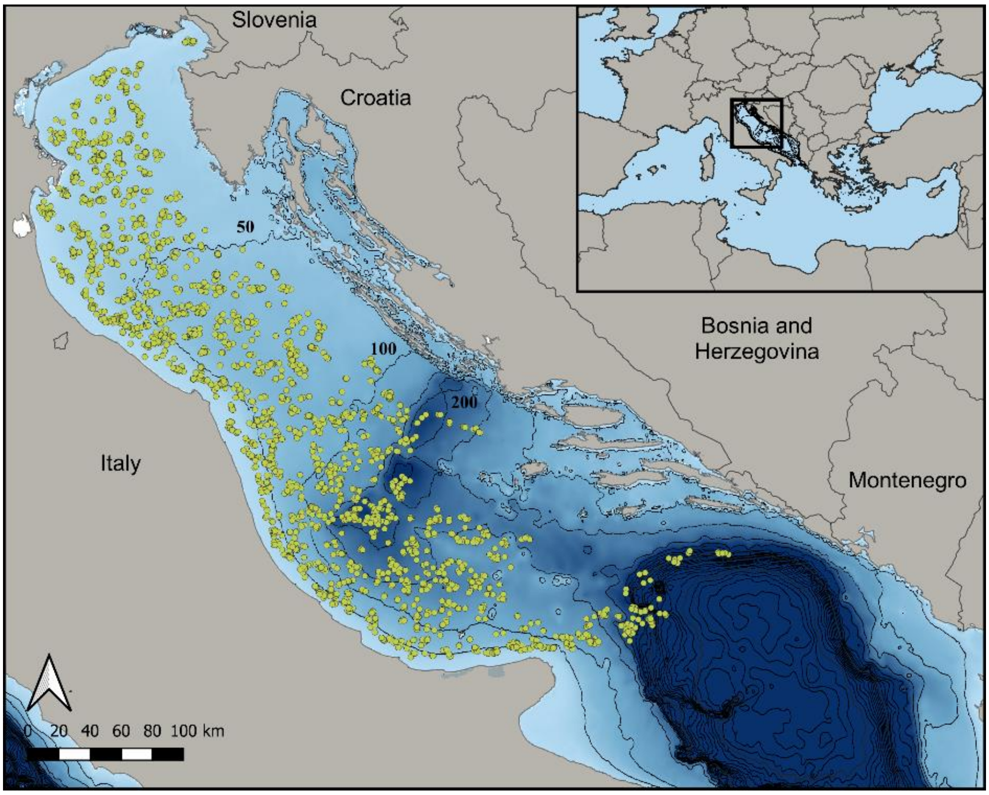


Figure 5.1. Study area and sampling stations (green circles) of the Italian MEDITS trawl surveys carried out in the period 1998–2020. Numbers indicate the values of the bathymetric lines.

5.2.2 MEDITS survey data

Data on gadiform species were collected during the scientific survey Mediterranean International Trawl Survey (MEDITS) (Spedicato et al., 2020) by the Laboratory of Marine Biology and Fisheries of Fano (University of Bologna), carried out usually during the late spring-summer period (May to September) on an annual basis since 1994, although in some years sampling has been extended to the autumn period. This survey used a stratified sampling design based on depth strata covering 10 to 500 m.

The sampling gear utilised was the GOC-73 experimental bottom otter trawl, which featured a horizontal opening of 16–22 m, a vertical opening of approximately 2.4 m, and a codend with a 20 mm (stretched) diamond mesh (Bertrand et al., 2002). The dataset included occurrence and abundance indexes (i.e., the number of fish per km^2 of trawled area) of five gadiform species, as well as depth data for each haul.

5.2.3 Environmental covariates, species traits, and phylogeny

Two different mean values of sea temperature, chlorophyll, and log-transformed depth were chosen to explain the environmental contribution to the occurrence pattern and variation of the abundance index. Considering the demersal nature of the study species, we extracted the monthly mean of Sea Bottom Temperature (SBT, in °C) from the Copernicus Marine Service Data with spatial resolution of 4 km^2 (Escudier et al., 2021) and then calculated the winter (January–March, SBTw) and the annual mean (SBTy) values to take into account the possibility that these covariates may explain different processes (e.g., abundance and/or occurrence pattern). Indeed, considering that the study species are mostly winter spawners and most of the hauls were carried out during the spring, we assumed the winter mean to be a reliable predictor of spawning and recruitment success (Hidalgo et al., 2019). Chlorophyll-a satellite data in µg l^{-1} were obtained from the Copernicus Marine Service Data with a spatial resolution of 1 km^2 (Volpe et al., 2019). Considering the relationship between phytoplankton blooms (mainly in springtime) and recruitment success (Platt et al., 2003), we calculated the spring average value (April–June) of chlorophyll-a and used it as a proxy for primary production and thus resource availability. In order to use data with the same spatial resolution, all environmental data were aggregated to a spatial resolution of 4 km^2 using the *raster* package (Hijmans and van Etten, 2018) in the software R (R Core Team, 2022). The environmental variables were then integrated with the haul data, coupling the data from each haul with the nearest spatial point of the variables and matching the temporal scale of the data. Depth data for each haul was obtained directly from the data collected onboard during the MEDITS survey. All the above-mentioned covariates were tested for multi-collinearity, ensuring they were not strongly correlated with each other ($- 0.7 < r < 0.7$) (Supplementary Figure 5.5).

We included in the model framework information about some life history traits to investigate their influence on the spatio-temporal dynamics and responses to environmental variability of the community, selecting seven traits to represent species' growth, reproduction, and diet patterns. Trait values for each species were collected from the available literature and authors' unpublished data, giving priority to the one collected in the Adriatic Sea (Table 5.1). To account for the possible influence of phylogenesis in determining the species' responses, we included the phylogenetic relationships of the included species, building a phylogenetic tree based on their taxonomic structure including order, family, genus, and species, and assuming an equal branch length between each node. This step was done using, as a reference, the gadiform phylogenesis of Teletchea et al. (2006) and the R-package *ape* (Paradis and Schliep, 2019).

Table 5.1. Life history traits of the species included in the study. Fecundity values are expressed on a logarithmic scale. k = growth rate (year^{-1}); L_{max} = maximum size (TL, cm); L_{inf} = Asymptotic length (cm).

Species	Trophic level	k	L_{max}	Lifespan	Age maturity	Fecundity	L_{inf}
Merlangius merlangus	4.36	1.89	37	3	1	12.21	23
Micromesistius poutassou	4.13	1.33	35	9	1	11.46	26
Trisopterus capelanus	3.56	0.70	28	4	1.3	11.49	20
Merluccius merluccius	4.42	0.15	82	20	2.5	12.89	70
Gadiculus argenteus	3.60	0.20	13	4	1.3	9.08	12

5.2.4 Modelling framework

We used the Hierarchical Modelling of Species Community (HMSC) (Ovaskainen et al., 2017; Tikhonov et al., 2020) model framework to investigate the spatio-temporal pattern of abundance of gadiforms in response to environmental variations and compare the two time series, including information on traits and phylogeny. We employed the R-package *Hmsc* (Ovaskainen and Abrego, 2020; Tikhonov et al., 2020), which allows for quantifying the proportion of variation explained within the community by including a given group of environmental covariates as well as through random effects. The inclusion of random effects allows for quantification of the residual variation not explained by the selected covariates, e.g., the one that comes from the spatial and temporal stochasticity of the data or underlying ecological processes (positive or negative interactions between species). By including spatial and temporal variation as latent variables, *Hmsc* creates matrices representing pair-wise species co-occurrence patterns in space or time in addition to information about the species' responses to the covariates (Montanyès et al., 2023). Since the study species showed different frequencies of occurrence and hence proportions of zero observations, we applied a hurdle model (Maunder and Punt, 2004). This modelling approach has been successfully applied to deal with zero-inflated data (Ciannelli et al., 2008; Pulcinella et al., 2019; Maioli et al., 2023). Occurrence probability was modelled using a binary response variable through probit regression in the presence-absence (PA) model, while data from haul with positive values of abundance, log-transformed, were modelled through a log-linear regression in the abundance (ABU) model.

To investigate the temporal trend of sea temperature and successively potential variations in species response to sea warming, we used the sequential t-test analysis of regime shift (STARS v. 6.3), first developed by Rodionov (2004). In particular, we aimed to detect potential abrupt changes in the annual mean of Sea Surface Temperature (SST) in the GSA 17 between 1998 and 2020. The cut-off length was set at 10 years, the significance level at 0.05, and Huber's weight parameter at 2. Then, we decided to split the whole dataset into two time series (henceforth called "before thermal shift" - BTS and "after thermal shift" - ATS, respectively) to compare their model outputs in terms of species responses to environmental covariates. For each model type, we considered two sub-models in relation to the thermal difference highlighted through the STARS analysis, thus fitting a total of four models: PA-BTS, PA-ATS, ABU-BTS, and ABU-ATS. The linear fixed effects in our analysis included SBTw, SBTy, chlorophyll-a concentration, and depth. As for the random variables, we included year as a temporal unstructured random effect and cell ID (spatial resolution of 4 km^2), as a spatially explicit random effect. The models were fitted assuming the default *Hmsc* priors (Tikhonov et al., 2020) and sampling the posterior distribution resulting from eight Markov chain Monte Carlo (MCMC) simulations, each collecting 250 samples and being run for 370,500 iterations, of which the first 125,000 were discarded as burn-in and applying a thinning of 1000. After the model fitting, we evaluated quantitatively the convergence of the Markov Chain Monte Carlo (MCMC) simulations in terms of sample sizes and potential scale reduction factors (Supplementary Figures 5.6 and

5.7) (Gelman and Rubin, 1992; Brooks and Gelman, 1998). The explanatory power of the model was evaluated by computing the coefficient of discrimination Tjur's R^2 (Tjur, 2009) together with the Area Under the Curve (AUC) (Pearce and Ferrier, 2000) for the PA model and by computing the R^2 for the ABU model. We then summarized the overall explanatory power of each model using a mean value of explanatory power across species. The proportional variance partitioning among fixed and random factors of both the PA models and the ABU models was calculated, following Ovaskainen et al. (2017). We explored how species and traits respond to environmental variables through a visual representation of the so-called *beta* and *gamma* parameters, respectively, applying a threshold of statistical support of 95% posterior probability. We also investigated the phylogenetic correlation, denoted as parameter *rho*, which is constrained between 0 and 1. The greater the value of *rho*, the stronger the correlation between environmental niches and the evolutionary history of the species (i.e., species distribution patterns are influenced mainly by their phylogenetic affinity rather than selective pressures due to environmental variability). Finally, we assessed species co-occurrence patterns at the levels of the spatial and temporal random effects included in the model, which could be useful to highlight pairs of species that co-occur more (or less) frequently than by random after accounting for their environmental preferences. However, since our model structure is spatially explicit, attention is needed in interpreting the results because the highlighted patterns could also represent spatial variation of unobserved covariates. Statistical analyses were performed in R version 4.1.0.

5.3 Results

A total of 2866 hauls carried out between 1998 and 2020 were considered in our analyses, after removing the first 4 years of the MEDITS data series because of the unavailability of satellite chlorophyll data until 1998 from the Copernicus Marine Service Data. The application of the STARS method to the SST annual mean in the GSA 17 allowed us to detect two dominant thermal regimes, identifying a thermal shift that occurred between 2010 and 2011. The SST mean value between these years changed abruptly from 17.7 to 18.3 °C, remaining steadily above 18 °C after 2011.

Accordingly, we identified as BTS and AFS the periods 1998–2010 and 2011–2020, respectively.

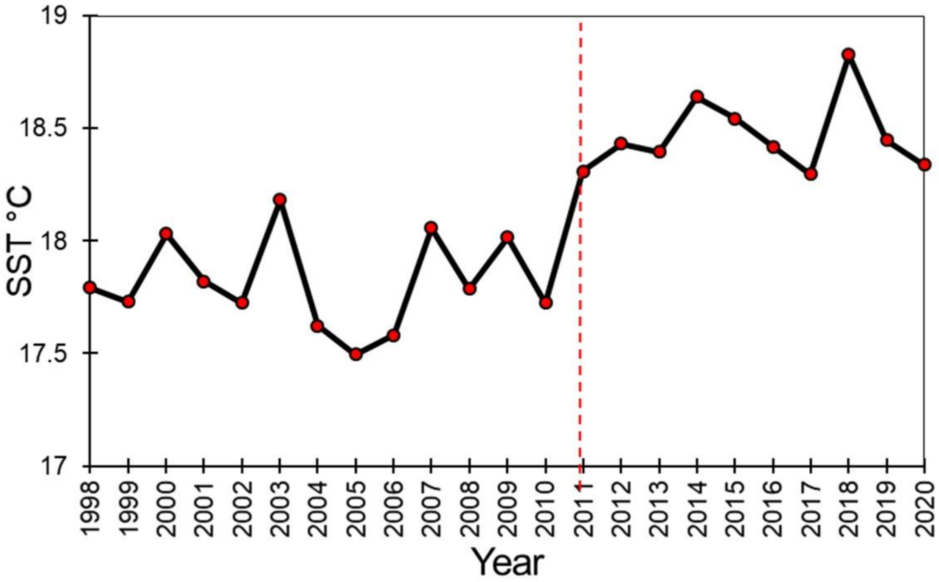


Figure 5.2. Trend of the mean annual values of sea surface temperature (SST) in the northern-central Adriatic Sea from 1998 to 2020. The red dotted line indicates the year of the thermal shift identified using the sequential t-test analysis of regime shift (STARS) method. Satellite data from Copernicus Marine Service, Mediterranean Sea - High Resolution L4 Sea Surface Temperature Reprocessed. https://doi.org/10.48670/moi-00173.

5.3.1 Model evaluation

The MCMC convergence was considered satisfactory, as evidenced by the mean (and standard deviation) of the potential scale reduction factor for both beta, gamma, and omega parameters being very close to 1. These values reflect the species and traits (community-weighed) responses to the environment and the co-occurrence patterns, respectively (Supplementary Figures 5.6 and 5.7). Assuming that the effective sample size of the MCMC was approximately equal to the number of posterior samples, the autocorrelation of the samples can be considered not significant (Supplementary Figures 5.6 and 5.7). Both PA and the ABU models showed a satisfactory fit to the data, showing values of mean Tjur's R^2 (AUC) of 0.61 (0.97) for the PA models, while the explanatory power (R^2) of the ABU models was 0.52.

5.3.2 Influence of environmental covariates

The species ABU and PA patterns were both affected by environmental variables, although we found a different pattern in the proportion of variance explained by the fixed vs dynamic covariates. Variance partitioning over the explanatory covariates highlighted that a high amount of variation was explained by fixed effect accounting for around 63% and 55% of the total variance explained by the PA and ABU models, respectively (averaged values between the BTS and ATS periods) (Figure 5.3). While in the PA models, depth explained around 90% of the variance explained by the fixed covariates, in the ABU models, all the fixed covariates contributed to explaining the variation of species abundance. Random effects at the spatial level (cell ID) explained on average 35% and 36% of the variance in PA and ABU models, respectively; at the temporal level, the random effects explained only a small share of the variance, on average accounting for 2% and 8% in PA and ABU models, respectively.

Depth was the main factor influencing the occurrence pattern of gadiform species, explaining most of the variance in blue whiting, European hake, and silvery pout, while, in whiting and poor cod the contribution of depth as an explanatory variable was lower. The contribution of chlorophyll-a in both PA and ABU models was only observable in the deep-water species blue-whiting and silvery pout. Comparing the BTS and ATS PA models, we observed a consistent pattern in the proportions of variance explained, with small differences in the species-specific share of proportion between spatial random factor and depth. The only difference noticeable is related to the increase in the variance explained by chlorophyll-a in blue whiting and silvery pout. On the other hand, the comparison of the BTS and ATS ABU models highlighted a common pattern of variation among gadiform species, with an overall reduction of the variance explained by the random factors (from 55% to 34%) and the increase of components explained by the fixed covariates (from 45% to 66%). Interestingly, this variation was mainly driven by the temperature covariates, which increased their share of variance from 5–8% to 21–22%.

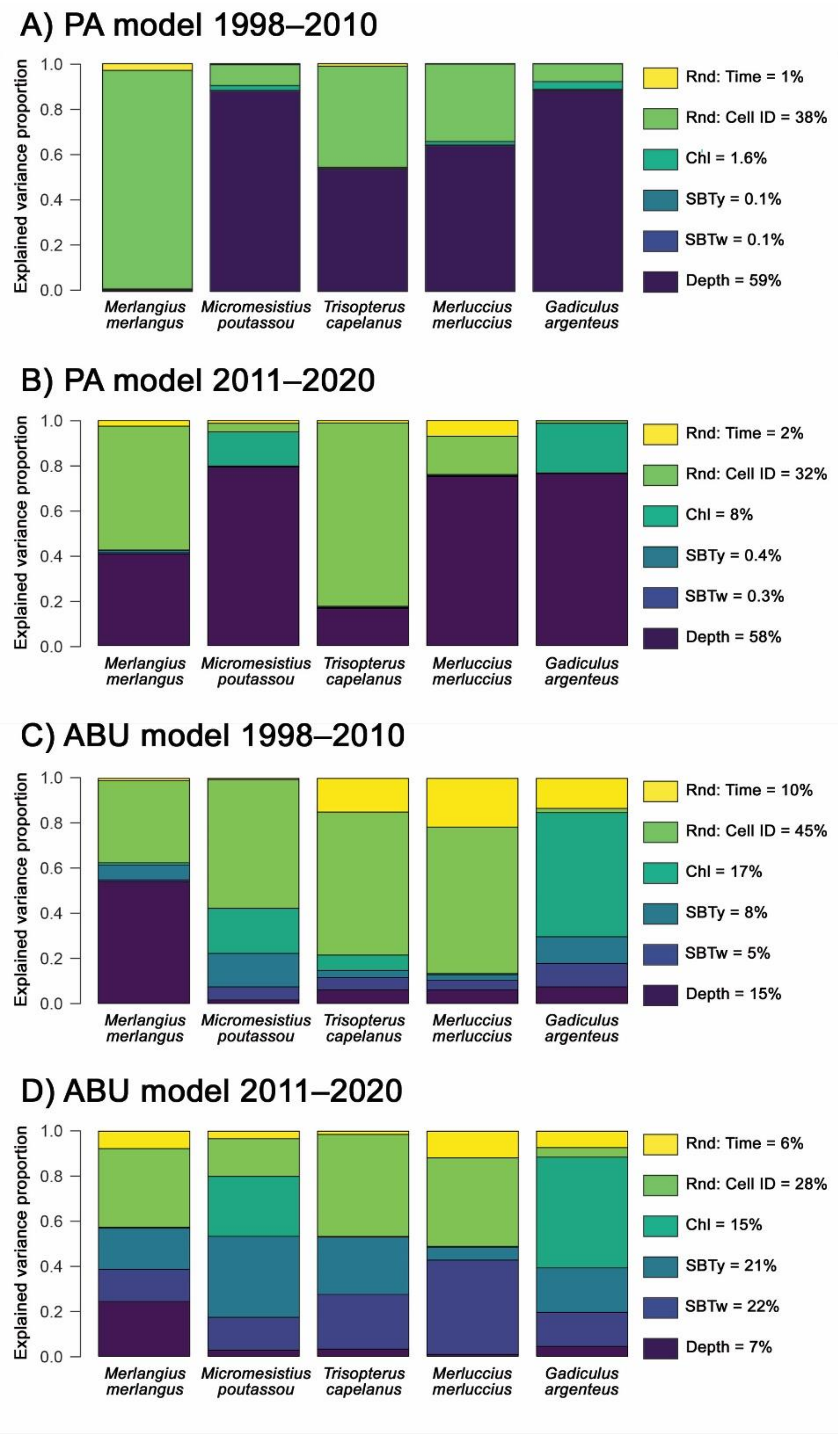


Figure 5.3. Variance partitioning among the explanatory variables included in the presence-absence (PA; A, B) and abundance (ABU; C, D) models. The average

proportions of variance across all species are indicated between brackets and the legend. Chl = chlorophyll-a; SBTy = annual mean Sea Bottom Temperature; SBTw = winter mean Sea Bottom Temperature; Random: grid.cell = spatial random effects at the cell ID level; Random: year = temporal random effects.

The species-specific responses to the environmental covariates, considering the results with a high level of statistical support (posterior probability > 0.95) showed a different scale of variation comparing the PA and ABU models, with some differences between BTS and ATS periods. In the PA models, the key role of depth was confirmed, with almost all the species responding positively to higher depth values, except for whiting. Despite their low importance overall, in all the species only negative responses were observed with chlorophyll-a and bottom temperature. In the ABU models, the environmental-related responses showed a higher degree of variability depending on the species and the time series. The only species not showing a relationship between abundance and environmental variability was the silvery pout (Figure 5.4 C, D).

The species-environment relationships derived from the occurrence data of the BTS and ATS time series revealed some differences in species responses, both in the PA and ABU models (Figure 5.4 B, D). Among the different species-specific variations in response to environmental covariates, the most intriguing aspect is that all the species showed variations in their response to the temperature covariates. In particular, whiting, blue whiting, and poor cod showed negative variations in their response to increasing temperature; on the other hand, European hake showed a positive influence with temperature in both BTS and ATS time series.

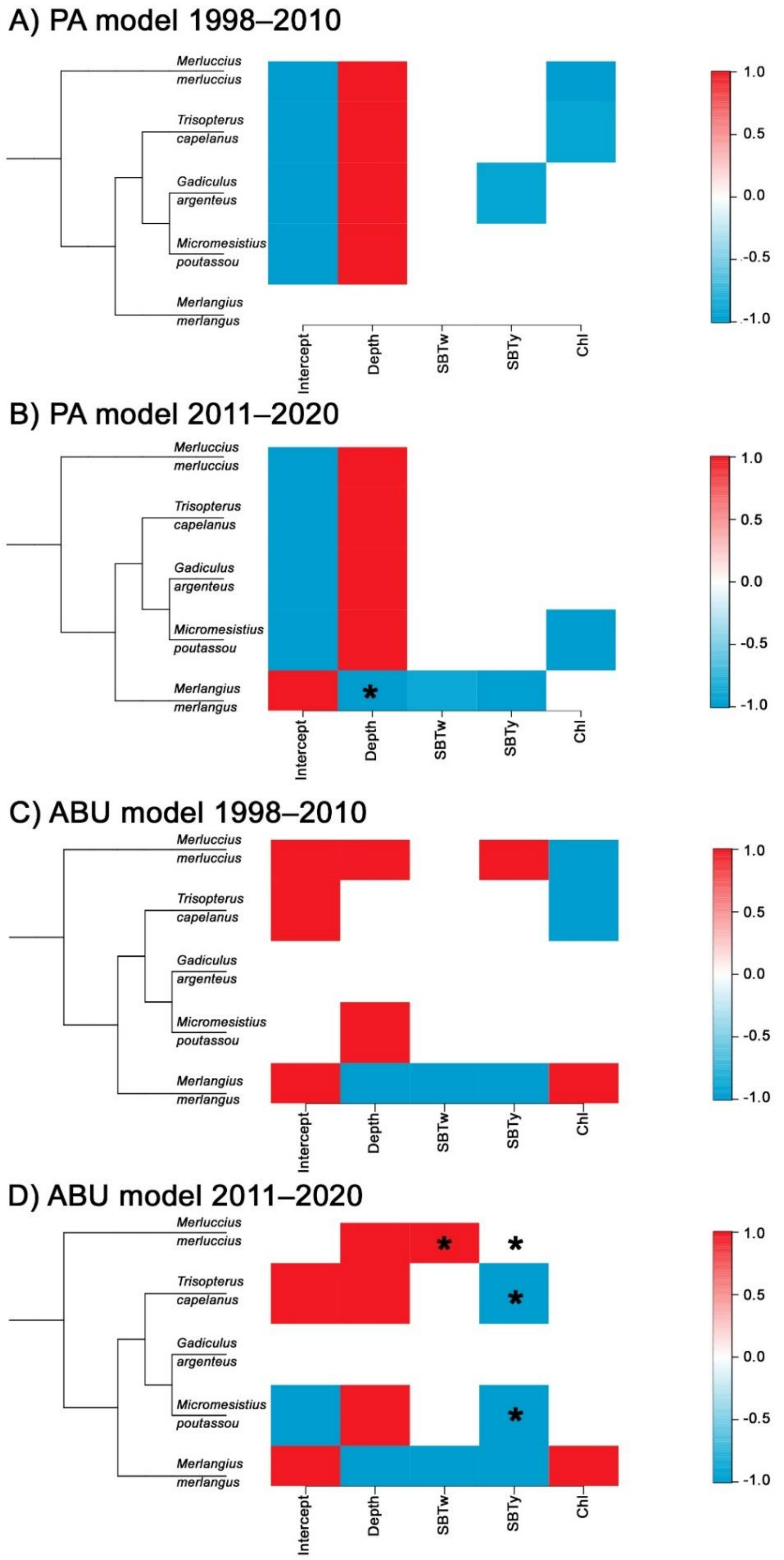


Figure 5.4. Estimated β parameters for the presence-absence (PA; A, B) and abundance (ABU; C, D) models, showing the responses of species to environmental covariates, represented as a heatmap. Using a minimum 95% posterior probability of

support, red squares indicate positive responses and blue squares indicate negative responses. White squares indicate responses that did not receive substantial statistical support. Asterisks indicate a meaningful variation in the response between the 1998–2010 and 2011–2020 time series. Chl = chlorophyll-a; SBTy = annual mean Sea Bottom Temperature; SBTw = winter mean Sea Bottom Temperature.

5.3.3 Influence of life history traits and co-occurrence/co-variation patterns

As regards the traits included in the model, we found that, on average, they explained 40% and 57% of the total variance in species responses to environmental covariates, respectively. Despite the substantial proportion of variance explained by traits in determining species responses to different environmental features, we only found a significant positive relationship (posterior support > 0.95) between lifespan and depth. However, we did not find strong support for phylogenetic niche conservatism, as the rho parameter (indicating the phylogenetic signal) was 0.30 and 0.50 in the PA and ABU models, respectively. This indicates that, despite the phylogenetic closeness between gadiform species, their response patterns were diversified and species-specific. Considering that the spatial random factor accounted for a significant proportion of variance in both models, we investigated the residual species associations at the spatial scales (cell ID). In addition, we investigated the temporal random effect only for the ABU models, taking into account its contribution to explaining abundance variations. The co-occurrence pattern of the PA model showed that all species are strongly correlated in space among them, with the exception of the European hake, which showed a lower correlation, albeit present, with all the other species (Figure 5.5 A, B). No differences were found between the BTS and ATF periods, confirming that the occurrence pattern of gadiform species did not show any particular trend over the last decades. Looking at the species association matrices of the ABU models, a high degree of variability is observed between the species pairs when comparing the time series (Figure 5.5 C, D). Species associations, potentially explained by biotic interactions or other unaccounted variables, varied at the level of both spatial and temporal random effects. Co-occurrence patterns between species at the spatial level changed mainly in their intensity but also in their direction (i.e., the onset of negative interactions between poor cod with European hake and blue whiting). At the temporal level, we observed differences in all the interactions between species pairs, which were mainly negative both in the BTS and ATS periods.

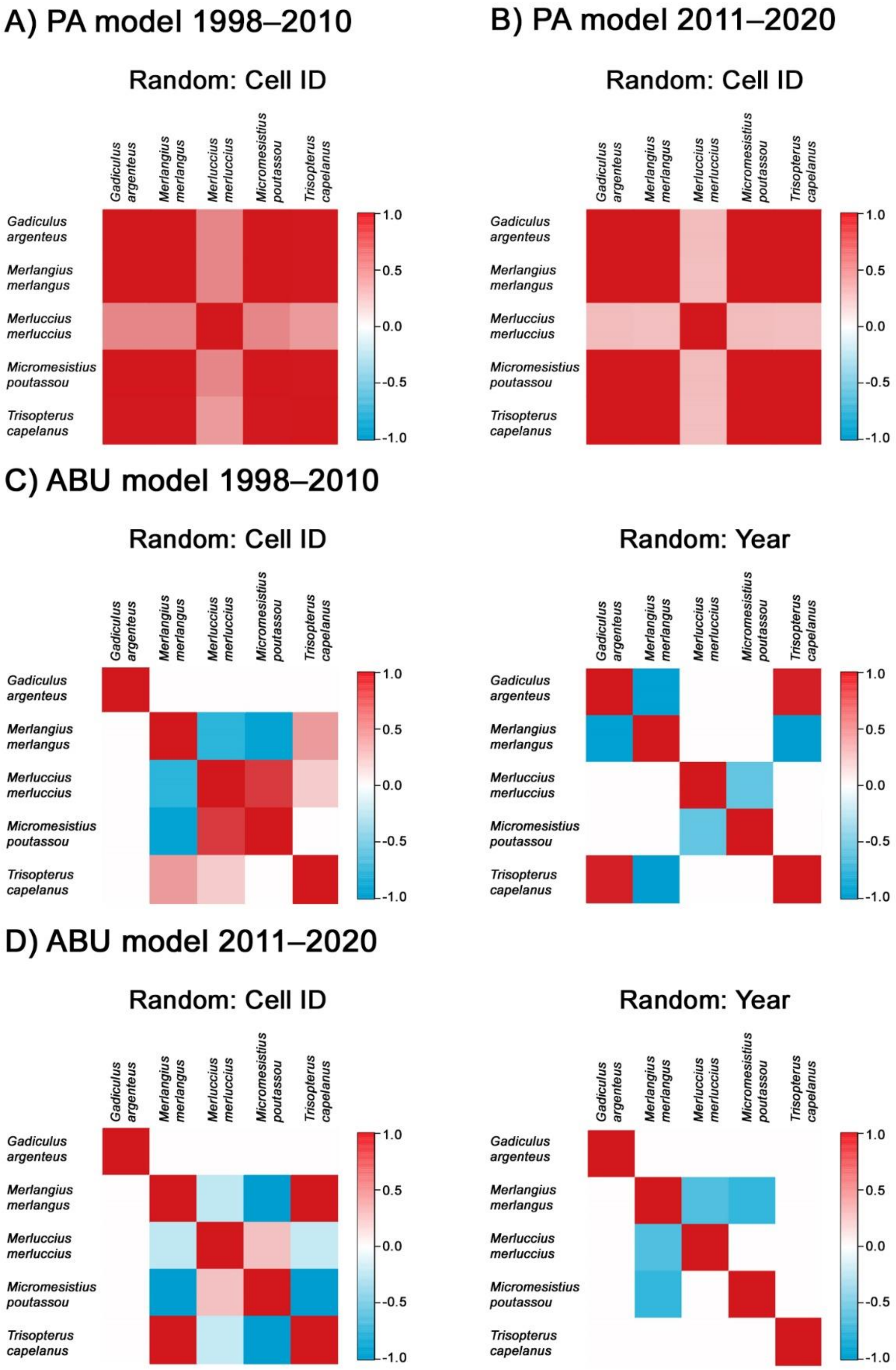


Figure 5.5. Residual species correlation matrices at the random levels: spatial random effects (cell ID) in presence-absence models (PA; A, B); spatial and temporal random effects in abundance models (ABU; C, D) models. The red and blue colours show species with positive and negative pair-wise associations (with at least a posterior probability of 0.95), respectively.

5.4. Discussion

We applied a joint species distribution model framework over a fish group more prone to cold thermal habitats but with high intra-group diversity, with the integration of data on life history traits and phylogeny. The analysis allowed us to identify both consistent and species-specific environmental factors influencing the occurrence and abundance pattern of the gadiform community in the northern-central Adriatic Sea over the last 20 years. Moreover, the comparison of model results related to the periods before (BTS) and after (ATS) the thermal shift of SST values that occurred in the area highlighted some differences in the species' responses to the temperature covariates and co-occurrence patterns. While the gadiform species occurrence was mainly driven by depth, the variation in abundance was explained by different combinations of the other covariates. The comparison of PA models between BTS and ATS did not highlight significant differences, suggesting that species occurrence patterns in the area are mainly under the control of conditions associated with bottom depth. On the other hand, comparing the factors involved in the abundance variations between BTS and ATS, we observed an overall increase through the time of the variance explained by the temperature covariates that we interpreted as an increase in the species' sensitivity to the temperature. Another significant result coming from the comparison is that gadiform species showed different responses to increasing temperature, allowing us to determine their potential vulnerability to the warming process.

The use of the STARS method on the SST data of the northern-central Adriatic Sea allowed us to identify the existence of two different thermal regimes in the period between 1998 and 2020, with a transition phase between 2010 and 2011. This result is consistent with Sguotti et al. (2022), which identified in 2011, through a Bayesian Change Point Analysis (Barry and Hartigan, 1993), the presence of an abrupt change in the landing trend of one of the major fishing fleets of the Adriatic Sea. The demersal community shift of the northern Adriatic Sea was thought to be linked to the combined effect of high levels of fishing pressure in the area (historically acting as a stressor), but also to the step-like increase of SST of nearly 1°C between 2010 and 2011 that occurred in the northern Adriatic Sea. Increasing values of SST have been widely reported in the whole Mediterranean Sea, with the Adriatic Sea being one of the most relevant hotspots, with an increase in the mean value of SST of more than 1 °C (Bonacci and Vrsalović, 2022; García-Monteiro et al., 2022; Calì et al., 2023a, 2023b).

There are multiple factors potentially contributing to explaining this phenomenon. Firstly, the peculiar shallowness and geographical positioning of the northern-central Adriatic Sea make it more susceptible to temperature variations. In this sub-basin, which has a mean depth lower than 100 m, the sea temperature is strongly linked to the seasonal cycle of air temperature, showing a wider range of variation compared to the other Mediterranean areas (Russo and Artegiani, 1996). Considering that higher warming trends were observed at higher latitudes (Fossheim et al., 2015; Bonacci and Vrsalović, 2022), the shallowness of the northern-central Adriatic Sea, together with its northern positioning in the Mediterranean context, determines an overall high susceptibility to warming.

Secondly, observational data based on the frequency and intensity of winter storms in the northern part of the Adriatic Sea suggested a decreasing trend over the second half of the 20th century (Lionello et al., 2012). The occurrence of winter storms, associated with strong northerly winds, is essential to maintain the dynamics of water circulation in this basin and to allow for the formation of cold and dense waters, which contribute to the overall thermal balance not only of the Adriatic Sea but also at a Mediterranean scale (Schroeder et al., 2017). Hence, it is plausible to hypothesise that less severe and frequent storms may have contributed to higher rates of heat retention in this area. Thirdly, another possible explanation is related to the effects of the overall reduction of freshwater inputs, mainly driven by the negative trend that occurred over the last 50 years of the largest tributary river Po (Marini and Grilli, 2023). The Adriatic Sea circulation and hydrology are strongly influenced by weather conditions and freshwater inputs (Vodopivec et al., 2022), which have a key role in controlling the heat balance as they have a cooling effect during the winter season (Gačić, 1997). Therefore, the decreased cooling effect of the river inputs may have acted as an additional factor contributing to the warming trend of the area.

The proportion of variance explained by the fixed factors (63% and 55% in PA and ABU models, respectively) clearly indicates that the environmental covariates incorporated in our models are highly relevant in explaining variations in occurrence and abundance of gadiform species in the northern-central Adriatic Sea. Our results show that their occurrence pattern is strongly affected by depth, confirming the results obtained in previous studies on spatial patterns of gadiform species (Kerby et al., 2013; Post et al., 2019; Mir-Arguimbau et al., 2020) and on spatio-temporal dynamics of demersal species in the Adriatic Sea (Maioli et al., 2023; Panzeri et al., 2023). Interestingly, gadiform species showed different bathymetric ranges of occurrence, with some species showing some similarities. Overall, the occurrence probability of all the species increases with depth, within the range explored by our data. The only species showing a completely different pattern is the whiting, which is a typical shallow-water species whose catch is rare to be observed at depths > 150 m (Cohen et al., 1990). Over the period considered in the present study, we found whiting specimens at a maximum depth of 120 m in the southernmost part of the study area. Even if our aim was not to evaluate the occurrence of temporal shifts in depth, we observed a slight difference in the depth range of almost all the species, showing a higher variability in the ATS compared to the BTS period (Supplementary Figure 5.1 A, B). Moreover, the estimation of the importance of environmental factors is probably conservative due to the inability to rule out the potential influence of unaccounted environmental variables that could be incorporated into the model's random component (Ovaskainen et al., 2017).

The most important result emerging from this work was the difference in the variance explained by the temperature covariates between the two thermal regimes in the ABU models. Indeed, the increase in the proportion of variance explained by the fixed effect observed, at the expense of the random component, can be attributed to their contribution. Both annual and winter mean values of SBT contributed to the observed variation, confirming the importance of including seasonal mean values to highlight some features of the population dynamics of the study species (Hidalgo et al., 2012, 2019). In our study, the use of both winter and annual means of SBT allowed us to disentangle their effect, as in the case of European hake, where almost all the variance explained by the temperature covariates in the BTS abundance model is related to SBTw. To properly discuss the implications of these results, it is necessary to take into account the species-specific relationship between abundance and temperature. Almost all the gadiform species showed a negative effect of increasing temperature on abundance values (with different slopes), except for European hake, which showed a positive pattern (Supplementary Figure 5.2). Silvery pout was the only species not showing a significant trend, probably in relation to the low number of records as it is considered rare compared to the other gadiform species. The negative response observed in whiting, blue whiting, and poor cod put in evidence their cold-water preference and the increased negative response to higher temperatures could be related to the fact that the populations inhabiting the Adriatic Sea are at the trailing-edge of their latitudinal range (Pinsky et al., 2020). Indeed, along the edges of their distribution ranges, species are expected to respond more strongly to climate change, as hypothesised by Rijnsdorp et al. (2009) and reported in several studies (Engelhard et al., 2011; Olafsdottir et al., 2019). On the other hand, European hake, showing a wider distribution and being abundant in the whole Mediterranean basin, resulted in being an outgroup member of the study group and showed a positive response of abundance values to increased temperatures, which was significant in the ATS period. It is worth noting that around 40% of the variance explained in this species is related to SBTw. Considering that this species shows the highest thermophilic attitude within the study group (Froese and Pauly, 2022), it is therefore possible to hypothesise that the winter temperature in the Adriatic area could have acted as a limiting factor before the thermal shift. This result is supported by experimental results on the effect of temperature on the development of European hake eggs, reporting that 12.7 °C is the threshold temperature below which the egg mortality rate increases significantly (Guevara-Fletcher et al., 2016). Indeed, before 2011, the mean sea temperature was rarely higher than this threshold (Supplementary Figure 5.3), providing a straightforward explanation of the positive response of this species.

Chlorophyll-a values showed a significant contribution in explaining the variation patterns only in the strict deep-water species blue whiting and silvery pout, both in ABU and PA models. Almost all the species showed a correlation with the strength of primary production in spring, except for the whiting abundance, which was positively correlated. This negative relationship between primary production and marine resource production has already been observed in the Mediterranean and is attributed to inter-specific competition (Puerta et al., 2015). Therefore, it can be hypothesised that years characterised by high productivity in the deep areas of the Adriatic Sea (which are usually poor in nutrients) during the spring season lead to an overall increase in the abundance of the nektobenthic community. This heightened abundance subsequently intensifies the competition between gadiform species, potentially resulting in food scarcity and reduced survival rates. The opposite pattern observed in whiting supports this hypothesis, being the only species having highly productive areas as favourable habitats and being more abundant in the northern sector of the Adriatic Sea (Calì et al., 2023b). Thus, the low overlap of whiting with other gadiform species may prevent the triggering of inter-specific competition and resource limitation dynamics, explaining the positive relationship between its abundance and primary productivity (which can be considered a proxy of prey availability).

Although the traits included explained 40% of the variation in species occurrence and 57% of the variation in species abundance in response to environmental covariates, only the positive relationship between lifespan and depth in both ABU models was significant. This finding is consistent with the general trend observed when comparing fish species inhabiting different bathymetric ranges, with deep-water species showing clear “K-selected” life history characteristics, for example, high longevity, slow growth, and low fecundity (Koslow et al., 2000; Lloret et al., 2021). This gradient is noticeable in our study group even if we considered a small number of correlated species, showing the highest predicted value (community-weighted) in the Pomo/Jabuka Pits area (Supplementary Figure 5.4). The variance explained by the random effect in our models (35–40%) was lower compared to previous studies applying the same model framework (Weigel et al., 2021; Maioli et al., 2023; Montanyès et al., 2023), indicating that the fixed covariates we selected were appropriate to explain most of the variation in occurrence and abundance patterns. However, the presence of the random component indicates the existence of additional spatially-dependent and stochastic processes beyond those accounted for by environmental drivers that influence species distribution and occurrence. Despite the fact that the processes affecting the random parts can be linked to other unaccounted environmental variables, the main part of these patterns can presumably be attributed to interactions between species (Montanyès et al., 2023). The residual species association matrices, which were obtained from the spatial random effect (PA and ABU models) and the temporal random effect (ABU models), highlighted some interesting and significant patterns. For example, from the spatial co-occurrence pattern of the whole period considered, it is possible to observe that European hake was the only species showing a lower value in the positive correlation with the other species. Even if more specific research is needed to better understand species co-occurrence patterns, the overall positive correlation between all the species might be related to their peculiar trophic ecology. Indeed, although they show a certain degree of overlap in their trophic spectra (being considered generalist predators), the characteristics of each trophic niche are species-specific (Sartor, 1995). Thus, as a general rule, they can coexist (after accounting for species niches) and exploit the same resources without incurring competitive phenomena. Finally, the lower positive correlation of European hake with all the other species could be explained by considering that this species, having the highest size and trophic level within the study group, can prey upon the other ones, as reported by Riccioni et al. (2022).

5.4.1 Conclusions

In conclusion, the present study presents significant findings regarding the impact of some environmental factors on the distribution and abundance of five cold-water species. Notably, the analysis revealed that while species occurrence is predominantly influenced by depth, the variance in abundance is affected by a combination of other covariates, especially temperature. The distinct responses of gadiform species to increasing temperatures highlight the varying vulnerabilities of these species to climate change. This is particularly evident in the increased sensitivity to temperature changes in the period after the thermal shift, suggesting a potential risk of alteration in the species' population dynamics due to warming waters.

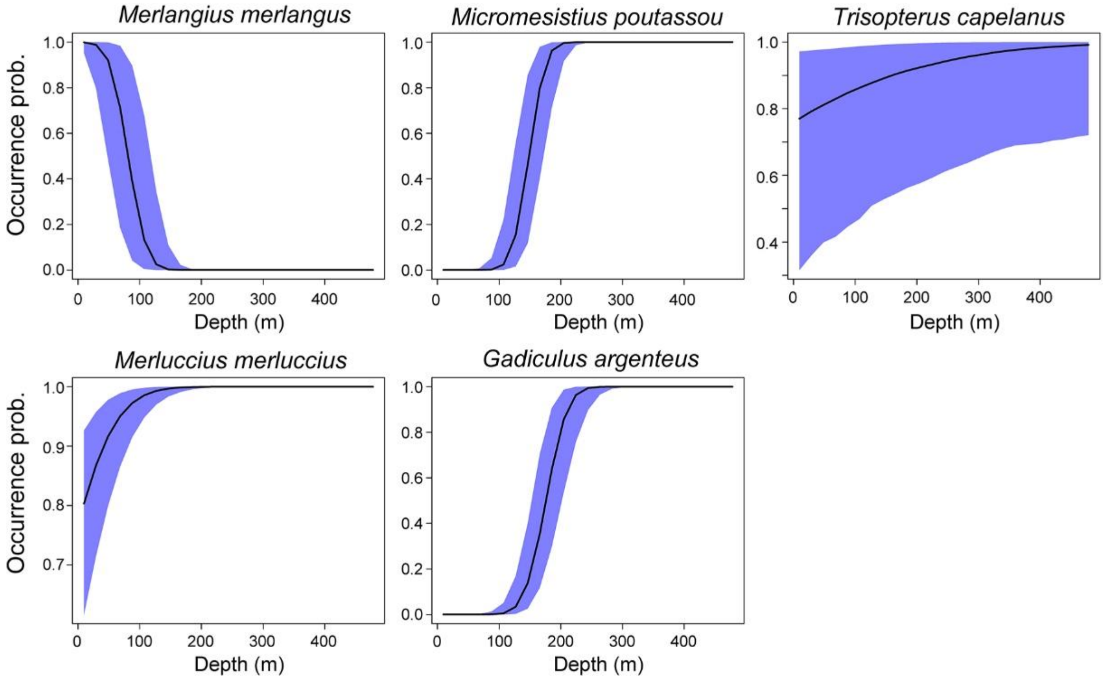
The implications of these findings are substantial for conservation and fishery management in the Adriatic Sea. The differential vulnerability of gadiform species to increasing temperatures indicates the need to consider species-specific responses when setting conservation strategies to counteract the effects of climate change. The present study underscores the importance of monitoring and adapting to ongoing climatic shifts, particularly in ecologically sensitive areas like the northern-central Adriatic Sea. Furthermore, the insights gained about species-specific depth preferences and responses to temperature and other environmental variables can guide sustainable fishing practices and habitat protection efforts. The variability in species' responses to environmental factors within a small group of related species exemplifies the complexity of marine ecosystems and the need for multi-faceted approaches to marine conservation and resource management. As climate change continues to impact marine environments, studies like ours provide crucial data for predicting and mitigating its effects on marine biodiversity and the fisheries that depend on it.

Acknowledgments

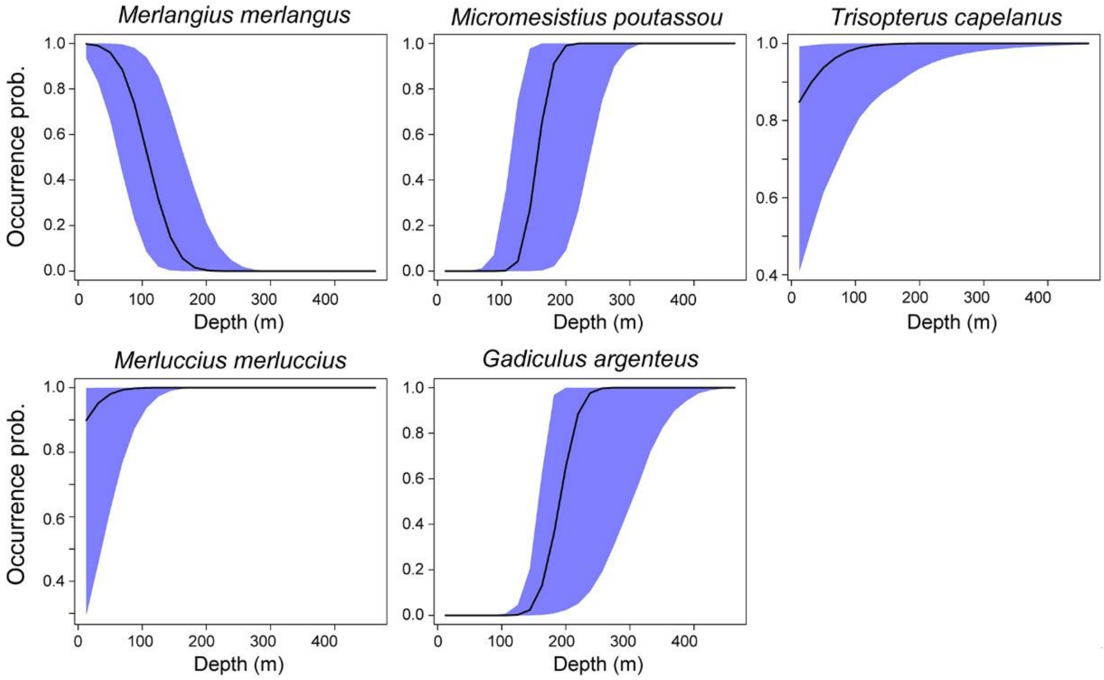
We thank the MEDITS staff involved in the scientific surveys and analysis of data. The research leading to these results was conceived under the International Ph.D. program “Innovative Technologies and Sustainable Use of Mediterranean Sea Fishery and Biological Resources” (www.FishMed-PhD.org, accessed July 10, 2023). This study represents partial fulfillment of the requirements for the Ph.D. thesis of Federico Calì.

Supplementary Material

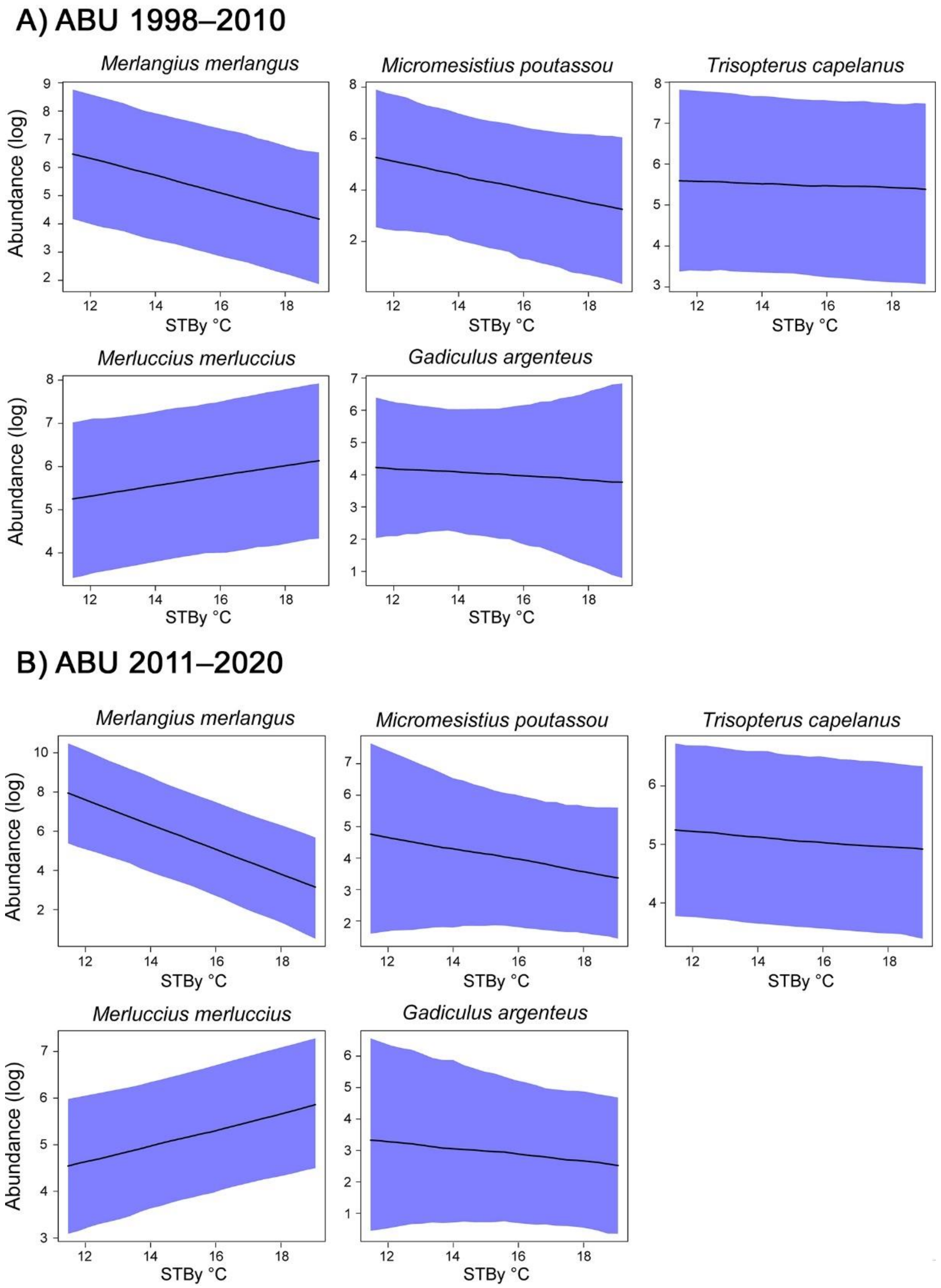
A) PA 1998–2010



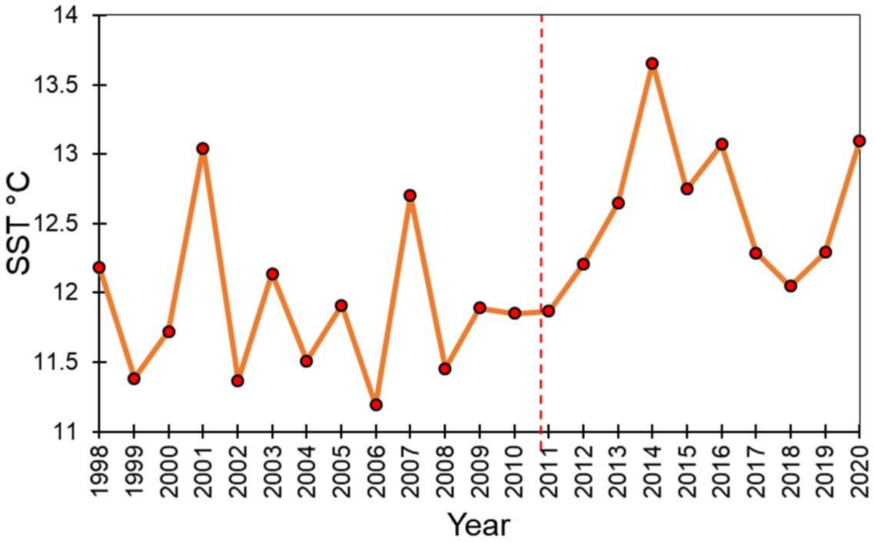
B) PA 2011–2020



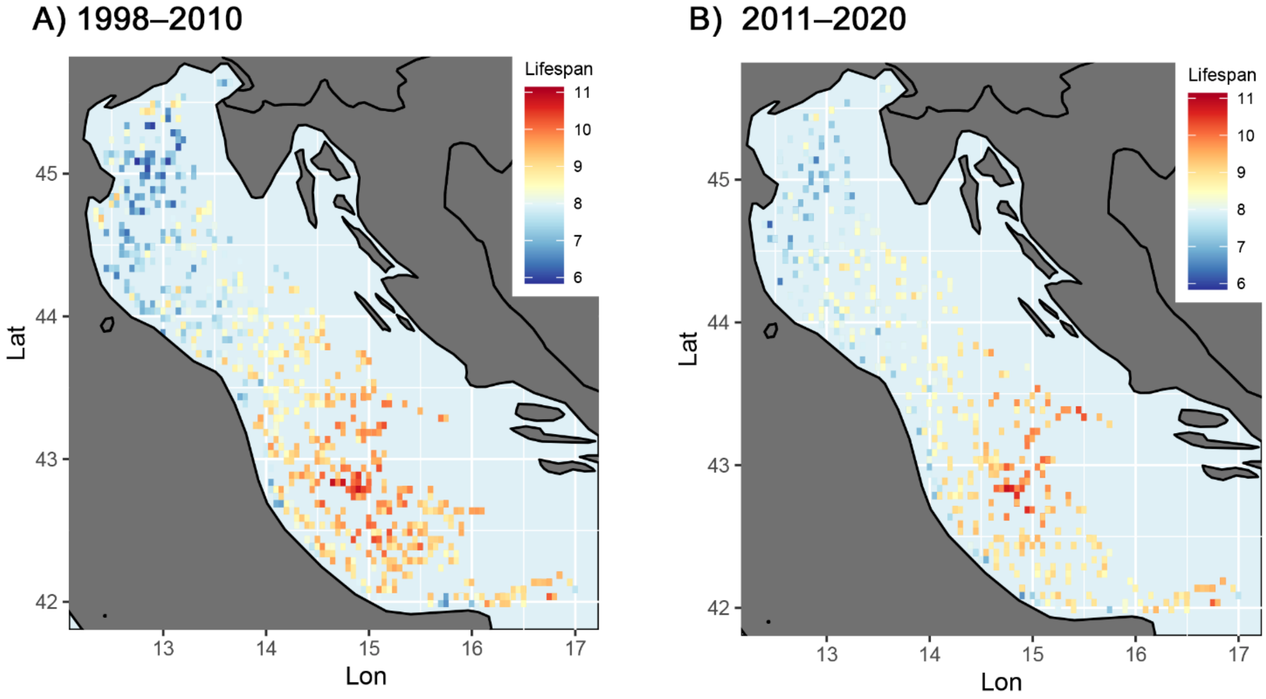
Supplementary Figure 5.1. Marginal effects of depth on the probability of occurrence of gadiform species in the northern-central Adriatic Sea. Shaded areas represent 95% credible intervals. Effects in the manuscript are only reported and discussed with probabilities > 0.95.



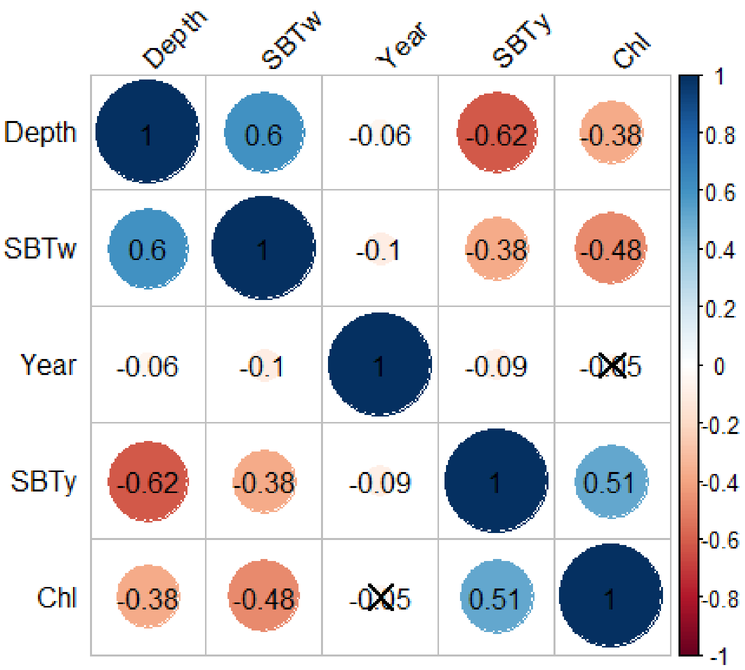
Supplementary Figure 5.2. Marginal effects of annual mean of Sea Bottom Temperature (SBTy) on the abundance (log-transformed) of gadiform species in the northern-central Adriatic Sea. Shaded areas represent 95% credible intervals. Effects in the manuscript are only reported and discussed with probabilities > 0.95.



Supplementary Figure 5.3. Temporal trend of the mean winter values of sea surface temperature (SST) in the northern-central Adriatic Sea from 1998 to 2020. The red dotted line indicates the year of the thermal shift identified using the sequential t-test analysis of regime shift method. Satellite data from Copernicus Marine Service, Mediterranean Sea - High Resolution L4 Sea Surface Temperature Reprocessed. https://doi.org/10.48670/moi-00173.

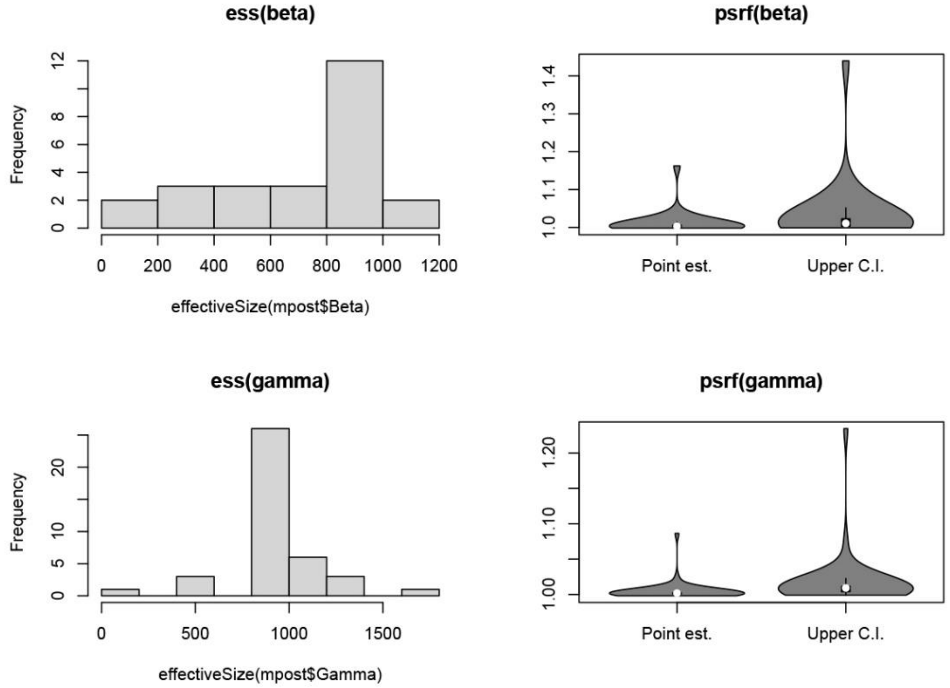


Supplementary Figure 5.4. Predicted community-weighted mean traits based on the abundance models. The maps show the posterior mean estimate of the lifespan for the 1998-2010 (A) and the 2011-2020 (B) periods.

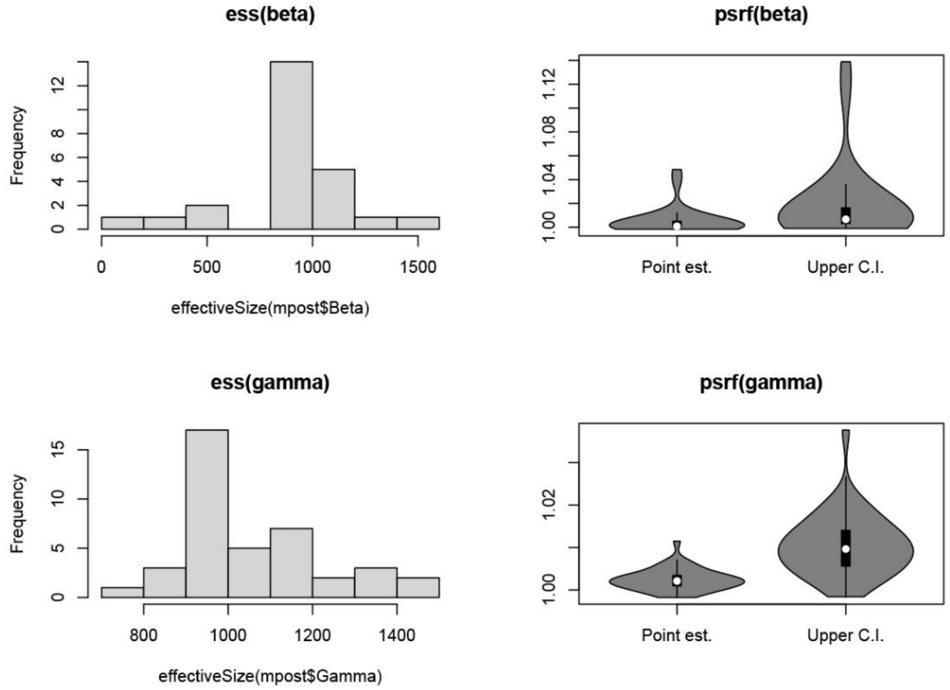


Supplementary Figure 5.5. Pearson pairwise correlation coefficients for the environmental covariates included in the analysis. The red and blue colours indicate positive and negative coefficients (reported inside the circles), respectively. Chl = chlorophyll-a; SBTy = annual mean Sea Bottom Temperature; SBTw = winter mean Sea Bottom Temperature.

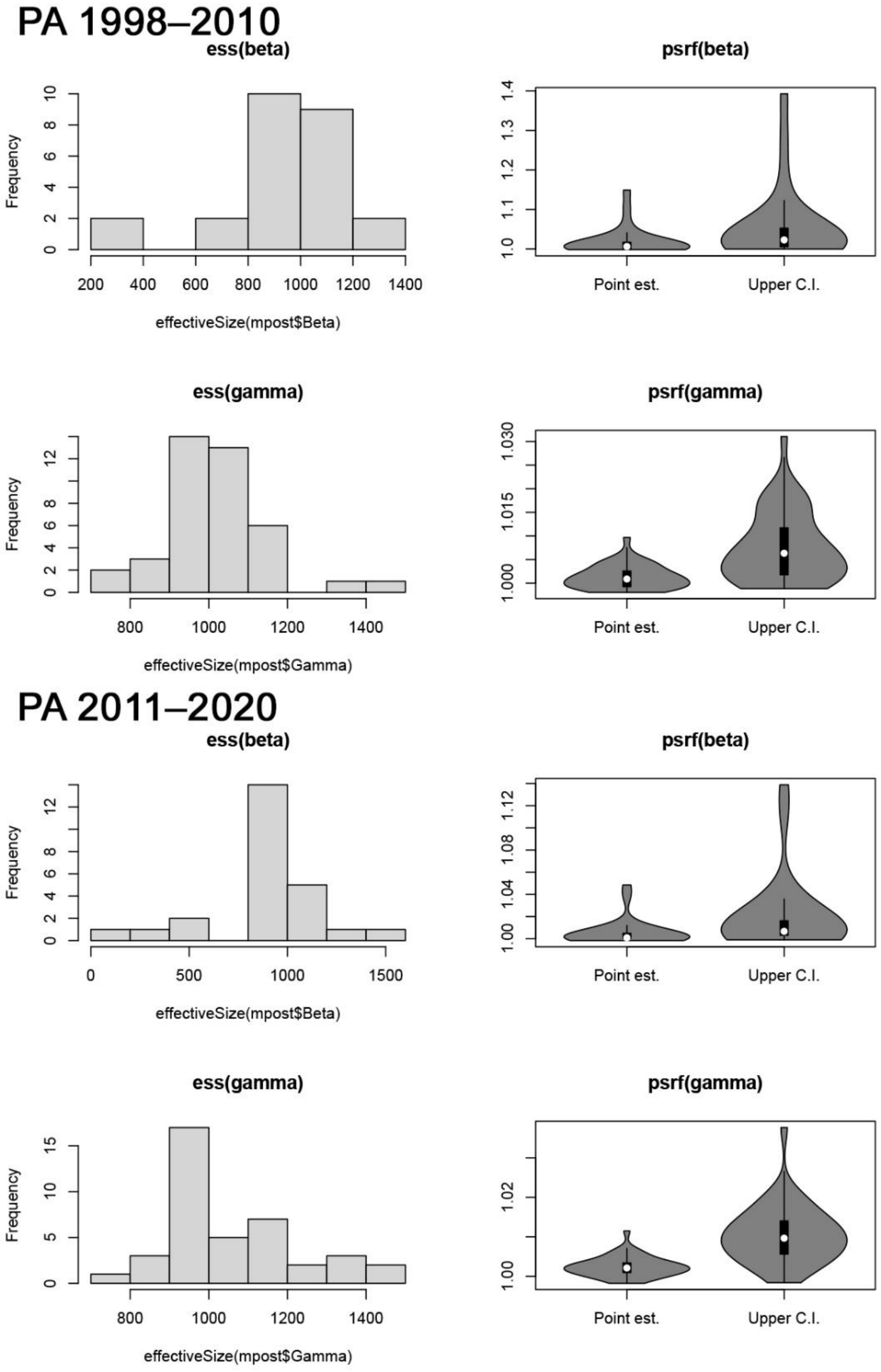
ABU 1998–2010



ABU 2011–2020



Supplementary Figure 5.6. Model diagnostics for the abundance (ABU) models. The panels correspond to the beta (species-environment relation) and gamma (trait-environment relation) parameters. The panels on the left measure MCMC in terms of the effective sample size (ess) and the panels on the right in terms of the potential scale reduction factor (psrf).



Supplementary Figure 5.7. Model diagnostics for the presence-absence (PA) models. The panels correspond to the beta (species-environment relation) and gamma (trait-environment relation) parameters. The panels on the left measure MCMC in terms of the effective sample size (ess) and the panels on the right in terms of the potential scale reduction factor (psrf).

References

Albouy, C., Guilhaumon, F., Leprieur, F., Lasram, F. B. R., Somot, S., Aznar, R., et al. (2013). Projected climate change and the changing biogeography of coastal Mediterranean fishes. *J. Biogeogr. 40*, 534-547.

Barausse, A., Michieli, A., Riginella, E., Palmeri, L., and Mazzoldi, C. (2011). Long-term changes in community composition and life history traits in a highly exploited basin (northern Adriatic Sea): The role of environment and anthropogenic pressures. *J. Fish Biol.* 79, 1453–1486. doi: 10.1111/j.1095-8649.2011.03139.x.

Barry, D., and Hartigan, J. A. (1993). A Bayesian Analysis for Change Point Problems A Bayesian Analysis for Change Point Problems. *J. Am. Stat. Assoc.* 88, 309–319. Available at: https://www.jstor.org/stable/2290726.

Ben Rais Lasram, F., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W., and Mouillot, D. (2010). The Mediterranean Sea as a “cul-de-sac” for endemic fishes facing climate change. *Glob. Chang. Biol.* 16, 3233–3245. doi: 10.1111/j.1365-2486.2010.02224.x.

Bertrand, J. A., de Sola, L. G., Papaconstantinou, C., Relini, G., and Souplet, A. (2002). The general specifications of the MEDITS surveys. *Sci. Mar.* 66, 9–17. Available at: https://doi.org/10.3989/scimar.2002.66s2.

Bonacci, O., and Vrsalović, A. (2022). Differences in Air and Sea Surface Temperatures in the Northern and Southern Part of the Adriatic Sea. *Atmosphere* 13, 1158. doi: 10.3390/atmos13071158.

Brooks, S. P., and Gelman, A. (1998). General Methods for Monitoring Convergence of Iterative Simulations. *J. Comput. Graph. Stat.* 7, 434–455. Available at: https://www.jstor.org/stable/1390675.

Calì, F., La Mesa, M., Donato, F., Mazzoldi, C., Martinelli, M., and Santojanni, A. (2023a). Life history traits and historical comparison of blue whiting (*Micromesistius poutassou*) growth performance from the western Pomo / Jabuka Pits area (central Adriatic Sea). doi: 10.3389/fmars.2023.1291173.

Calì, F., Stranci, F., La Mesa, M., Mazzoldi, C., Arneri, E., and Santojanni, A. (2023b). Whiting (*Merlangius merlangus*) Grows Slower and Smaller in the Adriatic Sea :

New Insights from a Comparison of Two Populations with a Time Interval of 30 Years. *Fishes* 8, 341. Available at: https://doi.org/10.3390/fishes8070341.

Ciannelli, L., Fauchald, P., Chan, K. S., Agostini, V. N., and Dingsør, G. E. (2008). Spatial fisheries ecology : Recent progress and future prospects. *J. Mar. Syst.* 71, 223–236. doi: 10.1016/j.jmarsys.2007.02.031.

Cohen, D. M., Inada, T., Iwamoto, T., and Scialabba, N. (1990). *Fao Species Catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date.*

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., et al. (2010). The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. *PLoS One* 5. doi: 10.1371/journal.pone.0011842.

Costello, M. J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., and Miloslavich, P. (2010). A census of marine biodiversity knowledge, resources, and future challenges. *PLoS One* 5. doi: 10.1371/journal.pone.0012110.

de Juan, S., and Lleonart, J. (2010). A conceptual framework for the protection of vulnerable habitats impacted by fishing activities in the Mediterranean high seas. *Ocean Coast. Manag.* 53, 717–723. doi: 10.1016/j.ocecoaman.2010.10.005.

Debes, P. V., Zachos, F. E., and Hanel, R. (2008). Mitochondrial phylogeography of the European sprat (*Sprattus sprattus* L ., Clupeidae) reveals isolated climatically vulnerable populations in the Mediterranean Sea and range expansion in the northeast Atlantic. *Mol. Ecol.* 17, 3873–3888. doi: 10.1111/j.1365-294X.2008.03872.x.

Druon, J. N., Fiorentino, F., Murenu, M., Knittweis, L., Colloca, F., Osio, C., et al. (2015). Modelling of European hake nurseries in the Mediterranean Sea: An ecological niche approach. *Prog. Oceanogr.* 130, 188–204. doi: 10.1016/j.pocean.2014.11.005.

Engelhard, G. H., Pinnegar, J. K., Kell, L. T., and Rijnsdorp, A. D. (2011). Nine decades of North Sea sole and plaice distribution. *ICES J. Mar. Sci.* 68, 1090–1104. doi: 10.1093/icesjms/fsr031.

Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Glob. Chang. Biol.* 20, 2473–2483. doi: 10.1111/gcb.12513.

Escudier, R., Clementi, E., Cipollone, A., Pistoia, J., Drudi, M., Grandi, A. et al. (2021). A high resolution reanalysis for the Mediterranean Sea. *Front. Earth Sci. 9*, 702285.

Fanelli, E., Ros, Z. Da, Menicucci, S., Malavolti, S., Biagiotti, I., Canduci, G., et al. (2023). The pelagic food web of the Western Adriatic Sea : a focus on the role of small pelagics. *Sci. Rep.* 13, 1–17. doi: 10.1038/s41598-023-40665-w.

Ferrà, C., Tassetti, A. N., Grati, F., Pellini, G., Polidori, P., Scarcella, G., et al. (2018). Mapping change in bottom trawling activity in the Mediterranean Sea through AIS data. *Mar. Policy* 94, 275–281. doi: 10.1016/j.marpol.2017.12.013.

Fortibuoni, T., Giovanardi, O., Pranovi, F., Raicevich, S., Solidoro, C., and Libralato, S. (2017). Analysis of long-term changes in a Mediterranean marine ecosystem based on fishery landings. *Front. Mar. Sci.* 4. doi: 10.3389/FMARS.2017.00033.

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Chang.* 5, 673–677. doi: 10.1038/nclimate2647.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science* 365, 979–983. doi: 10.1126/science.aax5721.

Froese, R., and Pauly, D. (2022). FishBase. *World Wide Web Electron. Publ. (Accessed 8 December 2022).* Available at: https://fishbase.mnhn.fr.

Gačić, M. (1997). Analysis of the seasonal and interannual variability of the sea surface temperature field in the Adriatic Sea from AVHRR data (1984-1992). *J. Geophys. Res. Ocean.* 102, 22937–22946. doi: 10.1029/97JC01720.

García-Monteiro, S., Sobrino, J. A., Julien, Y., Sòria, G., and Skokovic, D. (2022). Surface Temperature trends in the Mediterranean Sea from MODIS data during years 2003–2019. *Reg. Stud. Mar. Sci.* 49, 102086. doi:

10.1016/j.rsma.2021.102086.

Gelman, A., and Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Stat. Sci.* 7, 457–472.

Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., Mchugh, M., et al. (2010). Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Glob. Chang. Biol.* 16, 517–527. doi: 10.1111/j.1365-2486.2009.02027.x.

Guevara-Fletcher, C., Alvarez, P., Sanchez, J., and Iglesias, J. (2016). Effect of temperature on the development and mortality of European hake (*Merluccius merluccius* L.) eggs from southern stock under laboratory conditions. *J. Exp. Mar. Bio. Ecol. 476*, 50-57.

Hidalgo, M., El-Haweet, A. E., Tsikliras, A. C., Tirasin, E. M., Fortibuoni, T., Ronchi, F., et al. (2022). Risks and adaptation options for the Mediterranean fisheries in the face of multiple climate change drivers and impacts. *ICES J. Mar. Sci.* 79, 2473–2488. doi: 10.1093/icesjms/fsac185.

Hidalgo, M., Ligas, A., Bellido, J. M., Bitetto, I., Carbonara, P., Carlucci, R., et al. (2019). Size-dependent survival of European hake juveniles in the Mediterranean Sea. *Sci. Mar.* 83, 207–221. doi: 10.3989/scimar.04857.16A.

Hidalgo, M., Rouyer, T., Bartolino, V., Cerviño, S., Ciannelli, L., Massutí, E., et al. (2012). Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. *Ecography* 35, 637–649. doi: 10.1111/j.1600-0587.2011.07314.x.

Hijmans, R. J., and van Etten, J. (2018). Raster: Geographic Analysis and Modeling With Raster Data. R package version 2.7-15.

Hoegh-Guldberg, O., Rongshuo, C., Poloczanska, E. S., Brewer, P. G., Sundby, S., Hilmi, K., et al. (2014). “The Ocean,” in *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds. V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, et al. (Cambridge University Press, Cambridge, United

Kingdom and New York, NY, USA), 1655–1731.

Hopkins, T. S. (1992). The structure of Ionian and Levantine Seas. *Reports Meteorol. Oceanogr.* 41, 35–36.

Kerby, T. K., Cheung, W. W. L., Van Oosterhout, C., and Engelhard, G. H. (2013). Wondering about wandering whiting: Distribution of North Sea whiting between the 1920s and 2000s. *Fish. Res.* 145, 54–65. doi: 10.1016/j.fishres.2013.02.012.

Koslow, J. A., Boehlert, G. W., Gordon, J. D. M., Haedrich, R. L., Lorance, P., and Parin, N. (2000). Continental slope and deep-sea fisheries : implications for a fragile ecosystem. *ICES J. Mar. Sci.* 57, 548–557. doi: 10.1006/jmsc.2000.0722.

Kuparinen, A., and Hutchings, J. A. (2012). Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proc. R. Soc. B Biol. Sci.* 279, 2571–2579. doi: 10.1098/rspb.2012.0120.

Lionello, P., Cavaleri, L., Nissen, K. M., Pino, C., Raicich, F., and Ulbrich, U. (2012). Severe marine storms in the Northern Adriatic : Characteristics and trends. *Phys. Chem. Earth* 40–41, 93–105. doi: 10.1016/j.pce.2010.10.002.

Lipej, L., Kovačić, M., and Dulčić, J. (2022). An Analysis of Adriatic Ichthyofauna — Ecology, Zoogeography, and Conservation Status. *Fishes* 7, 58. doi: 10.3390/fishes7020058.

Lloret, J., Sabatés, A., Muñoz, M., Demestre, M., Solé, I., Font, T., et al. (2015). How a multidisciplinary approach involving ethnoecology, biology and fisheries can help explain the spatio-temporal changes in marine fish abundance resulting from climate change. *Glob. Ecol. Biogeogr.* 24, 448–461. doi: 10.1111/geb.12276.

Lloret, J., Serrat, A., Thordarson, G., Helle, K., Jadaud, A., Bruno, I., et al. (2021). The poor health of deep-water species in the context of fishing activity and a warming climate: will populations of *Molva* species rebuild or collapse? *J. Fish Biol.* 98, 1572–1584. doi: 10.1111/jfb.14347.

Lotze, H. K., Coll, M., and Dunne, J. A. (2011). Historical Changes in Marine Resources, Food-web Structure and Ecosystem Functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14, 198–222. doi: 10.1007/s10021-010-9404-8.

Maioli, F., Weigel, B., Chiarabelli, E., Manfredi, C., Anibaldi, A., Isailović, I., et al.

(2023). Influence of ecological traits on spatio-temporal dynamics of an elasmobranch community in a heavily exploited basin. *Sci. Rep.* 13, 1–15. doi: 10.1038/s41598-023-36038-y.

Marini, M., and Grilli, F. (2023). The Role of Nitrogen and Phosphorus in Eutrophication of the Northern Adriatic Sea: History and Future Scenarios. *Appl. Sci.* 13, 9267. Available at: https://doi.org/10.3390/app13169267.

Marini, M., Maselli, V., Campanelli, A., Foglini, F., and Grilli, F. (2016). Role of the Mid-Adriatic deep in dense water interception and modification. *Mar. Geol.* 375, 5–14. doi: 10.1016/j.margeo.2015.08.015.

Maunder, M. N., and Punt, A. E. (2004). Standardizing catch and effort data: A review of recent approaches. *Fish. Res.* 70, 141–159. doi: 10.1016/j.fishres.2004.08.002.

Merino, G., Coll, M., Granado, I., Gee, J., Kroodsma, D., Miller, N. A., et al. (2019). “FAO Area 37 - AIS-based fishing activity in the Mediterranean and Black Sea,” in *Global Atlas of AIS-based fishing activity - Challenges and opportunities*, eds. M. Taconet, D. Kroodsma, and J. A. Fernandes (Rome: FAO). Available at: www.fao.org/documents/card/en/c/ca7012en.

Mir-Arguimbau, J., Balcells, M., Raventós, N., Martín, P., and Sabatés, A. (2020). Growth, reproduction and their interplay in blue whiting (*Micromesistius poutassou*, Risso, 1827) from the NW Mediterranean. *Fish. Res.* 227, 105540. doi: 10.1016/j.fishres.2020.105540.

Montanyès, M., Weigel, B., and Lindegren, M. (2023). Community assembly processes and drivers shaping marine fish community structure in the North Sea. *Ecography* 10, 1–14. doi: 10.1111/ecog.06642.

Norberg, A., Abrego, N., Blanchet, F. G., Adler, F. R., Anderson, B. J., Anttila, J., et al. (2019). A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. *Ecol. Monogr.* 89, 1–24. doi: 10.1002/ecm.1370.

Olafsdottir, A. H., Utne, K. R., Jacobsen, J. A., Jansen, T., Óskarsson, G. J., Nøttestad, L., et al. (2019). Geographical expansion of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2007 to 2016 was primarily driven by stock size and constrained by low temperatures. *Deep. Res. Part II Top. Stud. Oceanogr.* 159, 152–168. doi: 10.1016/j.dsr2.2018.05.023.

Orlic, M., Gacic, M., and Laviolette, P. E. (1992). The currents and circulation of the Adriatic Sea. *Oceanol. Acta 15*, 109-124.

Ovaskainen, O., and Abrego, N. (2020). *Joint species distribution modelling: With applications in R*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Ovaskainen, O., and Soininen, J. (2011). Making more out of sparse data: hierarchical modeling of species communities. *Ecology* 92, 289–295.

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, G., Duan, L., Dunson, D., et al. (2017). How to make more out of community data ? A conceptual framework and its implementation as models and software. *Ecol. Lett.* 20, 561–576. doi: 10.1111/ele.12757.

Panzeri, D., Russo, T., Arneri, E., Carlucci, R., Cossarini, G., Isajlović, I., et al. (2023). Identifying priority areas for spatial management of mixed fisheries using ensemble of multi-species distribution models. *Fish Fish. 25, 187–204*. doi: 10.1111/faf.12802.

Paradis, E., and Schliep, K. (2019). ape 5.0 : an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528. doi: 10.1093/bioinformatics/bty633.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. *Science* 279, 860–863. doi: 10.1126/science.279.5352.860.

Pearce, J., and Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Modell.* 133, 225–245.

Pinsky, M. L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J., and Cheung, W. W. L. (2018). Preparing ocean governance for species on the move. *Science* 360, 1189–1191. doi: 10.1126/science.aat2360.

Pitcher, C. R., Hiddink, J. G., Jennings, S., Collie, J., Parma, A. M., Amoroso, R., et al. (2022). Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. *Proc. Natl. Acad. Sci. U. S. A.* 119. doi: 10.1073/pnas.2109449119.

Platt, T., Fuentes-Yaco, C., and Frank, K. T. (2003). Spring algal bloom and larval fish survival. *Nature* 423, 398–399.

Poggiato, G., Münkemüller, T., Bystrova, D., Arbel, J., Clark, J. S., and Thuiller, W. (2021). On the Interpretations of Joint Modeling in Community Ecology. *Trends Ecol. Evol.* 36, 391–401. doi: 10.1016/j.tree.2021.01.002.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., Molinos, J. G., Halpern, B. S., Hoegh-Guldberg, O., et al. (2016). Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.* 3, 1–21. doi: 10.3389/fmars.2016.00062.

Post, S., Fock, H. O., and Jansen, T. (2019). Blue whiting distribution and migration in Greenland waters. *Fish. Res.* 212, 123–135. doi: 10.1016/j.fishres.2018.12.007.

Pranovi, F., Caccin, A., Franzoi, P., Malavasi, S., and Zucchetta, M. (2013). Vulnerability of artisanal fisheries to climate change. *J. Fish Biol.* 83, 847–864. doi: 10.1111/jfb.12124.

Puerta, P., Hunsicker, M. E., Quetglas, A., Álvarez-Berastegui, D., Esteban, A., González, M., et al. (2015). Spatially Explicit Modeling Reveals Cephalopod Distributions Match Contrasting Trophic Pathways in the Western Mediterranean Sea. *PLoS One* 10, 1–17. doi: 10.1371/journal.pone.0133439.

Pulcinella, J., Bonanomi, S., Colombelli, A., Fortuna, C. M., Moro, F., Lucchetti, A., et al. (2019). Bycatch of loggerhead turtle (*Caretta caretta*) in the Italian Adriatic midwater pair trawl fishery. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00365.

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available at: https://www.r-project.org/.

Riccioni, G., Stagioni, M., Manfredi, C., Tinti, F., Piccinetti, C., and Libralato, S. (2022). DNA metabarcoding suggests dietary niche partitioning in the Adriatic European hake. *Sci. Rep.* 12. doi: 10.1038/s41598-022-05346-0.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* 66, 1570–1583. Available at: https://doi.org/10.1093/icesjms/fsp056.

Rodionov, S. N. (2004). A sequential algorithm for testing climate regime shifts. *Geophys. Res. Lett.* 31, 2–5. doi: 10.1029/2004GL019448.

Roether, W., Manca, B. B., Klein, B., Bregant, D., Georgopoulos, D., Beitzel, V., et al. (1996). Recent Changes in Eastern Mediterranean Deep Waters. *Science* 271, 333–335.

Russo, A., and Artegiani, A. (1996). Adriatic Sea hydrography. *Sci. Mar.* 60, 33–43.

Russo, A., Carniel, S., Sclavo, M., and Krzelj, M. (2012). 07 Climatology of the Northern-Central Adriatic Sea. *Mod. Climatol.* 8, 177–212. doi: 10.5772/34693.

Santelli, A., Cvitković, I., Despalatović, M., Fabi, G., Grati, F., Marčeta, B., et al. (2017). Spatial persistence of megazoobenthic assemblages in the Adriatic Sea. *Mar. Ecol. Prog. Ser.* 566, 31–48. doi: 10.3354/meps12002.

Sartor, P. (1995). Regime alimentare di osteitti gadiformi nel mar Tirreno Settentrionale. *Atti Soc. Tosc. Sci. Nat., Mem., Ser. B* 102, 59–67.

Schroeder, K., Chiggiato, J., Josey, S. A., Borghini, M., Aracri, S., and Sparnocchia, S. (2017). Rapid response to climate change in a marginal sea. *Sci. Rep.* 7, 1–7. doi: 10.1038/s41598-017-04455-5.

Serrat, A., and Muñoz, M. (2022). Can the Life History Trait Divergence of Two Extremes of a Cold-Water Genus Distribution Offer Evidence for Their Vulnerability to Sea Warming? *Fishes* 7, 143. doi: 10.3390/fishes7040143.

Sguotti, C., Bischoff, A., Conversi, A., Mazzoldi, C., Möllmann, C., and Barausse, A. (2022). Stable landings mask irreversible community reorganizations in an overexploited Mediterranean ecosystem. *J. Anim. Ecol.* 91, 2465–2479. doi: 10.1111/1365-2656.13831.

Spedicato, M. T., Massutí, E., Mérigot, B., Tserpes, G., Jadaud, A., and Relini, G. (2020). The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Sci. Mar.* 83, 9–20.

Supić, N., Grbec, B., Vilibić, I., and Ivančić, I. (2004). Long-term changes in hydrographic conditions in northern Adriatic and its relationship to hydrological and atmospheric processes. *Ann. Geophys.* 22, 733–745. doi: 10.5194/angeo-22-733-2004.

Teletchea, F., Laudet, V., and Hänni, C. (2006). Phylogeny of the Gadidae (sensu Svetovidov, 1948) based on their morphology and two mitochondrial genes. *Mol. Phylogenet. Evol.* 38, 189–199. doi: 10.1016/j.ympev.2005.09.001.

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., Jonge, M. M. J. De, Oksanen, J., et al. (2020). Joint species distribution modelling with the r-package Hmsc. 11, 442–447. doi: 10.1111/2041-210X.13345.

Tjur, T. (2009). Coefficients of Determination in Logistic Regression Models ? A New Proposal: The Coefficient of Discrimination. *Am. Stat.* 63, 366–372. Available at: https://www.jstor.org/stable/25652317.

Tortonese, E. (1964). The Main Biogeographical Features and Problems of the Mediterranean Fish Fauna. *Copeia* 1964, 98–107.

Vodopivec, M., Zaimi, K., and Peliz, Á. J. (2022). The Freshwater Balance of the Adriatic Sea: A Sensitivity Study. *J. Geophys. Res. Ocean.* 127, 1–23. doi: 10.1029/2022JC018870.

Volpe, G., Colella, S., Brando, V. E., Forneris, V., Padula, F. L., Cicco, A. D., et al. (2019). Mediterranean ocean colour Level 3 operational multi-sensor processing. *Ocean Sci.* 15, 127-146.

Weigel, B., Mäkinen, J., Kallasvuo, M., and Vanhatalo, J. (2021). Exposing changing phenology of fish larvae by modeling climate effects on temporal early life-stage shifts. *Mar. Ecol. Prog. Ser.* 666, 135–148. doi: 10.3354/meps13676.

6 General Discussion and Conclusions

It is important to know in detail about the biology, ecological interactions, and population trends of the key marine species not only to improve our comprehension of ecosystem functioning but also to achieve sustainable management of marine resources through an ecosystem-based approach (Pauly et al., 2002). The cold-water group of Gadiformes plays important ecological and socio-economic roles in the Adriatic Sea, whose northern-central part is considered a cold refugium offering suitable environmental conditions for these cold-water species (Ben Rais Lasram et al., 2010). In the current scenario of increasing sea temperatures, in-depth knowledge of these species would enable us to better understand the effects of climate change on fish species exploited by fishing. In this thesis, I investigated the biological responses of some commercial gadiform species to fishing exploitation and climate change. Specifically, I have provided new findings on the life history traits of three gadid species of the Adriatic Sea, highlighting some changes that occurred in their population structures and growth patterns over the last 30 years. Moreover, by applying a joint species distribution model (HMSC framework), I included in the analysis two additional species, extending the investigation to a total of five gadiform species exploited by fishing, in order to explore their occurrence and abundance change over time and space in the northern-central Adriatic Sea. The combination of different methodological approaches and the comparison of closely related species allowed me to take a step forward in disentangling the effects of fishing and climate change, which represent challenging but fundamental information to implement effective management policies (Claireaux et al., 2021; Jones et al., 2023).

6.1 Life history traits of whiting, blue whiting, and poor cod (Case studies I, II, III)

This thesis provides a detailed picture of some key life history traits of three important commercial gadids (*M. merlangus*, *M. poutassou,* and *T. capelanus)* collected from the main Italian fishing fleets of the northern-central Adriatic Sea (GSA 17) during 2020 and 2021. The size ranges observed in all the species were comparable to the other areas of the Mediterranean Sea and lower compared to previous studies from the same area and to the Atlantic Ocean (if included in the species distribution range). This observation, at the Adriatic scale, is explainable through the ongoing process of decrease in maximum size, discussed in detail below (section 6.2). On the other hand, the size difference between the Atlantic and Mediterranean populations was commonly found in other gadoid species (Mir-Arguimbau et al., 2020; Calì et al., 2023a; Froese and Pauly, 2023) and can be attributed to several factors. Firstly, the Mediterranean Sea has higher water temperatures compared to the Atlantic Ocean. Warmer waters can limit the availability of oxygen and reduce the overall energy supply for fish. This can lead to smaller fish sizes as they may have limited energy for growth (Pauly and Cheung, 2018). Secondly, the Mediterranean Sea is a semi-enclosed sea with a relatively smaller surface area and fewer resources compared to the Atlantic Ocean. Limited space and resources can lead to increased competition among fish species for food, habitat, and breeding sites. In such competitive environments, fish may have lower energy resources, resulting in reduced body growth (Rueda et al., 2015). Lastly, the Mediterranean Sea has a long history of intense fishing activity, often characterised by the presence of several countries sharing the same resources and weak management policies, which lead to overfishing of the stock and subsequent reduction of the fish size through selective harvesting of the larger individuals. On the opposite, the Atlantic fish stocks are generally better managed and undergo lower levels of fishing pressure (Cardinale et al., 2013, 2017). The age range found in the three gadid species showed the same dissimilarity between the Adriatic (Mediterranean) and the Atlantic populations, showing a higher lifespan in whiting and blue whiting populations inhabiting higher latitudes (Froese and Pauly, 2023). In addition to the already discussed difference in fishing pressure that causes a stronger age truncation in Mediterranean populations, it should also be considered the latitudinal variation in lifespan within ectotherm species, which is related to the temperature and explained by the metabolic theory of ecology (Brown et al., 2004). The validity of this theory has been proven in a wide range of ectotherms in both controlled laboratory experiments and free-living populations, showing that several species tend to live longer at higher latitudes (Munch and Salinas, 2009). On the Mediterranean scale, the age ranges found were comparable to those reported in other areas. The only exception was found in whiting, whose Black Sea population seems to have a longer lifespan compared to the Adriatic one, despite similar length ranges (Giovanardi and Rizzoli, 1984; Polat and Gümücs, 1996; Mazlum and Bilgin, 2014; Calì et al., 2023b). In the interspecific comparison of lifespan, one interesting finding is the relationship between the bathymetric range and the maximum age of the three species. Indeed, whiting, which is a shallow-water species, shows the shortest lifespan, while, the deep-water species blue whiting has the longest one. Poor cod can be considered the intermediate species between them. Despite the low number of species considered and the limited bathymetric range of the study area (0−280 m), this finding supports the general bathymetric trend observed in fish life history strategies, for which deep-water species tend to have "K-selected" strategies, showing high longevity, late maturity, and slow growth compared to the shallow-water ones (Koslow et al., 2000; Lloret et al., 2021). However, despite different lifespans, these three species share an early sexual maturity, being mature within the first year of life. Comparing them to the other species of Gadiformes, all of them can be considered early-maturing species, and it is possible to hypothesise that their common phylogenetic history determined the same adaptive response in the acclimation process to the Mediterranean Sea (characterised by warmer waters promoting higher growth rates) in the late Miocene (Endo, 2002). The seasonal otolith deposition pattern showed common features in the three species, agreeing with the previous studies. Otolith growth is characterised by the formation of a wide opaque ring during the warm season (spring and summer, fast growth) and a narrow hyaline ring during the cold season (autumn and winter, slow growth).

Interestingly, the current Adriatic populations of whiting, blue whiting, and poor cod showed consistently the highest values of growth rate (k) and performance index (φ') e the lowest asymptotic length (L_∞) ever reported in the literature. There are two likely causes for this result: the first is related to the peculiarity of the Adriatic context, and the second is related to the data used to estimate the VBF growth parameters. Firstly, it is possible that the high biological productivity typical of the Adriatic Sea naturally promotes higher growth rates thanks to high prey availability (Fanelli et al., 2023); at the same time, the long-time history of fishing exploitation could represent another factor that has driven the local populations to grow faster at expenses of the maximum size, to increase the probability of reproducing before being caught (Trippel, 1995). Secondly, this might be a result of the inclusion in the analyses of the spring juveniles, which allowed a good fitting of the VBGF at the origin and contributed to the estimation of more accurate values of these parameters. Therefore, it may be possible that the parameters estimated in this thesis are higher compared to the literature because usually the data on early life stages and juveniles are not available, resulting in an underestimation of VBF growth parameters, especially the Brody growth rate coefficient (Mir-Arguimbau et al., 2020). In addition to the use of a wide range of sizes and ages, the use of the edge analysis method to validate the age readings together with species-specific otolith processing methodologies allowed me to provide high-quality data, serving as a reference for further studies on the growth of the investigated species.

As well as most gadiform fishes, the data collected in 2020−2021 confirmed that the study species are winter spawners (Cohen et al., 1990). The only species showing a more extended spawning season was *T. capelanus*, which spawns from December to June (though the spawning peak is in winter). Comparing the onset and duration of the spawning process between the Atlantic and Mediterranean populations of whiting and blue whiting, it is possible to observe that the spawning duration is shorter and restricted to mid-winter in the Mediterranean populations of the species. In the Atlantic Ocean, spawning generally starts in mid-winter and ends in spring (blue whiting) or summer (whiting), showing a longer duration (Bailey, 1982; González-Irusta and Wright, 2017). Therefore, it could be hypothesised that the timing of spawning in the Mediterranean population is strongly influenced by sea temperature, reaching the optimal values for the onset of spawning and the development of the planktonic early life stages only during winter.

6.2 Historical comparison of size/age structures and growth performances of whiting, blue whiting, and poor cod (Case studies I, II, III)

Overall, the results of this thesis suggest a decrease in body size over the last three decades that was observed consistently in the investigated species, though each species showed a different variation pattern in age structures and growth trajectories. The application of a comparative approach allowed me to make inferences about the influence and relative contribution of fishing and climate change in determining biological responses.

In case study I (whiting), the reduction in large individuals was not coupled with a reduction in old individuals, as expected to be found in populations subjected to high fishing pressure, which determines both size and age truncation (Barnett et al., 2017).

In fact, fishing exerts selective pressure by removing larger and, consequently, older individuals (Yemane et al., 2008; Edwards and Plagányi, 2011). Surprisingly, despite the difference in the number of large individuals, no differences were found between the age structures and maximum age of samples collected in 2020–2021 and in 1990–1991. The comparison of the mean length-at-age revealed larger sizes per age class in 1990–1991 compared to 2020–2021, suggesting that the observed reduction in large individuals is related to a decrease in growth performances, which may be explained by metabolic constraints. Considering that whiting is a cold-water species restricted to the coldest areas of the Mediterranean Sea (which represent the southern limit of its distribution) and that a severe increase in sea temperature has occurred in the northern-central Adriatic Sea over the last decades (García-Monteiro et al., 2022; Sguotti et al., 2022), it is possible to hypothesise that the decrease in growth performance and size is the adaptative response to increased metabolic rates determined by temperatures above the thermal optimum for this species. Consequently, due to the increased energy required to maintain homeostasis in warmer temperatures, the amount of energy available for body growth is reduced.

The historical comparison in blue whiting (case study II) highlighted a similar trend of decline in the number of large individuals and mean length-at-age. On the contrary, the age structures in this species were different between individuals sampled in 1985–1986 and 2020–2021. In fact, the 2020–2021 sample was characterised by a wider age range and a higher proportion of old specimens (9% were 4 or more years old) compared to 1985–86 (2% were 4 or more years old). While the only two old specimens from 1985–86 were close to the maximum size known for the Mediterranean populations of blue whiting (40 cm; Froese and Pauly, 2023), the old specimens from 2020–2021 measured between 25 and 30 cm TL and among them, many were close to the maximum age found in the Mediterranean Sea (Fiorentino et al., 2003; Mir-Arguimbau et al., 2020). This result strongly supports the idea that the fish's body size and growth potential have shrunk over the period considered. It is worth noting that the blue whiting study case exemplifies the impacts of both fishing and climate change on fish populations, even if in this case the specific effect of each stressor was observed in different periods. The trunked size/age structure of 1985–86, composed primarily of young individuals, was probably the result of the high fishing effort exerted by Italian trawlers in the central Adriatic Sea, which increased continuously from the 1960s to the 1980s, leading to an oversized fishing fleet compared to the available fish resources (Froglia, 1993). On the other hand, the effects of fishing were much lower in 2020–2021 because of the fishing regulations in the Pomo/Jabuka Pits area (from which blue whiting samples were collected). The effects of a reduced level of fishing exploitation are represented by the presence of old specimens in 2020–2021. Therefore, the observed reduction in size could be linked to environmental variations that occurred in the area and are attributable to climate change. In particular, it is known that the cold-water generation process in the northern Adriatic Sea, which is strongly influenced by environmental factors, regulates the oxygen and nutrient supply in the Pomo/Jabuka Pits (Marini et al., 2016). Since this process is triggered by strong northerly winds blowing during the winter, the weakening of winter storms reported in the area (Lionello et al., 2012; Nissen et al., 2014) could have reduced the frequency/amount of cooling events, which are essential to renew the water masses in the Pomo/Jabuka Pits and thus the trophic and metabolic resources available for blue whiting. The reduction of cold-water formation events is an ongoing process reported at a wider spatial and temporal scale that has determined detectable anomalies in the thermohaline circulation in the Mediterranean Sea (Bethoux et al., 1990).

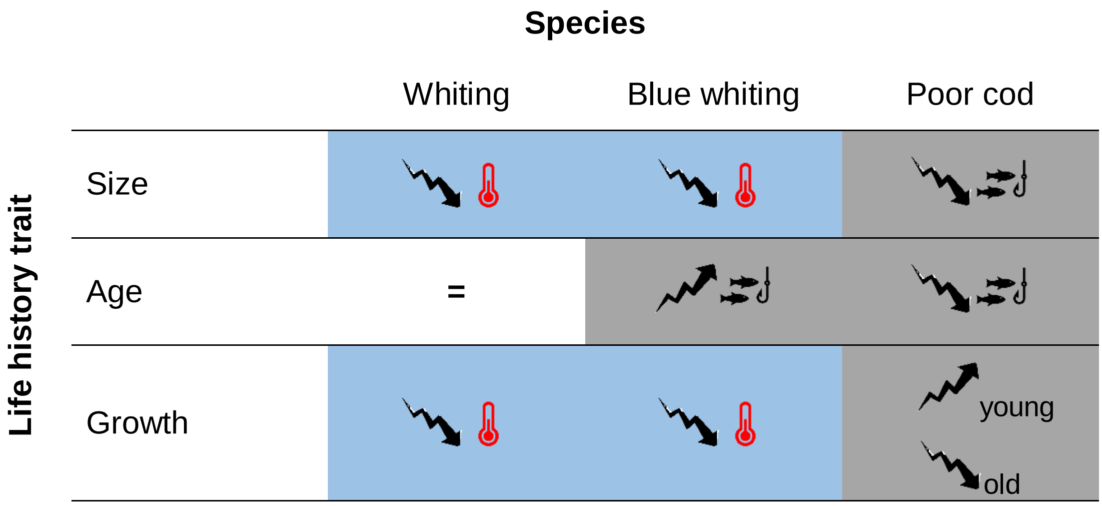
Case study III focused on poor cod and highlighted some common features but also differences from the other intraspecific comparisons. In this case, the reduction in large individuals (a common pattern in all case studies) was coupled with a reduction in old individuals (not observed in whiting and blue whiting). Moreover, the individuals sampled in 2020–2021 seemed to grow faster during the first two years of life but attained a smaller maximum size compared to 1986–1987. These results could represent clear examples of the effect of fishing exploitation, which has acted at different temporal scales. Indeed, the reduction in size and age is the most common short-term effect observed in fish populations subjected to overexploitation (Bianchi et al., 2000; Shin et al., 2005; Hidalgo et al., 2012). On the other hand, as a result of the significant and continuous fishing activity in the study area over the past few decades (Sguotti et al., 2022), coupled with the selective nature of this process, it is likely to lead to evolutionary changes (long-term effects). This selective pressure tends to favour individuals with faster growth rates and earlier sexual maturity, increasing their chances of reproducing before being caught (Trippel, 1995). Therefore, the difference in growth trajectories between 1986–1987 and 2020–2021 could be explained as an adaptive response of poor cod to fishing exploitation, which caused specimens to grow faster and mature earlier at the expense of long-term somatic growth (a result of the evolutionary trade-off). This hypothesis is further supported by the more evident dimorphism in size observed in the 2020–2021 sample, which may indicate a sex-dependent response to the size-selectivity of fishing. The potential difference in response between sexes may be related to the different energetic investments in gamete production and to the stronger influence of body size on the reproductive potential of females (Hayward and Gillooly, 2011). Given that the decrease in size would primarily affect the reproductive production of females (Barneche et al., 2018), it is plausible to hypothesise that the size reduction is more advantageous for male individuals, as it provides them greater adaptive benefits (i.e., decreased fishing mortality). The overall higher growth performance and the faster growth at the early stages of the 2020–2021 specimens suggest that this species may not have been negatively affected by the ongoing warming process. This finding is consistent with what is expected when taking into account the distribution range and the presumed thermal range of this species. In fact, poor cod is exclusively found in the Mediterranean region and is likely to have a greater tolerance for warm waters. In addition, it is worth noting that the prolonged spawning season of poor cod supports the hypothesis of a wider thermal optimum (and therefore metabolic adaptability) compared to whiting and blue whiting. Unfortunately, no specific data are available on the preferred thermal range of *T. capelanus* and the only data available are referred to its closest relative *T. minutus*, which has an Atlantic distribution (Froese and Pauly, 2023).

Although the results of the historical comparisons need to be interpreted with caution (the limitations of the approach used are discussed in section 6.4), by comparing the results at an interspecific level, it is possible to hypothesise that the differences observed between old and current samples represent the adaptive responses to specific combinations (in time and space) of disturbance levels exerted by fishing and climate change. Moreover, it is worth mentioning that, since each species shows a different level of vulnerability depending on its physiology and life history traits (Dulvy et al., 2003), it is possible to observe differences in responses to the same external stressors. In summary, from the evidence of the three case studies, it is possible to conclude that (Table 6.1):

i) climate change (i.e., sea warming) played a major role in determining the growth and body size reduction in whiting;

ii) the effects of both fishing and climate change were presumably observed, even if they succeeded in time, determining differences in the age structures of the samples and the growth and body size reduction in blue whiting, respectively;

iii) fishing played a major role in determining the age/size truncation and the modification of growth trajectories in poor cod.



	Species		
Life history trait	Whiting	Blue whiting	Poor cod
Size	↘ 🌡	↘ 🌡	↘ 🎣
Age	=	↗ 🎣	↘ 🎣
Growth	↘ 🌡	↘ 🌡	↗ young ↘ old

Table 6.1. Summary of the effects observed in the intraspecific historical comparisons between samples of whiting, blue whiting, and poor cod. The upward and downward arrows indicate increasing and decreasing values, respectively, between 1985–1991 and 2020–2021. Blue and grey indicate climate change and fishing exploitation, respectively, as potential main contributors to explain the trait differences. “=” indicates no variations.

6.3 Using multispecies distribution models to complement the experimental results and shed light on the adaptive responses of Gadiformes (Case studies I, II, III, IV)

The last step of this thesis was the application of a modelling approach through the use of a Hierarchical model of species communities (HMSC). In case study IV, standardised data from the Italian MEDITS survey carried out in the period 1998–2020 were used to test the influence of some environmental factors on spatio-temporal variations of the occurrence and abundance of five gadiform species. As environmental covariates, I included chlorophyll-a, depth, and sea bottom temperature. Chlorophyll-a is a widely used proxy for primary production and thus resource availability, potentially having a strong influence on the recruitment success of fish species (Platt et al., 2003). Depth is a key factor in determining the distribution patterns of the study species, as can be observed by looking at their different preferred bathymetric ranges (Froese and Pauly, 2023). This factor assumes particular ecological significance in a context such as the Adriatic, which is characterised by a pronounced bathymetric gradient along its latitudinal axis (Russo and Artegiani, 1996). Considering the demersal nature of the study species and the potential link between sea warming and the difference observed in the historical comparisons of gadid species, I chose to include in the analysis two different mean values of sea bottom temperature. In particular, I calculated the winter mean and the annual mean (correlation coefficient < 0.4) to take into account the possibility of explaining different processes. In fact, considering that the study species are mostly winter spawners and most of the hauls were carried out during the spring, we assumed the winter mean to be a reliable predictor of spawning, recruitment success, and then abundance (Hidalgo et al., 2019). On the other hand, the annual mean could be a good predictor of habitat preferences or thermal niches, influencing the species distribution. In addition to the species covered by the first three case studies, in case study IV I extended the scope of my investigation to silvery pout (*G. argenteus*) and European hake (*M. merluccius*), two gadiform species showing interesting thermal preferences to compare the species responses to sea warming.

The results of the presence-absence models showed that depth had a significant influence on the occurrence pattern of gadiform species in the northern-central Adriatic Sea, with temperature covariates having little effect (Figure 5.3 A, B). This finding is in agreement with the species-specific preferred bathymetric ranges, which determine the distribution patterns of the study species in the area (Figure 6.1).

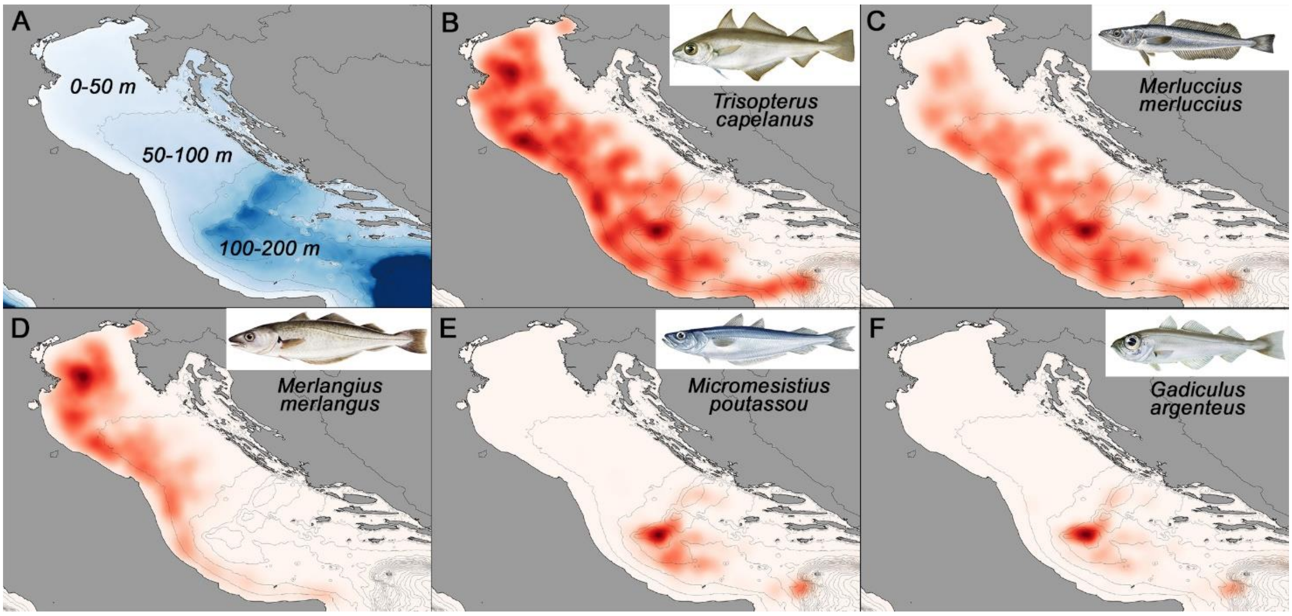


Figure 6.1. Bathymetric features of the northern-central Adriatic Sea (A) and heatmaps of abundance data (N/km2) of gadiform species from the Italian MEDITS surveys carried out between 1998 and 2020 (B–F). Darker colours indicate higher abundance.

On the other hand, the output of the abundance models highlighted a remarkable influence of environmental covariates and a low contribution of depth in explaining the abundance variation patterns, particularly in the period 2011–2020 (Figure 5.3 C, D). One interesting finding was represented by the identification of two thermal regimes in the period 1998–2020. This finding was used to fit and compare two different models, aiming to investigate the presence of differences in species responses to environmental covariates during the different thermal regimes. Indeed, the comparison of the variance partitioning among the explanatory variables of the abundance models highlighted a significant increase in variance explained by both thermal covariates (Figure 5.3 C, D). This finding suggests that the species' response to the temperature (in terms of abundance variation) increased after the thermal shift (2011–2020). In particular, almost all the species showed negative correlations between their abundance and the sea bottom temperature, except for European hake, which showed the opposite trend (Supplementary Figure 5.2). Moreover, the intensity of the responses (indicated by the slopes of the abundance-temperature relationships) increased in the period after the thermal shift, suggesting that the same temperature variation determined stronger responses in 2011–2020 compared to 1998–2010. Overall, the abundance model results demonstrate clearly how, among a small group of related species, the responses to temperature variations (and therefore climate change) can be different. This implies that each species has different levels of vulnerability to the warming process caused by climate change (Moullec et al., 2019).

It is worth noting that, despite the use of different data sources, there are similarities between the hypothesis proposed to explain the historical variations in case studies I, II, and III (Table 6.1) and the species-specific responses to temperature of the abundance models (Supplementary Figure 5.2). Whiting and blue whiting, which are the species whose decrease in size and growth performance was linked to the climate change effects, showed evident negative correlations between their abundance and temperature. On the other hand, poor cod, which was the species that exhibited a variation pattern similar to that expected for species highly exploited by fishing, showed a weak negative correlation between its abundance and temperature. Regarding the additional species, the model results suggested that silvery pout abundance is negatively correlated with temperature, as expected from belonging to the cold-water group of Gadidae. European hake was the only species showing a positive (and increasing over the two periods) correlation between its abundance and temperature. Results regarding silvery pout were not strongly supported because of the low number of records (this species showed the lowest value of R^2). On the contrary, European hake results showed strong statistical support and indicated a marked contrast in comparison with the other species. This species is considered to have a cold thermal preference, but it shows a broader thermal range compared to the other study species (Dulvy et al., 2008; Froese and Pauly, 2023). Nevertheless, such a strong positive correlation between abundance and temperature, together with the increased slope after the thermal shift, was unexpected and suggests that the European hake represents an exception within the study group, showing a high adaptative potential in the current scenario of increasing sea temperature. In addition to the slightly higher thermal optimum, this species shows particularly advantageous life history traits, which may have a strong influence on the resilience and adaptive capability of exploited species. Indeed, its larger size guarantees high fecundity rates, as is known from the positive relationship between the fish size and the number of eggs produced (Barneche et al., 2018; Serrat et al., 2019b). Moreover, the spawning period of this species is extended throughout the year, with two peaks of reproductive activity observed in the northern-central Adriatic Sea: one during winter and another during summer (Follesa and Carbonara, 2019). Recently, Serrat et al. (2019b) reported that European hake from Galician waters shows even three different spawning peaks per year, and their onset is under the control of photoperiod, food availability, and temperature. In contrast to the Adriatic gadids, whose spawning is restricted to the winter period (in correspondence with the temperature minimum), European hake spawning occurs over a wide range of environmental conditions, proving a high degree of metabolic adaptability. Hence, it could conceivably be hypothesised that the positive correlation between abundance and temperature is the result of the natural predisposition of the species to adapt its metabolism within a wide range of temperatures. A possible explanation for the higher adaptive capability of European hake compared to the Adriatic gadids is linked with the lifespan. In fact, in European hake, the greater phenotypic plasticity could be interpreted as an adaptative response to a slower evolutionary rate due to the long lifespan (up to 25 years) and relatively late maturity (3-4 years) (Vrgoc et al., 2004; Vitale et al., 2016). This high plasticity may increase the biological performance (and then fitness) of European hake individuals, making them less vulnerable to short-term environmental anomalies (Chirgwin et al., 2018). In the other gadid species, which have shorter lifespans and generation times, it should be expected to observe a faster adaptation process throughout the action of natural selection across several generations (Pinsky et al., 2020). However, the combined impact of the ongoing warming process and fishing exploitation may have caused an imbalance so great that it cannot be recovered through across-generational adaptative mechanisms, providing a possible explanation for the decline of some of these species (Lloret et al., 2021; Serrat and Muñoz, 2022; Calì et al., 2023a). Therefore, it could be hypothesised that the landing declines observed in blue whiting and poor cod (Figures 1.8A and 1.11A) are the consequence of this process. The absence of this trend in the landings of whiting, which is the species with the coldest thermal preference, could be a result of a trailing-edge contraction (Pinsky et al., 2020) of the population in the northern sub-basin, which may have increased the local population exploited by fishing, masking the decline of this species in the whole Adriatic Sea. Indeed, the northern sector, being the coldest part of the Mediterranean, is expected to become a cold-water species refugium in the future (Ben Rais Lasram et al., 2010). In contrast, European hake landings show a quite stable fluctuating trend over the last 50 years, despite being the primary and specifically targeted species for fishing activities (FAO, 2022b). These results support the idea that *M. merluccius* could have the highest adaptive potential among the study species, enabling it to better withstand the impacts of fishing and climate change.

The most novel aspect of this research is the integration of various approaches and data sources, along with an interspecific comparison of closely related species. This approach allowed for validating the hypotheses of the case studies and attempting to disentangle the effects of fishing from those of climate change. Indeed, using the findings from all the case studies, it has been possible to build a comprehensive framework capable of providing new insights useful to explain the variations that occurred in gadiform populations of the northern-central Adriatic Sea over the last decades.

6.4 Limitations of the study and future steps

While this study has provided valuable insights into the ecological responses of gadiform fish populations in the northern-central Adriatic Sea to climate change, it is essential to acknowledge certain limitations that may have influenced our findings.

Firstly, the historical comparison of case studies I, II, and III has been possible using samples collected with slightly different methodologies between the two periods sampled. All the 2020–2021 samples were collected using a fisheries-dependent approach (from bottom trawlers) in the northern-central Adriatic Sea. On the other hand, the samples collected between 1985 and 1991 were gathered during research cruises (fishery-independent approach), even if the sampling areas were comparable and the gear used was always a commercial gear type (Italian-type bottom otter trawl). The main difference in the gears used between the two periods was the codend mesh size, which was slightly smaller in the 1985–1991 samplings (30–35 mm versus 40 mm). However, in each intraspecific comparison, it is reasonable to assume comparable selectivity on adult individuals because it has been reported that a 40 mm mesh size at the codend fully selects juveniles smaller than 10 cm TL (Mir-Arguimbau et al., 2022b). Fisheries-dependent data, although valuable, may not capture all aspects of fish ecology and population dynamics. In fact, this kind of data can provide long time series and wide spatial coverage but they can be affected by the fishing strategy, which is commercially driven. On the other hand, fishery-independent data are usually carried out over relatively short periods and are not well suitable to study in detail the seasonal patterns (i.e., reproductive cycle, recruitment dynamics) (Pennino et al., 2016).

Another source of uncertainty shared by all the intraspecific historical comparisons is due to the fact that the conclusions drawn were based essentially on two discrete sampling periods with a long time shift (30–35 years). This kind of data can provide detailed snapshots of two restricted periods but could not be appropriated to describe multidecadal trends. Hypothetically, using data from only two spot samplings, it is possible that the biological variations found are exclusively attributable to the difference in fishing and/or environment in those particular periods, which could have been characterised by anomalies and then they are not useful to highlight long-term variations. Nevertheless, the agreement of some variation patterns (i.e., decrease in size) observed with the trend reported in several studies (Forster et al., 2012; Kuparinen and Hutchings, 2012; Albo-Puigserver et al., 2021; Lindmark et al., 2022) suggests that the data used were appropriate to describe the processes investigated. As regards the life history traits, I explored in detail only the historical differences in growth-related traits, because no data on the reproductive aspects were available for the samples collected between 1985 and 1991. The lack of this data represents one of the main limitations because growth and reproduction are closely related processes that can be influenced by both fishing and environmental variations (Lambert, 2008). Indeed, as somatic growth slows upon maturation, it is plausible that a shift towards early maturation could have determined the decrease in maximum size in the three gadid species. The results of this thesis support the hypothesis that in whiting and blue whiting the variation in size and growth was mainly due to climate change. Nevertheless, it cannot be excluded that fishing played a significant role. The availability of comparable data on the maturity size is fundamental to understand the impact of fishing on fish populations. Indeed, if there had been a decreasing trend in the maturity size of all the species, it would have indicated that fishing likely exerted a selective pressure on fish species, causing them to mature earlier and at lower sizes over time (Hunter et al., 2015). Furthermore, the lack of a long-time series of spatialised data on fishing pressure, due to the relatively recent implementation of VMS and AIS technologies (2009 and 2011, respectively), prevented the inclusion of fishing level as a covariate in the model. The inclusion of both climate- and fishing-related covariates would have allowed for clearer discrimination of their effects. For this reason, it is important to bear in mind that the use of the modelling approach did not provide any further information on the impact of fishing but only on the effect of the sea warming process.

An additional limitation, which emerged when combining the results of different approaches, was represented by the limited temporal coverage of the survey data used to fit the models. In fact, the analysis was limited to the period 1998–2020 because the MEDITS survey data collection started in 1994 and some environmental data (i.e., chlorophyll) were available only starting from 1998. Thus, although the model results supported the experimental hypotheses, it was not possible to include a wider time series that would have allowed for a comprehensive historical understanding of the observed trends, increasing also the explanatory potential of the models. Furthermore, our study focused on a small number of gadiform species, and their responses may not fully represent the ecological diversity of the order Gadiformes, which accounts for at least 21 species in the Adriatic Sea (Lipej et al., 2022). As highlighted in the present thesis, variability in species-specific responses to environmental changes is common even in closely related species, and future research may benefit from including a broader range of species. As already discussed above, one of the main limitations of the fishery-independent data is the short temporal coverage of the annual sampling activity. In particular, the MEDITS survey is usually carried out in late spring-summer (Spedicato et al., 2020) and the data resulting from this sampling cannot be adequate to represent the whole population dynamics and/or seasonal processes. In the specific case of gadids, for example, recruitment mainly occurs during the spring-summer period and the high percentage of juveniles caught could determine the overestimation of the abundance/biomass indexes. This stage undergoes high mortality rates and is the most impacted by bottom trawl fisheries in the Mediterranean (Colloca et al., 2013), thus increasing the risk of producing unreliable estimates of the values.

In order to improve the knowledge acquired from this thesis and overcome its limitations, future research attempts should explore several pathways. Firstly, the inclusion of additional environmental variables and more species when modelling spatio-temporal dynamics could improve our understanding of the factors influencing gadiform fish populations in the Adriatic Sea. Then, investigating how other ecological variables, such as prey availability and predation pressure, interact with temperature and fishing effort changes is crucial. In this context, it could be important to gain updated information on the trophic ecology of prey and predatory species of the study area and compare them with old data available, to investigate the variation of the dietary aspects. Doing so would help to understand in detail the factors involved in the reduced growth potential observed, given the primary role of the availability of food resources in determining growth performances (Ross et al., 2018). Experimental studies aiming to elucidate the physiological processes behind the variations we observed could be useful in the future to better understand the potential effect of warming on the metabolic performances of the study species. Moreover, considering that most of the cold-water species inhabiting the Mediterranean Sea show spawning peaks occurring in correspondence with the thermal minimum, a comparative study of the relationship between sea temperature and the reproductive traits (i.e., gametogenesis, fecundity) could be used to obtain essential information for evaluating the vulnerability of these species.

Further modelling efforts are essential for assessing how gadiform populations may respond to ongoing climate change in the Adriatic Sea. Incorporating predictive modelling techniques can help forecast potential future scenarios and inform adaptive management strategies. At present, the assessment and management of gadiform species is not a priority at the Mediterranean scale but, to achieve an ecosystem-based management, gaining information from the species not routinely evaluated will become increasingly important in the near future. Finally, collaboration with stakeholders and fisheries management authorities will be imperative to develop and implement effective management measures aimed at safeguarding climatically vulnerable species in the face of climate change. In summary, while this thesis has shed light on the biological responses of some commercial gadiform fish populations to climate change and fishing in the Adriatic Sea, there is a need for continued research and collaborative efforts (as most of the Adriatic stocks are shared between different countries) to ensure the long-term resilience and sustainability of these valuable marine resources in a changing environment.

7 References General sections

Albo-Puigserver, M., Pennino, M. G., Bellido, J. M., Colmenero, A. I., Giráldez, A., Hidalgo, M., et al. (2021). Changes in Life History Traits of Small Pelagic Fish in the Western Mediterranean Sea. *Front. Mar. Sci.* 8, 570354. doi: 10.3389/fmars.2021.570354.

Álvarez-Noriega, M., White, C. R., Kozłowski, J., Day, T., and Marshall, D. J. (2023). Life history optimisation drives latitudinal gradients and responses to global change in marine fishes. *PLoS Biol.* 21, e3002114. doi: 10.1371/journal.pbio.3002114.

Artegiani, A., Paschini, E., Russo, A., Bregant, D., Raicich, F., and Pinardi, N. (1997). The Adriatic Sea General Circulation. Part II: Baroclinic Circulation Structure. *J. Phys. Oceanogr.* 27, 1515–1532.

Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., et al. (2020). Fish body sizes change with temperature but not all species shrink with warming. *Nat. Ecol. Evol.* 4, 809–814. doi: 10.1038/s41559-020-1171-0.

Bailey, R. S. (1982). The population biology of blue whiting in the north atlantic. *Adv. Mar. Biol.* 19, 257–355. doi: 10.1016/S0065-2881(08)60089-9.

Barausse, A., Michieli, A., Riginella, E., Palmeri, L., and Mazzoldi, C. (2011). Long-term changes in community composition and life history traits in a highly exploited basin (northern Adriatic Sea): The role of environment and anthropogenic pressures. *J. Fish Biol.* 79, 1453–1486. doi: 10.1111/j.1095-8649.2011.03139.x.

Barneche, D. R., White, C. R., and Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science* 645, 642–645.

Barnett, L. A. K., Branch, T. A., Ranasinghe, R. A., and Essington, T. E. (2017). Old-Growth Fishes Become Scarce under Fishing. *Curr. Biol.* 27, 2843-2848.e2. doi: 10.1016/j.cub.2017.07.069.

Ben Rais Lasram, F., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W., and Mouillot, D. (2010). The Mediterranean Sea as a “cul-de-sac” for endemic fishes facing climate change. *Glob. Chang. Biol.* 16, 3233–3245. doi: 10.1111/j.1365-2486.2010.02224.x.

Bethoux, J. P., Gentili, B., Raunet, J., and Tailliez, D. (1990). Warming trend in the western Mediterranean deep water. *Nature* 347, 660–662. doi: 10.1093/nq/s6-XI.272.208-b.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., et al. (2000). Impact of fishing on size composition and diversity of demersal fish communities. *ICES J. Mar. Sci.* 57, 558–571. doi: 10.1006/jmsc.2000.0727.

Bohnsack, J. A. (1994). How marine fishery reserves can improve reef fisheries. In *Proceedings of the Gulf and Caribbean Fisheries Institute, 43*, 217–241. Available at: http://hdl.handle.net/1834/28594.

Bonacci, O., and Vrsalović, A. (2022). Differences in Air and Sea Surface Temperatures in the Northern and Southern Part of the Adriatic Sea. *Atmosphere* 13, 1158. doi: 10.3390/atmos13071158.

Botter, L., Giovanardi, O., and Raicevich, S. (2006). Chioggia’s fleet fishery migration in the Adriatic Sea between the 19th and the 20th centuries. *J Mediterr Stud* 16, 27–44.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.

Calì, F., La Mesa, M., Donato, F., Mazzoldi, C., Martinelli, M., and Santojanni, A. (2023a). Life history traits and historical comparison of blue whiting (*Micromesistius poutassou*) growth performance from the western Pomo/Jabuka Pits area (central Adriatic Sea). *Front. Mar. Sci.* 10, 1291173. doi: 10.3389/fmars.2023.1291173.

Calì, F., Stranci, F., La Mesa, M., Mazzoldi, C., Arneri, E., and Santojanni, A. (2023b). Whiting (*Merlangius merlangus*) Grows Slower and Smaller in the Adriatic Sea: New Insights from a Comparison of Two Populations with a Time Interval of 30 Years. *Fishes* 8, 341. Available at: https://doi.org/10.3390/fishes8070341.

Cardinale, M., Dörner, H., Abella, A., Andersen, J. L., Casey, J., Döring, R., et al. (2013). Rebuilding EU fish stocks and fisheries, a process under way? *Mar.*

Policy 39, 43–52. doi: 10.1016/j.marpol.2012.10.002.

Cardinale, M., Osio, G. C., and Scarcella, G. (2017). Mediterranean Sea: A failure of the European fisheries management system. *Front. Mar. Sci.* 4, 72. doi: 10.3389/fmars.2017.00072.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., et al. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob. Chang. Biol.* 16, 24–35. doi: 10.1111/j.1365-2486.2009.01995.x.

Chirgwin, E., Marshall, D. J., Sgro, C. M., and Monro, K. (2018). How does parental environment influence the potential for adaptation to global change? *Proc. R. Soc. B Biol. Sci.* 285, 20181374. doi: http://dx.doi.org/10.1098/rspb.2018.1374.

Civitarese, G., Gacic, M., Cardin, M., and Ibello, V. (2005). Winter Convection Continues in the Warming Southern Adriatic. *Eos, Trans. Am. Geophys. Union* 86, 445–451.

Claireaux, M., Dos Santos Schmidt, T. C., Olsen, E. M., Slotte, A., Varpe, Ø., Heino, M., et al. (2021). Eight decades of adaptive changes in herring reproductive investment: The joint effect of environment and exploitation. *ICES J. Mar. Sci.* 78, 631–639. doi: 10.1093/icesjms/fsaa123.

Clarke, A. (1992). Reproduction in the cold: Thorson revisited. *Invertebr. Reprod. Dev.* 22, 175–183. doi: 10.1080/07924259.1992.9672270.

Clodia Database (2022). Database of Fishery Data from Chioggia, Northern Adriatic Sea. Available at: http://chioggia.biologia.unipd.it/banche-dati/.

Cohen, D. M., Inada, T., Iwamoto, T., and Scialabba, N. (1990). FAO Species Catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date*. FAO Fish. Syn.* 125.

Coll, M., Santojanni, A., Palomera, I., and Arneri, E. (2009). Food-web changes in the Adriatic Sea over the last three decades. *Mar. Ecol. Prog. Ser.* 381, 17–37. doi: 10.3354/meps07944.

Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., et al.

(2013). Rebuilding Mediterranean fisheries: A new paradigm for ecological sustainability. *Fish Fish.* 14, 89–109. doi: 10.1111/j.1467-2979.2011.00453.x.

Danovaro, R., Dell'Anno, A., Fabiano, M., Pusceddu, A., and Tselepides, A. (2001). Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. *Trends Ecol. Evol.* 16, 505–510.

Darwin, C. R. (1871). *The descent of man and selection in relation to sex*. London: Murray.

Delling, B., Noren, M., Kullander, S. O., and González, J. A. (2011). Taxonomic review of the genus *Trisopterus* (Teleostei: Gadidae) with recognition of the capelan *Trisopterus capelanus* as a valid species. *J. Fish Biol.* 79, 1236–1260. doi: 10.1111/j.1095-8649.2011.03107.x.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *J. Appl. Ecol.* 45, 1029–1039. doi: 10.1111/j.1365-2664.2008.01488.x.

Dulvy, N. K., Sadovy, Y., and Reynolds, J. D. (2003). Extinction vulnerability in marine populations. *Fish Fish.* 4, 25–64. doi: 10.1046/j.1467-2979.2003.00105.x.

Edwards, C. T. T., and Plagányi, É. E. (2011). Protecting old fish through spatial management: Is there a benefit for sustainable exploitation? *J. Appl. Ecol.* 48, 853–863. doi: 10.1111/j.1365-2664.2011.01961.x.

Enberg, K., Jørgensen, C., Dunlop, E. S., Varpe, Ø., Boukal, D. S., Baulier, L., et al. (2012). Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. *Mar. Ecol.* 33, 1–25. doi: 10.1111/j.1439-0485.2011.00460.x.

Endo, H. (2002). Phylogeny of the Order Gadiformes (Teleostei, Paracanthopterygii). *Mem. Grad. Sch. Fish. Sci. Hokkaido Univ.* 49, 75–149. Available at: http://eprints2008.lib.hokudai.ac.jp/dspace/handle/2115/22016.

Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Glob. Chang. Biol.* 20, 2473–2483. doi: 10.1111/gcb.12513.

Fanelli, E., Ros, Z. Da, Menicucci, S., Malavolti, S., Biagiotti, I., Canduci, G., et al. (2023). The pelagic food web of the Western Adriatic Sea: a focus on the role of small pelagics. *Sci. Rep.* 13, 1–17. doi: 10.1038/s41598-023-40665-w.

FAO (2022a). *The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation.* Rome: FAO. Available at: https://doi.org/10.4060/cc0461en%0AThe.

FAO (2022b). *The State of Mediterranean and Black Sea Fisheries 2022*. Rome: General Fisheries Commission for the Mediterranean. Available at: https://doi.org/10.4060/cc3370en.

FAO (2023). FishStatJ - Universal software for fishery statistical time series. Available at: https://www.fao.org/fishery/en/topic/166235/en.

Ferrà, C., Tassetti, A. N., Grati, F., Pellini, G., Polidori, P., Scarcella, G., et al. (2018). Mapping change in bottom trawling activity in the Mediterranean Sea through AIS data. *Mar. Policy* 94, 275–281. doi: 10.1016/j.marpol.2017.12.013.

Fiorentino, F., Gancitano, S., Giusto, G. B., and Rizzo P. (2003). Stima della longevità in gadiformi dello stretto di sicilia sulla base della lettura di otoliti. *Biol. Mar. Mediterr.* 10, 814–818.

Follesa, M. C., and Carbonara, P. (2019). *Atlas of the maturity stages of Mediterranean fishery resources*. Studies and Reviews n. 99. Rome: FAO. Available at: https://policycommons.net/artifacts/1526159/atlas-of-the-maturity-stages-of-mediterranean-fishery-resources/2214270/.

Fonseca, V. F., and Cabral, H. N. (2007). Are fish early growth and condition patterns related to life history strategies? *Rev. Fish Biol. Fish.* 17, 545–564. doi: 10.1007/s11160-007-9054-x.

Forster, J., Hirst, A. G., and Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proc. Natl. Acad. Sci. U. S. A.* 109, 19310–19314. doi: 10.1073/pnas.1210460109.

Fortibuoni, T., Giovanardi, O., Pranovi, F., Raicevich, S., Solidoro, C., and Libralato, S. (2017). Analysis of long-term changes in a Mediterranean marine ecosystem based on fishery landings. *Front. Mar. Sci.* 4. doi: 10.3389/FMARS.2017.00033.

Fortibuoni, T., Libralato, S., Raicevich, S., Giovanardi, O., and Solidoro, C. (2010). Coding early naturalists' accounts into long-term fish community changes in the Adriatic Sea (1800-2000). *PLoS One* 5, 1–8. doi: 10.1371/journal.pone.0015502.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science* 365, 979–983. doi: 10.1126/science.aax5721.

Froese, R., and Pauly, D. (2023). FishBase. World Wide Web Electron. Publ. (Accessed 28 December 2023). Available at: https://fishbase.mnhn.fr.

Froglia, C. (1981). Summary of biological parameters on *Trisopterus minutus capelanus* (Risso) in the Adriatic. *Fao Fish. Reports* 253, 97–100.

Froglia, C. (1993). Indagine biologica sulle variazioni dei quantitativi commercializzati presso alcuni Mercati Ittici all' ingrosso dell'Alto Adriatico in relazione alla attuazione del fermo temporaneo di pesca a strascico. Ministero Marina Mercantile, Direzione Generale Pesca Marittima, Final Report.

Froglia, C., and Gramitto, M. (1981). Summary of biological parameters on *Micromesistius poutassou* (Risso) in the Adriatic. *Fao Fish. Reports* 253, 93–94.

Gaemers, P. A. M. (2016). Taxonomy, distribution and evolution of trisopterine gadidae by means of otoliths and other characteristics. *Fishes* 1, 18–52. doi: 10.3390/fishes1010018.

Gaemers, P. A. M., and Poulsen, J. Y. (2017). Recognition and distribution of two North Atlantic *Gadiculus* species, *G. argenteus* and *G. thori* (Gadidae), based on otolith morphology, larval pigmentation, molecular evidence, morphometrics and meristics. *Fishes*, 2, 15.

García-Monteiro, S., Sobrino, J. A., Julien, Y., Sòria, G., and Skokovic, D. (2022). Surface Temperature trends in the Mediterranean Sea from MODIS data during years 2003–2019. *Reg. Stud. Mar. Sci.* 49, 102086. doi: 10.1016/j.rsma.2021.102086.

Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., Mchugh, M., et al. (2010). Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Glob. Chang. Biol.* 16, 517–527. doi: 10.1111/j.1365-2486.2009.02027.x.

Giovanardi, O., and Rizzoli, M. (1984). Biological data, collected during the Pipeta expeditions, on the whiting, *Merlangius merlangus* (L.) in the Adriatic Sea. *Fao Fish. Reports* 290, 149–153.

González-Irusta, J. M., and Wright, P. J. (2017). Spawning grounds of whiting (*Merlangius merlangus*). *Fish. Res.* 195, 141–151. doi: 10.1016/j.fishres.2017.07.005.

Gramitto, M. E. (1999). Feeding habits and estimation of daily ration of poor cod *Trisopterus minutus capelanus* (gadidae) in the Adriatic Sea. *Cybium* 23, 115–130.

Hare, J. A., Alexander, M. A., Fogarty, M. J., Williams, E. H., and Scott, J. D. (2010). Forecasting the dynamics of a coastal fishery species using a coupled climate – population model. *Ecol. Appl.* 20, 452–464.

Hayward, A., and Gillooly, J. F. (2011). The cost of sex: Quantifying energetic investment in gamete production by males and females. *PLoS One* 6, e16557. doi: 10.1371/journal.pone.0016557.

Heino, M., Baulier, L., Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F. M., et al. (2013). Can fisheries-induced evolution shift reference points for fisheries management? *ICES J. Mar. Sci.* 70, 707–721. doi: 10.1093/icesjms/fst077 Review.

Heino, M., Dieckmann, U., and Godø, O. R. (2002). Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56, 669–678.

Hidalgo, M., Ligas, A., Bellido, J. M., Bitetto, I., Carbonara, P., Carlucci, R., et al. (2019). Size-dependent survival of European hake juveniles in the Mediterranean Sea. *Sci. Mar.* 83, 207–221. doi: 10.3989/scimar.04857.16A.

Hidalgo, M., Rouyer, T., Bartolino, V., Cerviño, S., Ciannelli, L., Massutí, E., et al. (2012). Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species.

Ecography 35, 637–649. doi: 10.1111/j.1600-0587.2011.07314.x.

Hopkins, T. S. (1992). The structure of Ionian and Levantine Seas. *Reports Meteorol. Oceanogr.* 41, 35–36.

Howes, G. J. (1991). Biogeography of Gadoid Fishes. *J. Biogeogr.* 18, 595–622. Available at: https://www.jstor.org/stable/2845542 Accessed:

IPCC (2014a). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. R. K. Pachauri and L. A. Meyer (eds.). Geneva, Switzerland.

IPCC (2014b). *Climate Change 2014 Impacts, Adaptation, and Vulnerability Part A: Global and Sectoral Aspects Working Group II Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L. L. White (eds.). Cambridge University Press, Cambrige, U. K.

Jardas, I. (1996). *Adriatic Ichthyofauna*. 1st ed. Zagreb, Croatia: Školska Knjiga.

Jennings, S., and Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. *Adv. Mar. Biol.*, 201–212. doi: 10.1016/s0065-2881(08)60212-6.

Jones, D. I., Miethe, T., Clarke, E. D., and Marshall, C. T. (2023). Disentangling the effects of fishing and temperature to explain increasing fish species richness in the North Sea. *Biodivers. Conserv.* 32, 3133–3155. doi: 10.1007/s10531-023-02643-6.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., et al. (2007). Managing evolving fish stocks. *Science* 318, 1247–1248. doi: 10.1126/science.1148089.

Kaschner, K., Rius-Barile, J., Kesner-Reyes, K., Garilao, C., Kullander, S. O., Rees, T., et al. (2022). AquaMaps: Predicted range maps for aquatic species. Available at: www.aquamaps.org.

Koslow, J. A., Boehlert, G. W., Gordon, J. D. M., Haedrich, R. L., Lorance, P., and

Parin, N. (2000). Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES J. Mar. Sci.* 57, 548–557. doi: 10.1006/jmsc.2000.0722.

Kuparinen, A., and Hutchings, J. A. (2012). Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proc. R. Soc. B Biol. Sci.* 279, 2571–2579. doi: 10.1098/rspb.2012.0120.

Kurlansky, M. (1997). *Cod: a biography of the fish that changed the world*. Penguin Book.

Lambert, Y. (2008). Why Should We Closely Monitor Fecundity in Marine Fish Populations? *J. Northwest Atl. Fish. Sci.* 41, 93–106. doi: 10.2960/J.v41.m628.

Laptikhovsky, V. (2006). Latitudinal and bathymetric trends in egg size variation: A new look at Thorson's and Rass's rules. *Mar. Ecol.* 27, 7–14. doi: 10.1111/j.1439-0485.2006.00077.x.

Levin, L. A., and Bridges, T. S. (2001). "Pattern and diversity in the reproduction and development," in *Ecology of Marine Invertebrate Larvae*. McEdward L. (eds.). London, U.K.

Lindmark, M., Audzijonyte, A., Blanchard, J. L., and Gårdmark, A. (2022). Temperature impacts on fish physiology and resource abundance lead to faster growth but smaller fish sizes and yields under warming. *Glob. Chang. Biol.* 28, 6239–6253. doi: 10.1111/gcb.16341.

Lionello, P., Cavaleri, L., Nissen, K. M., Pino, C., Raicich, F., and Ulbrich, U. (2012). Severe marine storms in the Northern Adriatic: Characteristics and trends. *Phys. Chem. Earth* 40–41, 93–105. doi: 10.1016/j.pce.2010.10.002.

Lipej, L., Kovačić, M., and Dulčić, J. (2022). An Analysis of Adriatic Ichthyofauna — Ecology, Zoogeography, and Conservation Status. *Fishes* 7, 58. doi: 10.3390/fishes7020058.

Lloret, J., Serrat, A., Thordarson, G., Helle, K., Jadaud, A., Bruno, I., et al. (2021). The poor health of deep-water species in the context of fishing activity and a warming climate: will populations of *Molva* species rebuild or collapse? *J. Fish Biol.* 98, 1572–1584. doi: 10.1111/jfb.14347.

Lloret, J., Shulman, G. and Love, R. M. (2013) *Condition and Health Indicators of Exploited Marine Fishes*. John Wiley & Sons. West Sussex, U. K.

Lotze, H. K., Coll, M., and Dunne, J. A. (2011). Historical Changes in Marine Resources, Food-web Structure and Ecosystem Functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14, 198–222. doi: 10.1007/s10021-010-9404-8.

Marini, M., Maselli, V., Campanelli, A., Foglini, F., and Grilli, F. (2016). Role of the Mid-Adriatic deep in dense water interception and modification. *Mar. Geol.* 375, 5–14. doi: 10.1016/j.margeo.2015.08.015.

Martin, P., Maynou, F., Recasens, L., and Sabatés, A. (2016). Cyclic fluctuations of blue whiting (*Micromesistius poutassou*) linked to open-sea convection processes in the northwestern Mediterranean. *Fish. Oceanogr.* 25, 229–240. doi: 10.1111/fog.12147.

Mazlum, R. E., and Bilgin, S. (2014). Age, growth, reproduction and diet of the whiting, *Merlangius merlangus euxinus* (Nordmann, 1840), in the southeastern Black Sea. *Cah. Biol. Mar.* 3, 463–474. Available at: https://www.researchgate.net/publication/274248550.

Merino, G., Coll, M., Granado, I., Gee, J., Kroodsma, D., Miller, N. A., et al. (2019). “FAO Area 37 - AIS-based fishing activity in the Mediterranean and Black Sea,” in *Global Atlas of AIS-based fishing activity - Challenges and opportunities*, eds. M. Taconet, D. Kroodsma, and J. A. Fernandes (Rome: FAO). Available at: www.fao.org/documents/card/en/c/ca7012en.

Mir-Arguimbau, J., Balcells, M., Raventós, N., Martín, P., and Sabatés, A. (2020). Growth, reproduction and their interplay in blue whiting (*Micromesistius poutassou*, Risso, 1827) from the NW Mediterranean. *Fish. Res.* 227, 105540. doi: 10.1016/j.fishres.2020.105540.

Mir-Arguimbau, J., Flexas, M. M., Salat, J., Martín, P., Balcells, M., Raventós, N., et al. (2022a). Severe winter conditions improve recruitment success of blue whiting (*Micromesistius poutassou*), a temperate water fish species, in the NW Mediterranean Sea. *Prog. Oceanogr.* 205. doi: 10.1016/j.pocean.2022.102818.

Mir-Arguimbau, J., Martín, P., Balcells, M., Sala-Coromina, J., and Sabatés, A.

(2022b). Fishery dynamics of blue whiting, *Micromesistius poutassou*, a highly discarded bycatch species in the NW Mediterranean Sea. *Sci. Mar.* 86, 1–12. doi: 10.3989/scimar.05240.025.

Mollet, F. M., Kraak, S. B. M., and Rijnsdorp, A. D. (2007). Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. *Mar. Ecol. Prog. Ser.* 351, 189–199. doi: 10.3354/meps07138.

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Marsaleix, P., Somot, S., et al. (2019). An end-to-end model reveals losers and winners in a warming Mediterranean Sea. *Front. Mar. Sci.* 6, 1–19. doi: 10.3389/fmars.2019.00345.

Munch, S. B., and Salinas, S. (2009). Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proc. Natl. Acad. Sci. U. S. A.* 106, 13860–13864. doi: 10.1073/pnas.0900300106.

Nissen, K. M., Leckebusch, G. C., Pinto, J. G., and Ulbrich, U. (2014). Mediterranean cyclones and windstorms in a changing climate. *Reg. Environ. Chang.* 14, 1873–1890. doi: 10.1007/s10113-012-0400-8.

O'Connor, M. I., Holding, J. M., Kappel, C. V., Duarte, C. M., Brander, K., Brown, C. J., et al. (2015). Strengthening confidence in climate change impact science. *Glob. Ecol. Biogeogr.* 24, 64–76. doi: 10.1111/geb.12218.

Panayotova, M., and Todorova, V. (2015). Diversity and community structure of fish in the Bulgarian Black Sea shelf area. *J. Res. Agric. Anim. Sci.* 3, 7–14.

Pauly, D. (2022). Why do fish reach first maturity when they do? *J. Fish Biol.* 101, 333–341. doi: 10.1111/jfb.14902.

Pauly, D., and Cheung, W. W. L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Glob. Chang. Biol.* 24, e15–e26. doi: 10.1111/gcb.13831.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. *Science* 279, 860–863. doi: 10.1126/science.279.5352.860.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., et al. (2002). Towards sustainability in world fisheries. *Nature* 418, 689–695.

doi: 10.1038/nature01017.

Pennino, M. G., Conesa, D., López-Quílez, A., Munoz, F., Fernández, A., and Bellido, J. M. (2016). Fishery-dependent and -independent data lead to consistent estimations of essential habitats. *ICES J. Mar. Sci.* 73, 2302–2310. doi: 10.2307/4451315.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. (2005). Climate Change and Distribution Shifts in Marine Fishes. *Science* 308, 1912–1916.

Pitcher, C. R., Hiddink, J. G., Jennings, S., Collie, J., Parma, A. M., Amoroso, R., et al. (2022). Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. *Proc. Natl. Acad. Sci. U. S. A.* 119, e2109449119. doi: 10.1073/pnas.2109449119.

Platt, T., Fuentes-Yaco, C., and Frank, K. T. (2003). Spring algal bloom and larval fish survival. *Nature* 423, 398–399.

Polat, N., and Gümücs, A. (1996). Ageing of whiting (*Merlangius merlangus euxinus*, Nord., 1840) based on broken and burnt otolith. *Fish. Res.* 28, 231–236.

Politou, C. Y., and Papaconstantinou, C. (1991). Population biology of poor cod (*Trisopterus minutus capelanus*) in the eastern coast of Greece. *Cybium* 15, 69–81.

Pranovi, F., Raicevich, S., Da Ponte, F., Libralato, S., and Giovanardi, O. (2005). "Trawl Fishing Disturbance and Medium-Term Macroinfaunal Recolonization Dynamics: A Functional Approach to the Comparison between Sand and Mud Habitats in the Adriatic Sea (Northern Mediterranean Sea)," in *Benthic habitats and the effects of fishing* (Bethesda, Maryland: American Fisheries Society).

Rass, T. S. (1935). Patterns of structure of fish eggs and larvae in the northern seas. *Dokl. Akad. Nauk SSSR* 2.

Rass, T. S. (1986). Biogeographic rule of inverse relation between egg size and environmental temperature in poikilothermous animals. *Tr. IOAN* 116, 152–168.

Roa-Varón, A., and Ortí, G. (2009). Phylogenetic relationships among families of Gadiformes (Teleostei, Paracanthopterygii) based on nuclear and mitochondrial data. *Mol. Phylogenet. Evol.* 52, 688–704. doi: 10.1016/j.ympev.2009.03.020.

Roether, W., and Schlitzer, R. (1991). Eastern Mediterranean deep water renewal on the basis of chlorofluoromethane and tritium data. *Dyn. Atmos. Ocean.* 15, 333–354.

Roether, W., Manca, B. B., Klein, B., Bregant, D., Georgopoulos, D., Beitzel, V., et al. (1996). Recent Changes in Eastern Mediterranean Deep Waters. *Science* 271, 333–335.

Roff, D. A. (1992). *The Evolution of Life Histories: theory and analysis*. Chapman & Hall. New York, U. S. A.

Roff, D. A. (2002). *Life History Evolution*. Sinauer Associates, Inc. Publisher Sunderland. Massachusetts, U. S. A.

Ross, S. D., Nielsen, J. R., Gislason, H., Nielsen, A., and Andersen, N. G. (2018). Growth and food consumption of whiting *Merlangius merlangus*. *J. Fish Biol.* 93, 334–343. doi: 10.1111/jfb.13763.

Rudstam, L. G., Aneer, G., and Hildén, M. (1994). Top-down control in the pelagic Baltic ecosystem. *Dana* 10, 105–129.

Rueda, L., Assutí, E. M., Alvarez-Berastegu, D., and Hidalgo, M. (2015). Effect of intra-specific competition, surface chlorophyll and fishing on spatial variation of gadoid's body condition. *Ecosphere* 6. doi: 10.1890/ES15-00087.1.

Russo, A., and Artegiani, A. (1996). Adriatic Sea hydrography. *Sci. Mar.* 60, 33–43.

Russo, A., Carniel, S., Sclavo, M., and Krzelj, M. (2012). 07 Climatology of the Northern-Central Adriatic Sea. *Mod. Climatol.* 8, 177–212. doi: 10.5772/34693.

Salat, J., Pascual, J., Flexas, M., Chin, T. M., and Vazquez-Cuervo, J. (2019). Forty-five years of oceanographic and meteorological observations at a coastal station in the NW Mediterranean: a ground truth for satellite observations. *Ocean Dyn.* 69, 1067–1084.

Sbrana, M. (2017). "*Trisopterus capelanus*," in *Sintesi delle conoscenze di biologia, ecologia e pesca delle specie ittiche dei mari italiani / Synthesis of the knowledge on biology, ecology and fishery of the halieutic resources of the Italian seas*, eds. P. Sartor, A. Mannini, R. Carlucci, E. Massaro, and S. Queirolo (Biol. Mar. Mediterr.), 467-478 (Suppl. 1).

Schroeder, K., Chiggiato, J., Josey, S. A., Borghini, M., Aracri, S., and Sparnocchia, S. (2017). Rapid response to climate change in a marginal sea. *Sci. Rep.* 7, 1–7. doi: 10.1038/s41598-017-04455-5.

Serrat, A., and Muñoz, M. (2022). Can the Life History Trait Divergence of Two Extremes of a Cold-Water Genus Distribution Offer Evidence for Their Vulnerability to Sea Warming? *Fishes* 7, 143. doi: 10.3390/fishes7040143.

Serrat, A., Lloret, J., Frigola-Tepe, X., and Muñoz, M. (2019a). Trade-offs between life history traits in a coldwater fish in the Mediterranean Sea: the case of blue whiting *Micromesistius poutassou*. *J. Fish Biol.* 95, 428–443. doi: 10.1111/jfb.13993.

Serrat, A., Saborido-Rey, F., Garcia-Fernandez, C., Muñoz, M., Lloret, J., Thorsen, A., et al. (2019b). New insights in oocyte dynamics shed light on the complexities associated with fish reproductive strategies. *Sci. Rep.* 9, 1–16. doi: 10.1038/s41598-019-54672-3.

Sguotti, C., Bischoff, A., Conversi, A., Mazzoldi, C., Möllmann, C., and Barausse, A. (2022). Stable landings mask irreversible community reorganizations in an overexploited Mediterranean ecosystem. *J. Anim. Ecol.* 91, 2465–2479. doi: 10.1111/1365-2656.13831.

Sheridan, J. A., and Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nat. Clim. Chang.* 1, 401–406. doi: 10.1038/nclimate1259.

Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G., and Gislason, H. (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396. doi: 10.1016/j.icesjms.2005.01.004.

Spedicato, M. T., Massutí, E., Mérigot, B., Tserpes, G., Jadaud, A., and Relini, G. (2020). The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Sci. Mar.* 83, 9–20.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Funct. Ecol.* 3, 259–268. Available at: https://www.jstor.org/stable/2389364%0AJSTOR.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press. Oxford, U. K.

Stearns, S. C. (2000). Life history evolution: Successes, limitations, and prospects. *Naturwissenschaften* 87, 476–486. doi: 10.1007/s001140050763.

Svetovidov, A. M. (1948). “Gadiformes,” in *Fauna of USSR, Vo IX No. 4. Fishes. Zoological.* Institute of the Academy of Sciences of the USSR (Translated by the Israel Program for Scientific Translations for the National Science Foundation and Smithsonian Institution as OTS 63– 11071).

Teletchea, F., Laudet, V., and Hänni, C. (2006). Phylogeny of the Gadidae (sensu Svetovidov, 1948) based on their morphology and two mitochondrial genes. *Mol. Phylogenet. Evol.* 38, 189–199. doi: 10.1016/j.ympev.2005.09.001.

Tortonese, E. (1964). The Main Biogeographical Features and Problems of the Mediterranean Fish Fauna. *Copeia* 1964, 98–107.

Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *Bioscience* 45, 759–771.

Vallisneri, M., Manfrin Piccinetti, G., and Piccinetti, C. (2003). Biologia riproduttiva di *Trisopterus minutus capelanus* (Lacepede, 1800) nel Mar Adriatico - Reproductive biology of *Trisopterus minutus capelanus* (Lacepede, 1800) in the Adriatic Sea. *Biol. Mar. Medit.* 10, 296–299.

Vallisneri, M., Vecchi, A., and Manfredi, C. (2004). The biological cycle of *Merlangius merlangus* (Linneus, 1758) (Osteichthyes, Gadidae) in the Northern and Middle Adriatic Sea. *Biol. Mar. Medit.* 11, 652–656.

Van Der Laan, R., Eschmeyer, W. N., and Fricke, R. (2014). Family-group names of Recent fishes. *Zootaxa* 3882, 1–230.

Vitale, S., Andrews, A. H., Rizzo, P., Gancitano, S., and Fiorentino, F. (2016). Twenty-five-year longevity of European hake (*Merluccius merluccius*) from novel use of bomb radiocarbon dating in the Mediterranean Sea. *Mar. Freshw. Res.* 67, 1077–1080. doi: 10.1071/MF15376.

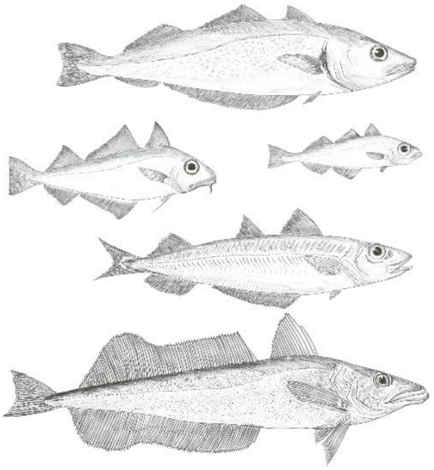
Vrgoc, N., Arneri, E., Jukic-Peladic, S., Krstulovic Šifner, S., Mannini, P., Marceta, B., et al. (2004). Review of current knowledge on shared demersal stocks of the Adriatic Sea. FAO-MiPAF Scientific Cooperation to Support Responsible Fisheries in the Adriatic Sea. GCP/RER/010/ITA/TD-12. *AdriaMed Tech. Doc.*, 91.

Watling, L., and Norse, E. A. (1998). Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conserv. Biol.* 12, 1180–1197. doi: 10.1046/j.1523-1739.1998.0120061180.x.

Wilbur, H. M., and Rudolf, V. H. W. (2006). Life history evolution in uncertain environments: Bet hedging in time. *Am. Nat.* 168, 398–411. doi: 10.1086/506258.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., et al. (2009). Rebuilding Global Fisheries. *Science* 325, 5478–585. Available at: https://www.jstor.org/stable/20544204.

Yemane, D., Field, J. G., and Leslie, R. W. (2008). Indicators of change in the size structure of fish communities: A case study from the south coast of South Africa. *Fish. Res.* 93, 163–172. doi: 10.1016/j.fishres.2008.03.005.



FINE