



Small pelagic fish dynamics: A review of mechanisms in the Gulf of Lions

Claire Saraux, Elisabeth van Beveren, Pablo Brosset, Quentin Queiros, Jean-Herve Bourdeix, Gilbert Dutto, Eric Gasset, Cyrielle Jac, Sylvain Bonhommeau, Jean-Marc Fromentin

► To cite this version:

Claire Saraux, Elisabeth van Beveren, Pablo Brosset, Quentin Queiros, Jean-Herve Bourdeix, et al.. Small pelagic fish dynamics: A review of mechanisms in the Gulf of Lions. Deep Sea Research Part II: Topical Studies in Oceanography, 2019, 159, pp.52–61. 10.1016/j.dsr2.2018.02.010 . hal-02439847

HAL Id: hal-02439847

<https://hal.science/hal-02439847>

Submitted on 21 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

**Small pelagic fish dynamics:
a review of mechanisms in the Gulf of Lions**

Claire Saraux^{a,*}, Elisabeth Van Beveren^{a,b}, Pablo Brosset^{a,b}, Quentin Queiros^a, Jean-Hervé Bourdeix^a,
Gilbert Dutto^c, Eric Gasset^a, Cyrielle Jac^a, Sylvain Bonhommeau^{a,d}, and Jean-Marc Fromentin^a

^a MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France

^b Fisheries and Oceans Canada, Institut Maurice-Lamontagne, 850 route de la mer, Mont-Joli, QC
G5H 3Z4, Canada

^c IFREMER (Institut Français de Recherche pour l'Exploitation de la MER), chemin de Maguelone,
34250 Palavas-les-Flots, France

^d IFREMER (Institut Français de Recherche pour l'Exploitation de la MER) Délégation de l'Océan
Indien, Rue Jean Bertho, BP60, 97822 Le Port CEDEX France

* Corresponding author: Claire Saraux, IFREMER, Av. Jean Monnet, 34200 Sète, FRANCE,
claire.saraux@ifremer.fr

List of emails:

claire.saraux@ifremer.fr

elisvb@hotmail.com

pablo.brosset@gmail.com

quentin.queiros@ifremer.fr

jean.herve.bourdeix@ifremer.fr

gilbert.dutto@ifremer.fr

eric.gasset@ifremer.fr

cyrielle.jac@ifremer.fr

sylvain.bonhommeau@ifremer.fr

jean.marc.fromentin@ifremer.fr

Abstract

Around 2008, an ecosystem shift occurred in the Gulf of Lions, highlighted by considerable changes in biomass and fish mean weight of its two main small pelagic fish stocks (European anchovy, *Engraulis encrasicolus*; European sardine, *Sardina pilchardus*). Surprisingly these changes did not appear to be mediated by a decrease in fish recruitment rates (which remained high) or by a high fishing pressure (exploitation rates being extremely low). Here, we review the current knowledge on the population's dynamics and its potential causes. We used an integrative ecosystem approach exploring alternative hypotheses, ranging from bottom-up to top-down control, not forgetting epizootic diseases. First, the study of multiple population characteristics highlighted a decrease in body condition for both species as well as an important decrease in size resulting both from a slower growth and a progressive disappearance of older sardines. Interestingly, older sardines were more affected by the decrease in condition than younger ones, another sign of an unbalanced population structure. While top-down

control by bluefin tuna or dolphins, emigration and disease were mostly discarded as important drivers, bottom-up control mediated by potential changes in the plankton community appeared to play an important role via a decrease in fish energy income and hence growth, condition and size. Isotopic and stomach content analyses indicated a dietary shift pre- and post-2008 and modeled mesozooplankton abundance was directly linked to fish condition. Despite low energy reserves from 2008 onwards, sardines and anchovies maintained if not increased their reproductive investment, likely altering the life-history trade-off between reproduction and survival and resulting in higher natural mortality. The current worrying situation might thus have resulted from changes in plankton availability/diversity, which remains to be thoroughly investigated together with fish phenotypic plasticity.

Keywords: population dynamics, top-down, disease, zooplankton, exploited species.

Introduction

Knowledge on population dynamics is key to understanding ecosystem functioning and managing exploited populations. Small pelagic fish are widely known for their rapid and important population fluctuations, rendering their management especially difficult (Bakun, 1997). Indeed, long time series of abundance proxies (i.e., fish scale deposition rates, Baumgartner et al., 1992; McClatchie et al., 2017) demonstrate that large fluctuations are an inherent characteristic of these populations and occur very rapidly, i.e. within a few years. As a consequence, fish landings may drop from thousands or millions of tons to almost nothing in a matter of years (e.g. Lluch-Belda et al., 1989). Such rapid population changes are usually explained by the short lifespan of small pelagic fish and fluctuating, environment-dependent recruitment success (Chambers and Trippel, 2012; Cushing, 1990). In addition, over the last decades, (over-)exploitation has also played a role in those fluctuations as fishing capacity and effort can hardly match such high level variations, generating collapses and longer periods of low abundance in small pelagic fish stocks (Essington et al., 2015; Toresen and Østved, 2000).

Sardine and anchovy have a worldwide distribution and are especially known for their prevalence in the five boundary current systems (Benguela, Humboldt, California, Canary, Kuroshio), although their populations are also important in other areas, such as the Northeast Atlantic, south-west Australia and the Mediterranean and Black Seas (Checkley et al., 2009). While the main causes (including environmental and climatic drivers) for population variations as well as the apparent synchrony of the sardine/anchovy alternation have been largely studied in these five major ecosystems (see references within Checkley et al., 2009; Schwartzlose et al., 1999), the question arises on whether results might be transferable to smaller or non-upwelling systems (but see Katara et al., 2011). For those ecosystems, understanding the mechanisms involved in population fluctuations remains a key objective, especially with a view of improving management schemes, benefitting both ecosystem and economy. With a better insight in past and hence future fluctuations, management procedures can be better evaluated and selected, decreasing the probability of overexploitation (Hilborn, 2007). Besides an obvious interest for management, the topic is also interesting from an ecological point of view. To date, most studies have focused on co-variations between climatic or oceanographic parameters and population abundance, biomass or catch. However, those usually lack a comprehensive mechanistic. Using the Gulf of Lions as a pilot area, we attempt to deliver an integrated insight in the population dynamics by tackling the question from several complementary angles.

The Gulf of Lions is one of the most productive areas in the Mediterranean Sea, due to a wide (for the Mediterranean Sea) continental shelf and a combination of high discharge by the Rhone river and small-scale upwellings created by strong and transient winds (Milot, 1990; Petrenko et al., 2005). Recently, significant changes have been observed in the pelagic ecosystem of the Gulf of Lions (Fig 1). Since 2008, the prevailing small pelagic species, i.e. sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) have exposed a lasting decrease in individual size and weight, making them far less profitable for fisheries in the absence of a market for fish of such a size. As a result, most pelagic trawlers that used to target sardine and anchovy have now turned towards other more valued species (such as European hake, *Merluccius merluccius*), or halted their activity altogether. Consequently, landings of both species, but especially sardine, have dropped to insignificant levels during the last years (GFCM, 2016; Fig 1). Conversely, the sprat (*Sprattus sprattus*) population which had been scanty present for the last two decades and is of no commercial interest in the region, showed a remarkable upsurge. Nonetheless, its mean size and body condition remained quite low or decreased (Fig 1).

Surprisingly, these changes in population dynamics neither appeared mediated by environmentally-driven changes in recruitment or overfishing (as often documented in small pelagic fish; see e.g. Barange et al., 2009; Cushing and Dickson, 1976; Lindegren et al., 2013), as recruitment over this period remained high and the exploitation rate was rather low, even before 2008 (sardine exploitation rate < 15% since 2002; GFCM, 2016).

Facing this situation, we launched the EcoPelGol project to understand the underlying causes of recent small pelagic population changes in the Gulf of Lions. As no similar regime shift (in terms of oceanography or other biological compartments) had been observed at that period in the Gulf of Lions, the objective of the project was to provide an integrative assessment of causal mechanisms affecting population dynamics by jointly investigating top-down (predation by tuna or marine mammals) and bottom-up (environmental effects) controls as well as diseases and energy allocation trade-offs (see Fig. 2). Although all studies provide a piece of the puzzle, all need to be combined to provide an in-depth answer to the question. Here, we present a summary and cross-discussion of our findings. First, we present a set of studies investigating changes in size, growth, condition and demographic composition over the last two decades and then assessing whether the present situation really is unusual compared to the last 150 years in terms of fish landings. Then, observations and results from these studies allowed us to build alternative hypotheses regarding the control mechanisms of the populations. Each of these hypotheses will be presented and discussed here: (1) changes in size distribution are due to mortality or emigration; (2) observed decreases in

small pelagic fish populations are due to top-down pressure exerted on small pelagics by the recently recovering bluefin tuna (*Thunnus thynnus*) population as well as dolphins (*Tursiops truncatus* and *Stenella coeruleoalba*); (3) changes in demographic composition and biological parameters of sardine and anchovy stocks are due to emigration or disease; (4) changes in population trends are due to bottom-up processes, such as environmental forcing and changes in planktonic preys. In the absence of long-term time series of plankton fields in the Gulf of Lions, we investigated potential changes in fish diet using a combination of stable isotope and stomach content data analyses. Finally, (5) we tested for the hypothesis that changes in fish size and mass should affect life-history trade-off between maintenance, growth and reproduction (Stearns, 1976). To do this, we estimated the reproductive investment of sardine and anchovy along years through different proxies such as the reproductive period duration, the gonado-somatic index or the length at first maturity.

Methods

This paper reviews the main findings of several studies. For clarity, we present here only an overview of the principal data and methods used in this project and refer to specific studies for more details.

Small pelagic data

Data on small pelagics come from two main sources: (i) data collected in July of each year since 1993 during scientific PELMED surveys, and (ii) fisheries data. PELMED surveys (Bourdeix and Saraux, 1985) are acoustic and trawl surveys specifically designed to sample and assess small pelagic fish biomasses in the Gulf of Lions. Acoustic sampling is performed along 9 parallel and regularly spaced transects by means of echosounders (Simrad ER60). Discrimination between species is done both by echo trace classification and trawl allocation (Simmons and MacLennan, 2005). Indeed, trawls are conducted each time new fish traces are observed on the echogram. The proportion of each species is then estimated by random sampling of the catch before sorting and weighing per species. Further, measurements such as weight, length, age and fat content are taken for the three main targeted species (anchovy, sardine and sprat) at each trawl. Depending on years, samples (entire fish or tissues) are also conserved (frozen at -20°C or in formol) and brought back to the lab for more complete analyses (e.g. histology, stomach contents, muscle lipid and isotopic analyses). Despite a very rich dataset with a high spatial resolution, these surveys only represent a snapshot of the summer situation and do not inform on potential seasonal patterns. To counteract this problem, a partnership with fishermen has been developed to acquire samples all year round. A few times a month, one crate of the catch is randomly sampled by fishermen on the boat and conserved on ice until they return to the harbour (note that fishing events last a maximum of 24h according to

regulation). Individual measurements are then computed in the laboratory in the evening or the next day.

These data (~30 years) were complemented by data on sardine and anchovy fish landings spanning 1865-2013. This long-term time series was compiled by subregion of the Gulf of Lions by extensive data mining of the Mediterranean French fisheries records (see Van Beveren et al., 2016a for details), and provided us with a historical perspective in this ecosystem.

Environmental data

In a first approach, climatic and environmental variables were used as proxies of habitat quality and prey availability. We also used different global climatic indices including the North Atlantic Oscillation (NAO) or the Western Mediterranean Oscillation (WeMO), that integrate fluctuations of temperature, rainfall and wind mixing over large spatial and temporal scales and may be more relevant in explaining population fluctuations (see Stenseth et al., 2003). In addition, Sea Surface Temperature (SST) and Chlorophyll a concentration (Chla) satellite-derived data were extracted from MODIS aqua data (<http://oceancolor.gsfc.nasa.gov>). Rhone outflow, an indicator of nutrient availability, is measured at the Beaucaire station and data is distributed by the Compagnie Nationale du Rhône.

Biological parameters

Several biological parameters have been studied in this project.

Body condition: Body condition is commonly defined as the quantity of individual's energetic reserves (Jakob et al., 1996) and reflects the amount of energy extracted from the environment. As such, it may inform on prey availability or foraging efficiency (Lloret et al., 2014). Body condition is also often considered as a good indicator of individual well-being or performance, as it represents the amount of nutrients that can be mobilized for the different vital traits, thus mediating life-history trade-offs (Schulte-Hostedde et al., 2001). We mostly used the LeCren body condition index (Le Cren, 1951) based on morphometrics measurements, as it allowed us to go back in time and investigate changes throughout the years. The Le Cren index is defined as the ratio between the weight of the fish and a theoretical weight for its length derived from measurements over the entire population: $K_n = \frac{W}{a L^b}$ where a and b are constants estimated from the length-weight relationships. This parameter has been shown to strongly correlate with bioenergetics measurements of fat contents using a fatmeter, as well as with direct biochemical measurements outside of the breeding period (Brosset et al., 2015a). During breeding, the morphometric index seems to represent a more integrative index of the fish condition (Brosset et al., 2015a).

Reproductive investment: Two parameters relating to reproduction were used. First, the length at first maturity L_{50} was defined as the length at which half of the population is mature using a sigmoid model. This was estimated each year or through periods of combined years. Second, the gonadosomatic index was used as a proxy of reproductive investment. It was estimated as the ratio between the weight of the gonad and the weight of the eviscerated fish.

Age: Age was assessed using otolith reading. However, as those were missing in some years, annual age compositions per species were computed using a Bayesian mixture model that uses age-length keys based on otolith readings as priors to slice size distributions (see Van Beveren et al., 2014 for more details).

Estimating predation on small pelagic fish

Predation by bluefin tuna: Top-down control by bluefin tuna was estimated by calculating the total amount of energy needed by bluefin tuna in the Gulf of Lions by combining (i) DEB (Dynamic Energy Budget) modeling to estimate the weight-specific energy requirement of an individual (adapted from Jusup et al., 2014), (ii) population weight structure information from fisheries and (iii) population abundance as estimated from aerial surveys (Bauer et al., 2015). This energy was then partitioned among the different consumed preys using stomach content analyses for 3 years of study and prey energy densities acquired from the literature. This allowed us to estimate the consumption of each prey species. As the PELMED survey delivers estimates of small pelagic fish stock abundances in the Gulf of Lions, we were then able to estimate the percentage of the population predated by bluefin tuna. To account for uncertainty associated with all parameters, calculations were bootstrapped (10 000 iterations) using the most appropriate error distributions for each parameter. Furthermore, as the predation pressure might have been more important on specific prey size classes, we also investigated bluefin tuna selectivity. To do so, we estimated the size distribution of consumed prey, based on undigested prey lengths and relationships between otolith and prey lengths for digested prey. Per species, prey size distribution was compared to the population size distribution, obtained from the PELMED survey. All methodological details can be found in Van Beveren et al., 2017.

Predation by dolphins: A similar approach was used to estimate predation by the two main dolphin species inhabiting the Gulf of Lions (*Tursiops truncatus* and *Stenella coeruleoalba*). Plane and boat surveys were used to estimate dolphin abundance and population structure, while allometric energetic models were used to estimate individual energy requirement and stomach contents of stranded dolphins were used to determine prey composition in the diet. Uncertainty was estimated using a simulation approach (more details in Queiros et al., subm.).

Pathogen and disease analyses

To assess whether pathogens might be an additional source of mortality for sardine in the Gulf of Lions, monthly sampling was performed for one year in 2014-2015 (see details in Van Beveren et al., 2016b). Nine sampling events of 150 sardines each were used to perform a large-band search for bacteria, parasites (micro and macro) and viruses. Fresh samples were obtained from fishermen or the PELMED survey and were analysed within 24h. All fish were first measured, weighed and their fat content was assessed using a fatmeter (Brosset et al., 2015a), so that we could investigate the link between fish morphological characteristics and pathogen prevalence and intensity. Regarding viruses, we used both broad-spectrum cell cultures and specific PCR analyses targeting the pilchard herpes virus known to decimate sardine populations (see Whittington et al., 2008) and the betanodavirus (the most common fish virus in the Mediterranean Sea). To check whether detected infectious agents could be harmful pathogens, we also ran tissue analyses through autopsy and histology.

Planktonic data analyses

The study of bottom-up processes requires detailed information on prey (plankton) availability. Unfortunately, surveys of phyto- and zooplankton are scarce in the Gulf of Lions and no historical datasets are available. Therefore, we used modeled plankton concentration estimates extracted from a coupled physical-biogeochemical model called SYMPHONIE – Eco3m-S (Auger et al., 2011; Baklouti et al., 2006; Marsaleix et al., 2012). This model includes 6 groups of plankton: picophytoplankton, nanophytoplankton, microphytoplankton (mainly diatoms), nanozoopankton (small ciliates and flagellates), microzooplankton (large ciliates and flagellates) and mesozooplankton (mainly copepods).

We investigated whether fish diet had changed across time and tested whether this could be related to changes in small pelagic fish populations. We compared the diet of small pelagics before and after 2008 (i.e. when most of the changes occurred). We used a combination of complementary approaches, i.e. stomach content and stable isotope analyses (Caut et al., 2006) on fish sampled from PELMED surveys. This ensured all samples were collected at a similar time of year and avoided any potential bias due to seasonal variation.

Results and Discussion

1. State of the population

As often in fisheries studies, the first alarming sign was observed from fish landings with a sudden crash in sardine landings around 2008, while anchovy landings had been decreasing at a slower rate over a longer time period. Looking at it from a historical perspective (Fig. 3) highlighted an even more alarming trend. Indeed, a first study describing the historical landings of sardine and anchovy in the Gulf of Lions showed that their present total landings are similar to those before the 1960s, when fishing was still non-industrial since sonars and large-scale trawlers had not yet appeared (Van Beveren et al., 2016a). Focusing on sardine, the recent situation (after 2008) is highly unusual, as recent landings are the lowest recorded over the past 150 years. Biomass and abundance estimates resulting from recent PELMED surveys did not reveal such drastic changes. Especially, fish abundance has been maintained if not increased lately contrary to the landings (Fig.1). The contradiction between the crash in landings and an increase in abundance suggests a decrease in fishing effort. One reason for this might be fish size. Indeed, the low price and quasi-absence of a market for small fish and the increase in fishing marginal costs (e.g. fuel) would lead to a halt in fishing effort. To test this hypothesis and obtain a better awareness of the current situation and population dynamics, we investigated changes in fish size, condition, age and length composition using PELMED survey data (Van Beveren et al., 2014). Sardine and anchovy size decreased around 2008 and fish remained small thereafter (Fig. 4). Annual anchovy size distributions are usually unimodal, so that the decrease in mean size corresponds to a shift of the entire mode towards small individuals due to a rather slow growth, as confirmed by von Bertalanffy growth curves (Van Beveren et al., 2014). Conversely, sardine distributions are bimodal and the decrease in size translated in the disappearance of the second mode containing large sardines. For sardine, which displayed the most significant size truncation, the shift towards smaller fish was explained by a combination of slower growth and the disappearance of older individuals (ages 2+, see Van Beveren et al., 2014).

Large old individuals might have disappeared because they emigrated towards different areas and/or they experienced a higher than usual mortality rate. If fish emigrated, they most likely did so towards Spanish waters, because of the main current direction and the presence of continental shelf in this area. However, a comparison between French and Spanish size distributions of the landings from 2002 to 2013 (Fig 5) reveals that size distributions are similar between both regions. In particular, when large fish disappeared from French landings, the same happened with Spanish landings. This not only suggests that large fish did not migrate to Spain, but also that the recent changes observed in the Gulf of Lions might take place at a larger scale in the North-Western Mediterranean Sea (although sardine exploitation has always been much more important in Spain; Palomera et al., 2007). As a consequence, it is more likely that large individuals experienced higher mortality rates. Higher mortality is expected to occur if fish are in a lower condition (Millar and Hickling, 1990).

Accordingly, since 2008 both sardine and anchovy populations have been characterized by a continuous trough of low body condition, compared to short, transient troughs in the past (Van Beveren et al., 2014, Fig 4). Thus, the current situation is the first to occur over such a long period. Interestingly, the decrease was most pronounced for sardine, for which the largest decline in size and age was observed. Moreover older sardines were more affected by the decrease in condition than younger ones, supporting the hypothesis that natural mortality rates primarily increased for larger size classes (Brosset et al., 2015b).

As expected when fish populations decline (e.g. Ballon et al., 2008), sardines and anchovies matured earlier (length at maturity for sardine was about 12.1 cm prior to 2009, but about 9.6 cm after 2009 for sardines). Further, despite poor energy reserves, they maintained, or in some cases even increased, their reproductive investment (as expressed by the reproductive period duration as well as their gonadosomatic index, see Brosset et al., 2016b). These findings might explain why abundance and recruitment remained surprisingly high throughout the last decade (Fig. 1). However, such changes might also come at a cost and explain the disappearance of older sardines through a change in the life-history trade-off between reproduction and maintenance. This is especially true for sardines, which act as capital breeders reproducing in winter when feeding conditions are poorer. An especially low condition at the start of winter (Albo-Puigserver et al., 2017) and reproduction associated with an important reproductive effort may thus result in increased adult mortality. The change in the reproduction/maintenance trade-off might incur costs in terms of immunity for instance, so that fish might be more susceptible to disease (Krams et al., 2017). Such a change may also affect the amount of energy a fish can mobilize for muscle activity and as such decrease its swimming efficiency, so that weaker individuals might be more prone to predation (Herting and Witt, 1967). Ultimately, fish might reach a critical condition for their survival and die from starvation, if they are not able to find large quantity of prey especially at the end of winter.

Regardless of the exogenous pressures, one hypothesis is that the observed changes in life-history traits (slower growth, decreased size at first maturity) and associated trade-offs might result from population adaptation. For instance, fish facing an important selective exploitation on large individuals have been shown to react towards slower growth and earlier maturation (Audzijonyte et al., 2013; Devine et al., 2012; Kuparinen et al., 2016; Mollet et al., 2016). Yet, whether such changes derive from phenotypic plasticity or genetic changes remains mostly unknown. We recently aimed at experimentally disentangling those effects by capturing wild sardines in October 2015, which we placed in 4.5 cubic meter tanks for three months. Our results highlighted phenotypic plasticity rather than genetic adaptation. Despite the winter period over which the experiment was conducted and low water temperature at that time, sardines fed daily to 1.5% of their body mass (as often

recommended in aquaculture) immediately exhibited compensatory growth ($13.0 \pm 0.1\text{cm}$ after 40 days vs. $11.2 \pm 0.1\text{cm}$ at t_0) and an important upsurge in their body condition (Le Cren index: 1.43 ± 0.02 at t_{40} vs. 0.93 ± 0.01 at t_0). Such an increase would take 6 months up to one year to occur in the wild according to the von Bertalanffy curves estimated between 1993 and 2012 confirming that observed changes are a direct consequence of a dietary restriction in the wild.

2. Factors affecting small pelagic populations

Although previously cited studies contributed to our general understanding of the core population dynamics, the underlying factors affecting population dynamics still needed to be determined. Given the exceptionality of the situation (high mortality of older fish rather than low recruitment), a large scope of potential mechanisms were scrutinised, including some which are commonly neglected in small pelagic fish research (e.g., predation and disease; Fig 2).

2.1 Top-down Control

First and foremost, fishing pressure was examined as overexploitation is a likely candidate when investigating decrease in fish size and condition. Due to differential catchability, fishing can cause or magnify a shift towards young, small and early-maturing individuals (Audzijonyte et al., 2013; Devine et al., 2012; Kuparinen et al., 2016; Mollet et al., 2016). Over the past 25 years, harvest rates (landings/population biomass) have generally been low (mean of 13% for anchovy and 10% for sardine) but varied significantly around these means (Fig. 6). A safe level of medium term exploitation for small pelagic fish is considered to be 0.4 (Patterson et al., 1992), a threshold that has only been crossed once in 1997 for sardine. This occurred right before sardine biomass peaked, indicating that there had been little effect on the population. Finally, since 2010 the sardine harvest rate has been reduced to 1% or less, but no signs of recovery in terms of growth, survival or condition have yet been recorded despite the high turnover rate of the species. These results suggest that fishery is not the main cause for high sardine and anchovy mortality. Further, stock assessments for sardines in this area based on a 2-stage biomass model, estimated an extremely low exploitation rate, confirming this vision (GFCM, 2016). As such, the General Fisheries Commission for the Mediterranean Sea judged the sardine stock ecologically unbalanced due to its lack of old individuals and problems of growth and body condition (GFCM, 2016).

Similarly to the fishery hypothesis, another top-down regulating mechanism could be the effect of predators removing an important part of the adult population. However, despite sardine and anchovy being the two main prey species of bluefin tuna (accounting for more than 80% of the diet in

terms of mass and abundance), top-down control by tuna has been estimated to be extremely limited, the percentages of each population consumed being lower than 2% (Van Beveren et al., 2017). Further, bluefin tuna seemed to be opportunistic in terms of prey size, as no consistent size-selective feeding was observed. Similarly, the fraction of the sardine and anchovy population ingested by dolphins was even lower (<0.1%, Queiros et al., submitted). The current situation of small pelagics in the Gulf of Lions is thus unlikely to be due to top-down processes.

2.2 Disease

A general veterinary study focusing at sardine was conducted, aiming to detect a wide range of potential pathogens, including parasites, viruses and bacteria (Van Beveren et al., 2016b). However, our analyses did not reveal any trace of macro-parasites or viruses (whether on culture or by specific PCRs) and detected only few bacteria, all of which with little prevalence (Van Beveren et al., 2016b). Only micro-parasites were observed in 77% of the fish (Van Beveren et al., 2016b). Those microparasites observed in the liver were coccidies, a hepatic parasite, whose effect is mostly unknown. However, no clear damage to tissues and no link between pathogen presence and host size or condition were highlighted (Van Beveren et al., 2016b). This study therefore suggested that the probability of pathogens acting as a key mechanism affecting the sardine population is fairly low, although further research on the prevalence and harmfulness of coccidies as well as occurrence in different waters needs to be conducted for this hypothesis to be entirely refuted.

2.3. Bottom-up control

Rather, changes in growth, size and condition, and hence possibly increased mortality, might reflect bottom-up controls mediated by changes in plankton composition and/or concentrations. Indeed, we showed that the concentration in mesozooplankton (from biogeochemical models) was the only variable significantly affecting body condition of both sardines and anchovies, while river runoff, sea surface temperature (SST) or microphytoplankton (i.e. diatom concentration) affected condition in only one of the two species (Brosset et al., 2015b). Following up on this analysis and suggestions in a previous review (Palomera et al., 2007), we compared pre- and post- 2008 diets for fish of similar size. Those exhibited important changes in carbon isotopic values as well as in consumed plankton composition and size for both sardines and anchovies (Brosset et al., 2016a). A principal component analysis on the diet composition of all sampled fish clearly showed segregation between the years prior to (2007 for sardines and 1994 for anchovies) and posterior to the changes (2011-2012) with a shift towards smaller prey species in both sardines and anchovies in recent years (Brosset et al., 2016a). Despite previous associations between small pelagic abundance and basic environmental parameters such as temperature (Palomera et al., 2007), a study on climatic (large-scale indices such

as NAO, AMO and WeMO) and oceanographic parameters (SST and river runoff) did not show any significant change in 2008, suggesting that the mechanisms behind small pelagic changes might be more complex (Van Beveren et al., 2016a). Also, a study at a larger scale including most of the northern side of the Mediterranean Sea showed that fish size and body condition decreased in almost all areas but not concomitantly and suggests that the causes of these declines might be different and occurring at subregional scales (Brosset et al., 2017). Nonetheless, smaller plankton species are known to be less energetic (Zarubin et al., 2014), which might explain why small pelagics have experienced a trough of low body condition. Still, this result might be surprising as a regime shift towards smaller plankton size is thought to be favourable for sardines (Van der Lingen et al., 2006). Indeed, sardines are known to feed on smaller plankton than anchovies probably because they are more efficient filter-foragers (Van der Lingen et al., 2002). Why then would sardines be the ones most affected by a change in plankton communities towards smaller sizes? This observation might reflect an important difference in sardine feeding strategies between upwelling systems and other areas. Sardines from upwelling areas might have developed adaptations increasing their filtering efficiency because of high plankton densities. In the Mediterranean Sea, which is known to be rather productive in spring but mostly oligotrophic otherwise, sardines seem to have developed both feeding modes, i.e. filter and particulate feeding (Nikolioudakis et al., 2012). Therefore, adaptations to filter-feeding might not have evolved so strongly in the Mediterranean Sea. Gill rakers for instance have a higher density in the upwelling area off the Iberian coast than in the North-Western Mediterranean Sea (Costalago et al., 2015). Also, traditional differences in diet between sardines and anchovies (Van der Lingen et al., 2002) are not clearly observed in the Mediterranean Sea (e.g. LeBourg et al., 2015). Therefore, a change towards smaller prey might thus not have been beneficial for Mediterranean sardines, in contrast to what would have been expected in other systems.

3. Further research

While bottom-up control seems the most likely explanation to recent declines in small pelagic fish populations in the Gulf of Lions, the detailed mechanisms underlying the effect of plankton size and composition on fish life-history traits remain to be tested. In particular, the use of an experimental approach (wild fish maintained in tanks) where food size, quantity and quality may be manipulated for might help refine the understanding of individual and combined effects of food on fish foraging behavior, energy expenditure and gain, growth and reproduction. Further, the reconstruction of high-resolution zooplankton fields as well as a better understanding of the energy density of different plankton species or size-classes is urgently needed. If this indeed confirms a change in plankton, then oceanographic, atmospheric and hydrological parameters would need to be further

analysed to better identify a potential regime shift of the ecosystem. In particular, we need to further examine the main factors affecting ocean productivity: nutrient input (through the Rhone river discharge) and water mixing (winds, local upwellings, and deep water convection). Additionally, density-dependence and competition might be important synergistic factors contributing to the dynamics of these populations, especially if resource partitioning is lower due to greater similarities in feeding behavior and prey preference. The total abundance of small pelagics in the Gulf of Lions has somewhat increased, in particular after the upsurge of sprats (Fig. 1). Further, these three species strongly co-occur in the Gulf of Lions (Saraux et al., 2014) and there has been an increase in the isotopic niche overlap of sardine and anchovy with sprat (Brosset et al., 2016a). A study of intra- and inter-specific competition within and among these three species would be of high interest. Finally, few ecotoxicological studies have been performed so far on small pelagic fish in the Gulf of Lions (but see COSTAS project; Tronczynski et al., 2013). Yet, pollution or a decreased water quality could elicit a decrease in fish condition with direct or indirect mortality. Given that the Gulf of Lions contains considerable concentrations of pollutants (Harmelin et al., 2012) and is the most polluted Mediterranean area in terms of PCBs (Bodiguel et al., 2008; Gomez-Gutierrez et al., 2007), this hypothesis would be worth a detailed examination. Pollutants might change fish physiology after ingestion (Heath, 1995), whether or not after bioaccumulation or biomagnification of the contaminants along the trophic web. However, for the few pollutants (PCB, PBDE, Hg and ¹³⁷Cs) looked at so far in anchovy and sardine of the Gulf of Lions (see Harmelin et al., 2012), no exceptionally high levels were found when compared to other European regions (Bocio et al., 2007; Martí-Cid et al., 2007; Naso et al., 2005). This indicates that it might be necessary to look at a mixture of pollutants, as the combined effect of numerous weakly present ones might become an influential cocktail. Further, pollutants might have an indirect effect on fish through the food web. In particular, planktonic species could be impacted (Tiano et al., 2014), potentially resulting in a community and/or abundance change (Arfi et al., 1981; Uriarte and Villate, 2005). However, a study on the aspects of PCBs (including multiple congeners) in the Gulf of Lions indicated that PCB biomagnification in plankton is relatively low, and concentrations are not correlated to the plankton biomass in the system (although such a relation might have been masked; Tiano et al., 2014). While first results, mostly on PCB, were not particularly significant, ecotoxicology of fish and plankton is an important research venue to consider in order to further understand dynamics of small pelagics.

4. Conclusions

In conclusion, the important decrease in small pelagic landings in the Gulf of Lions resulted from a decrease in fish size and condition rather than from a decrease in abundance. Changes in size resulted from a decrease in growth (anchovy and sardine) and disappearance of old individuals

(sardines). The EcoPelGol project enabled us to test for different control mechanisms that we discussed here. Namely, our results provide little evidence of top-down control by predators of those populations and suggested a very low probability of a control by disease and fisheries. Rather, our results suggest changes in diet of these species supporting a bottom-up control. Nonetheless, despite low energy reserves, the investment in reproduction does not appear to be impaired but might occur at a cost to adult maintenance. Future research should further explore the bottom-up control hypothesis to (1) confirm whether plankton communities have changed drastically in recent years and if so (2) examine which factors might explain such changes; and (3) investigate the ecophysiological mechanisms relating changes in diet to fish phenotypes.

Acknowledgements

We thank V.A. Viblanc, J. Alheit and two anonymous reviewers for their helpful suggestions to improve this manuscript. We thank the captain and the crew of the RV “L’Europe” as well as all the scientists on board for their assistance during the PELMED surveys. Our gratitude is extended to the fishermen who provided us with sardine samples all along the project as well as those who helped us capture wild sardines to keep them alive.

Funding: PELMED surveys are cofinanced by Europe through the Data Collection Framework. Most of this work derives from the EcoPelGol programme (Study of the Pelagic ecosystem in the Gulf of Lions), funded by France Filière Pêche (FFP) and the “Région Languedoc-Roussillon”. The rest of the work was funded through the FEAMP project MONALISA, which was co-funded by Europe and FFP.

References

- Albo-Puigserver, M., Muñoz, A., Navarro, J., Coll, M., Pethybridge, H., Sánchez, S., Palomera, I., 2017. Ecological energetics of forage fish from the Mediterranean Sea: Seasonal dynamics and interspecific differences. *Deep-Sea Res. II* 140, 74–82. <https://doi.org/10.1016/J.DSR2.2017.03.002>
- Arfi, R., Champalbert, G., Patriti, G., 1981. Système planctonique et pollution urbaine: un aspect des populations zooplanctoniques. *Mar. Biol.* 61, 133–141.
- Audzijonyte, A., Kuparinen, A., Fulton, E.A., 2013. How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. *Evol. Appl.* 6, 585–595.
- Auger, P.A., Diaz, F., Ulses, C., Estournel, C., Neveux, J., Joux, F., Pujo-Pay, M., Naudin, J., 2011. Functioning of the planktonic ecosystem on the Gulf of Lions shelf (NW Mediterranean) during spring and its impact on the carbon deposition: a field data and 3-D modelling combined approach. *Biogeosciences* 8, 3231–3261. doi: 10.5194/bg-8-3231-2011
- Baklouti, M., Diaz, F., Pinazo, C, Faure, V., Quéguiner, B., 2006. Investigation of mechanistic formulations depicting phytoplankton dynamics for models of marine pelagic ecosystems and description of a new model. *Prog. Oceanogr.* 71, 1–33. doi: 10.1016/j.pocean.2006.05.002
- Bakun, A., 1997. *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. California Sea Grant College System, National Oceanic and Atmospheric Administration, in cooperation with Centro de Investigaciones Biológicas del Noroeste, La Paz, Mexico.
- Ballón, M., Wosnitza-Mendo, C., Guevara-Carrasco, R., Bertrand, A., 2008. The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, *Merluccius gayi peruanus*. *Prog. Oceanogr.* 79(2), 300-307.
- Barange, M., Coetzee, J., Takasuka, A., Hill, K., Gutierrez, M., Oozeki, Y., van der Lingen, C., Agostini, V., 2009. Habitat expansion and contraction in anchovy and sardine populations. *Prog. Oceanogr.* 83, 251–260.
- Bauer, R.K., Bonhommeau, S., Brisset, B., and Fromentin, J.-M., 2015. Aerial surveys to monitor bluefin tuna abundance and track efficiency of management measures. *Mar. Ecol. Prog. Ser.* 534, 221-234. doi:10.3354/meps11392
- Baumgartner, T.R., Soutar, A., Ferreira-Bartrina, V., 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *CalCOFI Rep* 33, 24–40.
- Bocio, A., Domingo, J.L., Falcó, G., Llobet, J.M., 2007. Concentrations of PCDD/PCDFs and PCBs in fish and seafood from the Catalan (Spain) market: Estimated human intake. *Environ. Int.* 33, 170–175.

502 Bodiguel, X., Tronczynski, J., Loizeau, V., Munsch, C., Guiot, N., Le Guellec, A.M., Olivier, N.,
 503 Rounsard, F., Mellon, C., 2008. Classical and novel organohalogen compounds (PCBs and
 504 PBDEs) in hake (*M. merluccius*, L.) from the Mediterranean and Atlantic coasts (France).
 505 *Environmental Toxicology II* (eds A. Kungolos), M. Zamorano), pp. 157–166. Wit Press,
 506 Southampton.

507 Bourdeix, J.-H., Saraux, C., 1985. PELMED – PELAGIQUES MEDITERRANÉE
 508 <http://dx.doi.org/10.18142/19>

509 Brosset, P., Fromentin, J.M., Ménard, F., Bourdeix, J.H., Bigot, J.L., VanBeveren, E., Pernet, F., Saraux,
 510 C., 2015a. Measurement and analysis of small pelagic fish condition: a suitable method for
 511 rapid evaluation in the field. *J. Exp. Mar. Bio. Ecol.* 462, 90-97.

512 Brosset, P., Ménard, F., Fromentin, J.M., Bonhommeau, S., Ulses, C., Bourdeix, J.H., Bigot, J.L., Van
 513 Beveren, E., Roos, D., Saraux, C., 2015b. Influence of environmental variability and age on
 514 small pelagic fish body condition in the Gulf of Lions. *Mar. Ecol. Prog. Ser.* 529, 219-231.

515 Brosset, P., LeBourg, B., Costalago, D., Banaru, D., Bourdeix, JH, Van Beveren, E., Fromentin, J.M.,
 516 Ménard, F., Saraux, C., 2016a. Linking small pelagic dietary shifts and ecosystem changes in the
 517 Gulf of Lions. *Mar. Ecol. Prog. Ser.* 554, 157-171.

518 Brosset, P., Lloret, J., Muñoz, M., Fauvel, C., Van Beveren, E., Marques, V., Fromentin, J.M., Ménard,
 519 F., Saraux, C., 2016b. Biased allocation towards reproduction in small pelagic stocks under poor
 520 condition. *R. Soc. Open Sci.* 3, 160202.

521 Brosset, P., Fromentin, J.M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., Bonanno, A., Carpi,
 522 P., De Felice, A., Donato, F., Ferreri, R., Giraldez, A., Gücü, A., Iglesias, M., Keč, V., Leonori, I.,
 523 Palomera, I., Somarakis, S., Ticina, V., Torres, P., Ventero, A., Zorica, B., Menard, F., Saraux, C.,
 524 2017. Spatio-temporal patterns and environmental controls of small pelagic fish body
 525 condition from contrasted Mediterranean areas. *Prog. Oceanogr.* 151, 149-162.

526 Caut, S., Roemer, G.W., Donlan, C.J., Courchamp, F., 2006. Coupling stable isotopes with
 527 bioenergetics to estimate interspecific interactions. *Ecol. Appl.* 16, 1893–1900. doi:
 528 10.1890/1051-0761(2006)016[1893:CSIWBT]2.0.CO;2

529 Chambers, R.C., Trippel, E., 2012. Early Life History and Recruitment in Fish Populations. Springer
 530 Science & Business Media.

531 Checkley, D., Alheit, J., Oozeki, Y., Roy, C., 2009. Climate Change and Small Pelagic Fish. Cambridge
 532 University Press, New York, US.

533 Costalago, D., Garrido, S., Palomera, I., 2015. Comparison of the feeding apparatus and diet of
 534 European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters: ecological
 535 implications. *J.Fish Biol.* 86(4), 1348-1362.

536 Cushing, D.H., 1990. Plankton Production and Year-class Strength in Fish Populations: an Update of
 537 the Match/Mismatch Hypothesis. *Adv. Mar. Biol.* 26, 249–293.

538 Cushing, D.H., Dickson, R.R., 1976. The biological response in the sea to climatic changes. *Adv. Mar.*
 539 *Biol.* 14, 1-122

540 Devine, J.A., Wright, P.J., Pardoe, H.E., Heino, M., 2012. Comparing rates of contemporary evolution
 541 in life-history traits for exploited fish stocks. *Can. J. Fish. Aquat. Sci.* 69, 1105–1120.

542 Essington, T.E., Moriarty, P.E., Froehlich, H.E., Hodgson, E.E., Koehn, L.E., Oken, K.L., Siple, M.C.,
 543 Stawitz, C.C., 2015. Fishing amplifies forage fish population collapses. *Proc. Natl. Acad. Sci. U.*
 544 *S. A.* 112, 6648–52. <https://doi.org/10.1073/pnas.1422020112>

545 GFCM, Scientific Advisory Committee on Fisheries (SAC)., 2016. Report of the working group on stock
 546 assessment of small pelagic species.

547 Gomez-Gutierrez, A., Garnacho, E., Bayona, J.M., Albaiges, J., 2007. Assessment of the
 548 Mediterranean sediments contamination by persistent organic pollutants. *Environ. Pollut.* 148,
 549 396–408.

550 Harmelin, M.V., Mahe, K., Bodiguel, X., Mellon, C., 2012. Possible link between prey quality,
 551 condition and growth of juvenile hake (*Merluccius merluccius*) in the Gulf of Lions (NW
 552 Mediterranean). *Cybum* 36, 323–328.

553 Heath, A.G., 1995. *Water Pollution and Fish Physiology*. CRC Press.

554 Herting, G.E., Witt, A.J., 1967. The Role of Physical Fitness of Forage Fishes in Relation to their
 555 Vulnerability to Predation by Bowfin (*Amia calva*). *Trans. Am. Fish. Soc.* 96, 427–430.
 556 [https://doi.org/10.1577/1548-8659\(1967\)96\[427:TROPFO\]2.0.CO;2](https://doi.org/10.1577/1548-8659(1967)96[427:TROPFO]2.0.CO;2)

557 Hilborn, R., 2007. Moving to Sustainability by Learning from Successful Fisheries. *AMBIO A J. Hum.*
 558 *Environ.* 36, 296–303. [https://doi.org/10.1579/0044-7447\(2007\)36\[296:MTSBLF\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[296:MTSBLF]2.0.CO;2)

559 Jakob, E.M., Marshall, S.D., Uetz, G.W., 1996. Estimating Fitness: A Comparison of Body Condition
 560 Indices. *Oikos* 77, 61–67. doi: 10.2307/3545585

561 Jusup, M., Klanjšček, T., Matsuda, H., 2014. Simple measurements reveal the feeding history, the
 562 onset of reproduction, and energy conversion efficiencies in captive bluefin tuna. *J. Sea Res.*
 563 94, 144–155.

564 Katara, I., Pierce, G.J., Illian, J., Scott, B.E., 2011. Environmental drivers of the anchovy/sardine
 565 complex in the Eastern Mediterranean. *Hydrobiologia* 670, 49–65.
 566 <https://doi.org/10.1007/s10750-011-0693-5>

567 Krams, I.A., Rumvolt, K., Saks, L., Krams, R., Elferts, D., Vrublevska, J., Rantala, M.J., Kecko, S., Cīrule,
 568 D., Luoto, S., Krama, T., 2017. Reproduction compromises adaptive immunity in a cyprinid fish.
 569 *Ecol. Res.* 32, 559–566. <https://doi.org/10.1007/s11284-017-1467-y>

570 Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaix, H., Martinez, N.D., 2016. Fishing induced life-history
571 changes degrade and destabilize harvested ecosystems. *Sci. Rep.* 6, 22245.

572 Le Bourg, B., Banaru, D., Saraux, C., Nowaczyk, A., Le Luherne, E., Jadaud, A., Bigot, J.-L., Richard, P.,
573 2015. Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions
574 (NW Mediterranean Sea). *J. Sea Res.* 103, 138–146.

575 Le Cren, E.D., 1951. The Length-Weight Relationship and Seasonal Cycle in Gonad Weight and
576 Condition in the Perch (*Perca fluviatilis*). *J. Anim. Ecol.* 20, 201–219.

577 Lindegren, M., Checkley, D.M., Rouyer, T., MacCall, A.D., Stenseth, N.C., 2013. Climate, fishing, and
578 fluctuations of sardine and anchovy in the California Current. *Proc. Natl. Acad. Sci. U. S. A.* 110,
579 13672–7. <https://doi.org/10.1073/pnas.1305733110>

580 Lloret, J., Shulman, G., Love, R.M., 2014. Condition and Health Indicators of Exploited Marine Fishes.
581 John Wiley Sons, Oxford, U.K. 247 pp.

582 Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A., Smith,
583 P.E., 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. *South*
584 *African J. Mar. Sci.* 8, 195–205.

585 Marsaleix, P., Auclair, F., Duhaut, T., Estournel, C., Nguyen, C., Ulses, C., 2012. Alternatives to the
586 Robert-Asselin filter. *Ocean Model.* 41, 53–66. doi:10.1016/j.ocemod.2011.11.002

587 Martí-Cid, R., Bocio, A., Llobet, J.M., Domingo, J.L., 2007. Intake of chemical contaminants through
588 fish and seafood consumption by children of Catalonia, Spain: Health risks. *Food Chem.*
589 *Toxicol.* 45, 1968–1974.

590 McClatchie, S., Hendy, I. L., Thompson, A. R., Watson, W., 2017. Collapse and recovery of forage fish
591 populations prior to commercial exploitation, *Geophys. Res. Lett.* 44, 1877–1885.
592 doi:10.1002/2016GL071751.

593 Millar, J.S., Hickling, G.J., 1990. Fasting endurance and the evolution of mammalian body size. *Funct.*
594 *Ecol.* 4, 5–12. doi: 10.2307/2389646

595 Millot, C., 1990. The Gulf of Lions' hydrodynamics. *Cont. Shelf Res.* 10, 885–894.
596 [https://doi.org/10.1016/0278-4343\(90\)90065-T](https://doi.org/10.1016/0278-4343(90)90065-T)

597 Mollet, F.M., Dieckmann, U., Rijnsdorp, A.D., 2016. Reconstructing the effects of fishing on life-
598 history evolution in North Sea plaice *Pleuronectes platessa*. *Mar. Ecol. Prog. Ser.* 542, 195–208.

599 Naso, B., Perrone, D., Ferrante, M.C., Bilancione, M., Lucisano, A., 2005. Persistent organic pollutants
600 in edible marine species from the Gulf of Naples, Southern Italy. *Sci. Total Environ.* 343, 83–95.

601 Nikolioudakis, N., Isari, S., Pitta, P., Somarakis, S., 2012. Diet of sardine *Sardina pilchardus*: an 'end-
602 to-end' field study. *Mar. Ecol. Prog. Ser.* 453, 173–188.

603 Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., García, A., Morales-Nin, B., 2007. Small
 604 pelagic fish in the NW Mediterranean Sea: An ecological review. *Prog. Oceanogr.* 74, 377–396.
 605 <https://doi.org/10.1016/j.pocean.2007.04.012>
 606 Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management
 607 targets. *Rev. Fish Biol. Fish.* 2, 321–338.
 608 Petrenko, A., Leredde, Y., Marsaleix, P., 2005. Circulation in a stratified and wind-forced Gulf of Lions,
 609 NW Mediterranean Sea: in situ and modeling data. *Cont. Shelf Res.* 25, 7–27.
 610 <https://doi.org/10.1016/J.CSR.2004.09.004>
 611 Queiros, Q., Fromentin, J-M., Astruc, G., Bauer, R., Saraux, C., 2017. Marked differences in the effect
 612 of dolphin predation on hake and small pelagic fish stocks in the Northwestern Mediterranean
 613 Sea. *submitted*
 614 Saraux, C., Fromentin, J.M., Bigot, J.L., Bourdeix, J.H., Morfin, M., Roos, D., VanBeveren, E., Bez, N.,
 615 2014. Spatial structure and distribution of small pelagic fish in the NorthWestern
 616 Mediterranean Sea. *PLoS One* 9(11), e111211.
 617 Schulte-Hostedde, A.I., Millar, J.S., Hickling, G.J., 2001. Evaluating body condition in small mammals.
 618 *Can. J. Zool.* 79, 1021–1029. doi: 10.1139/z01-073
 619 Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher,
 620 W. J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, D. B., MacCall, A. D.,
 621 Matsuura, Y., Nevarez-Martinez, M. O., Parrish, R. H., Roy, C., Serra, R., Shust, K. V., Ward, M.
 622 N., Zuzunaga, J. Z., 1999. Worldwide large-scale fluctuations of sardine and anchovy
 623 populations. *South African J. Mar. Sci.* 21, 289–347.
 624 Simmons, E. J., MacLennan, D. N., 2005. Fisheries acoustics. Chapman and Hall, London.
 625 Stearns, S. C., 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51(1), 3–47.
 626 Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N.G.,
 627 Ådlandsvik, B., 2003. Review article. Studying climate effects on ecology through the use of
 628 climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc.*
 629 *R. Soc. B Biol. Sci.* 270, 2087–2096.
 630 Tiano, M., Tronczynski, J., Harmelin-Vivien, M., Tixier, C., Carlotti, F., 2014. PCB concentrations in
 631 plankton size classes, a temporal study in Marseille Bay, Western Mediterranean Sea. *Mar.*
 632 *Pollut. Bull.* 89, 331–339.
 633 Toresen, R., Østved, J., 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea*
 634 *harengus*, Clupeidae) throughout the 20th century and the influence of climatic variations. *Fish*
 635 *Fish.* 1, 231–256.

- Tronczynski, J., Carlotti, F., Bodin, N., Radakovitch, O., 2013. Contaminants bioaccumulation and biomagnification in a short trophic system: phytoplankton, zooplankton, anchovy, sardine (COSTAS). Marseille, France.
- Uriarte, I., Villate, F., 2005. Differences in the abundance and distribution of copepods in two estuaries of the Basque coast (Bay of Biscay) in relation to pollution. *J. Plankton Res.* 27, 863–874.
- Van Beveren, E., Bonhommeau, S., Fromentin, J.M., Bigot, J.L., Bourdeix, J.H., Brosset, P., Roos, D., Saraux, C., 2014. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Mar. Biol.* 161, 1809-1822.
- Van Beveren, E., Fromentin, J.M., Rouyer, T., Bonhommeau, S., Brosset, P., Saraux, C., 2016a. The fisheries history of small pelagics in the Northern Mediterranean. *ICES J. Mar. Sci.* 73, 1474-1484.
- Van Beveren, E., Keck, N., Fromentin, J.M., Laurence, S., Boulet, H., Labrut, S., Baud, M., Bigarré, L., Brosset, P., Bonhommeau, S., Saraux, C., 2016b. Can pathogens alter the population dynamics of sardine in the NW Mediterranean? *Mar. Biol.* 163(12), 240.
- Van Beveren, E., Fromentin, J.M., Bonhommeau, S., Nieblas, A.E., Metral, L., Brisset, B., Jusup, M., Bauer, R., Brosset, P., Saraux, C., 2017. Predator-prey interactions in the face of effective management strategies: changes in Mediterranean small pelagics are not due to increased tuna predation. *Can. J. Fish. Aquat. Sci.* 74, 1422–1430. <https://doi.org/10.1139/cjfas-2016-0152>
- Van Der Lingen, C. D., 2002. Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *South African J. Mar. Sci.* 24, 301-316
- Van der Lingen, C. D., Hutchings, L., Field, J. G., 2006. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African J. Mar. Sci.* 28, 465-477.
- Whittington, R.J., Crockford, M., Jordan, D., Jones, B., 2008. Herpesvirus that caused epizootic mortality in 1995 and 1998 in pilchard, *Sardinops sagax neopilchardus* (Steindachner), in Australia is now endemic. *J. Fish Dis.* 31, 97–105.
- Zarubin, M., Farstey, V., Wold, A., Falk-Petersen, S., Genin, A., 2014. Intraspecific differences in lipid content of calanoid copepods across fine-scale depth ranges within the photic layer. *PLoS ONE* 9, e92935. doi: 10.1371/journal.pone.0092935

Figure legends

Fig. 1. Biomass, abundance, landings and mean weight of anchovies (in green), sardines (in blue) and sprats (in black) in the Gulf of Lions.

Fig 2: Schematics on the main drivers of small pelagics population dynamics. Significant drivers appear in bold, while less important ones appear in grey and in italics. Green items are perspectives for future work.

Fig 3: Historical landings of sardines and anchovies adapted from Van Beveren et al., 2016a

Fig 4: Size distribution and mean body condition ($\pm$ SE) of sardines and anchovies in 1984 and 85 and from 1992 to 2015, adapted and updated from Van Beveren et al., 2014. N and n represent the number of trawls and the number of measured fish respectively.

Fig 5: Comparison of the annual size distributions of sardine and anchovy landed in Spain (blue) and France (red). Vertical lines indicate the median size of each distribution.

Fig 6: Harvest rates of sardine and anchovy as estimated by the total landings divided by the biomass of the stock assessed by acoustics. Dashed line indicates the reference point of Patterson (1996)

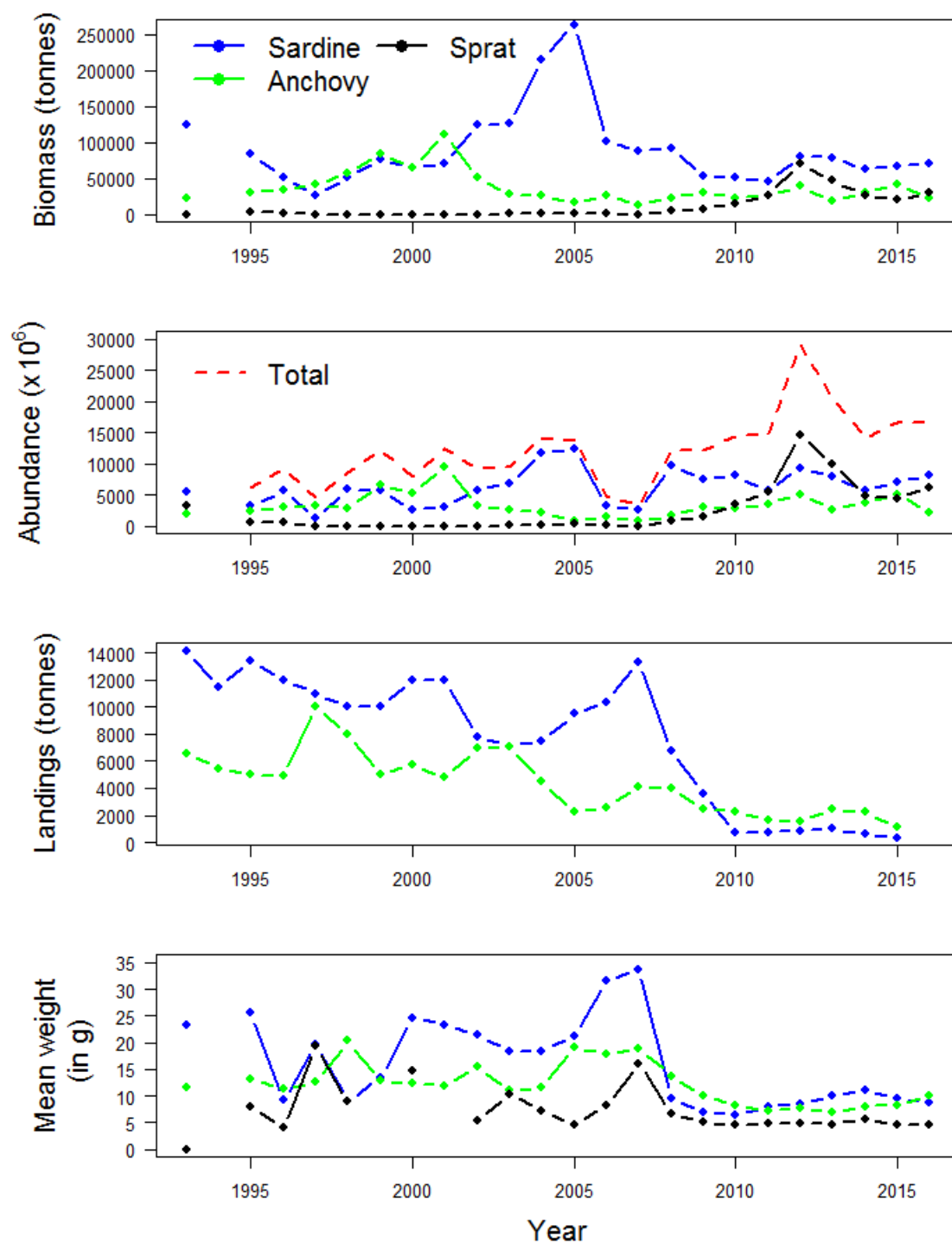
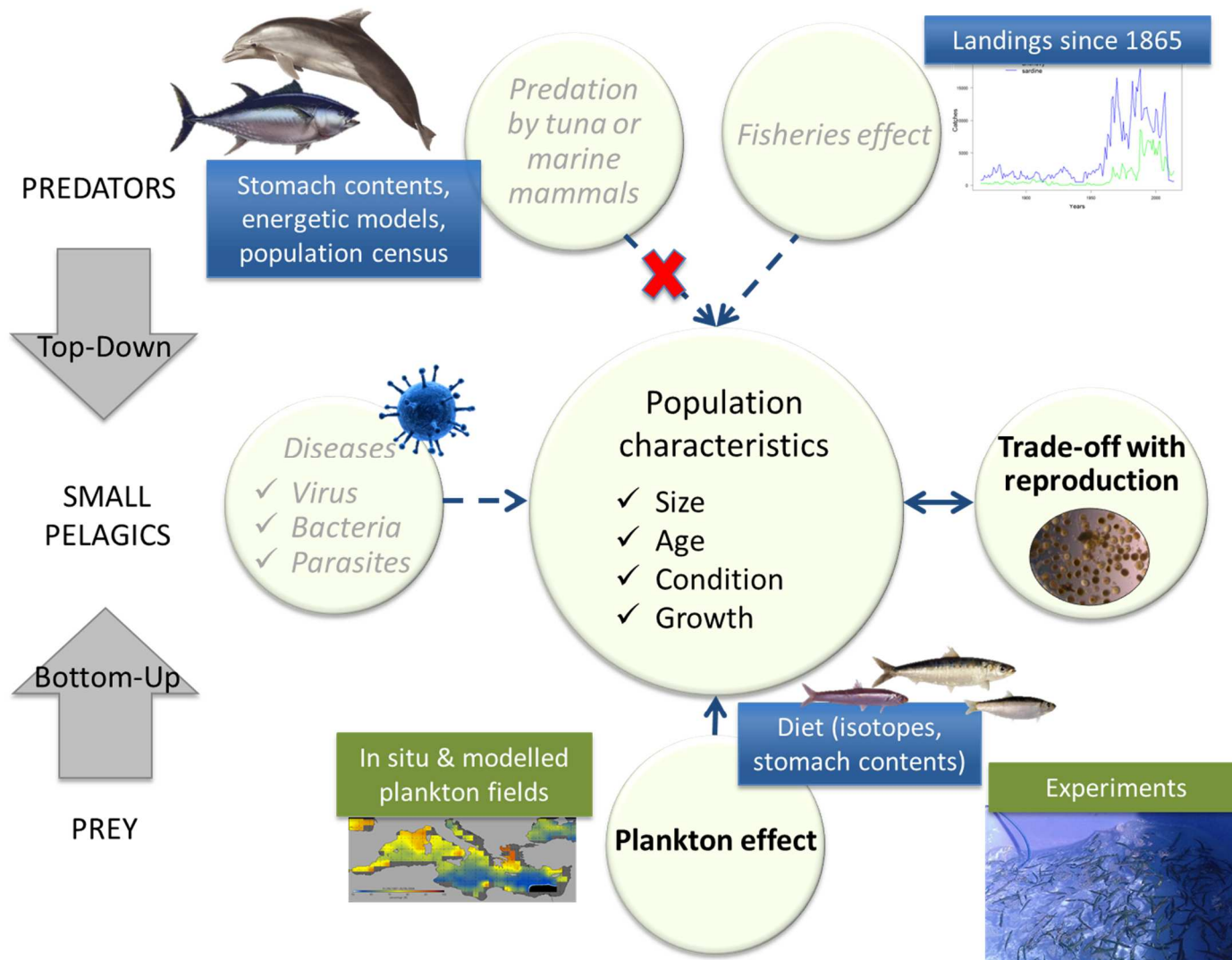


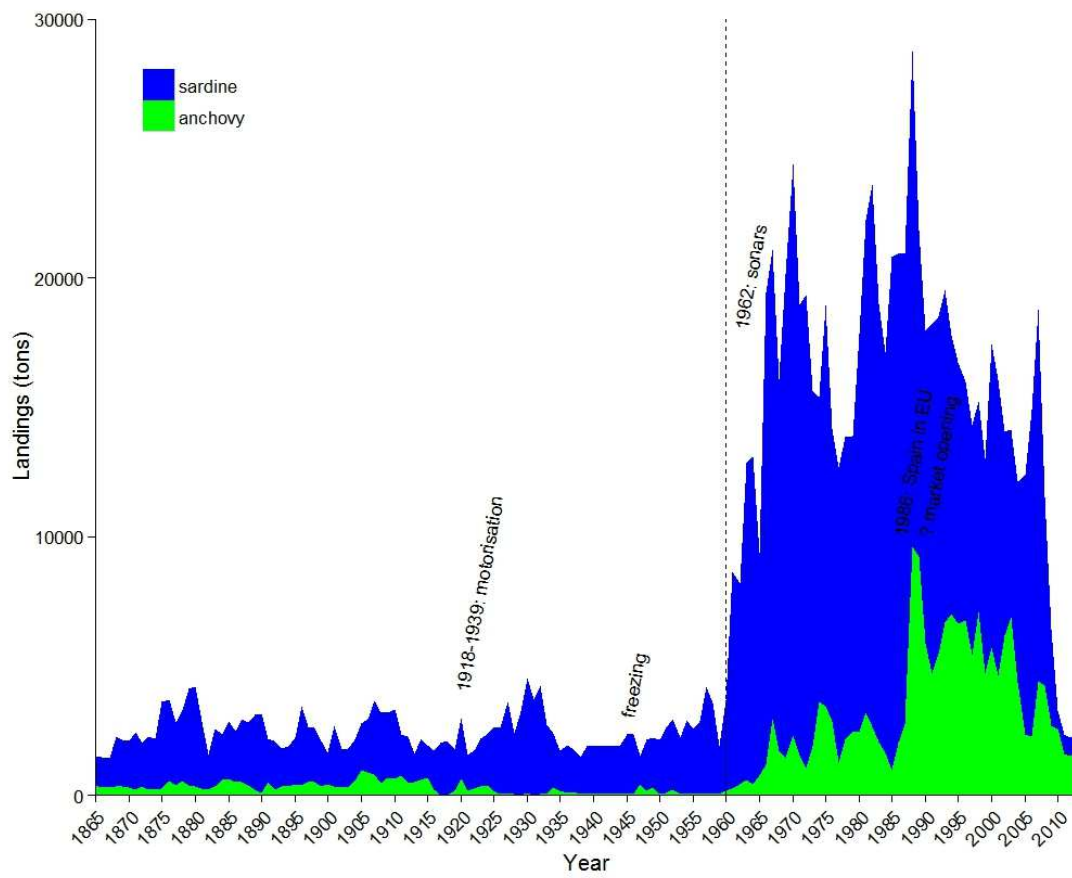
Fig. 1



694

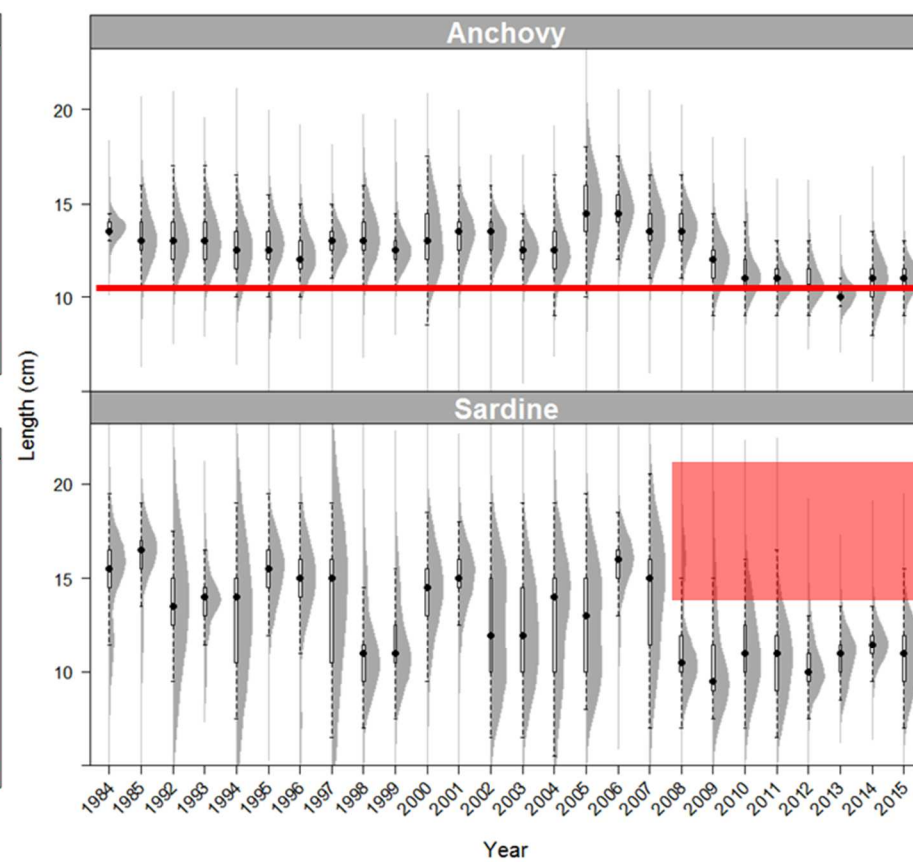
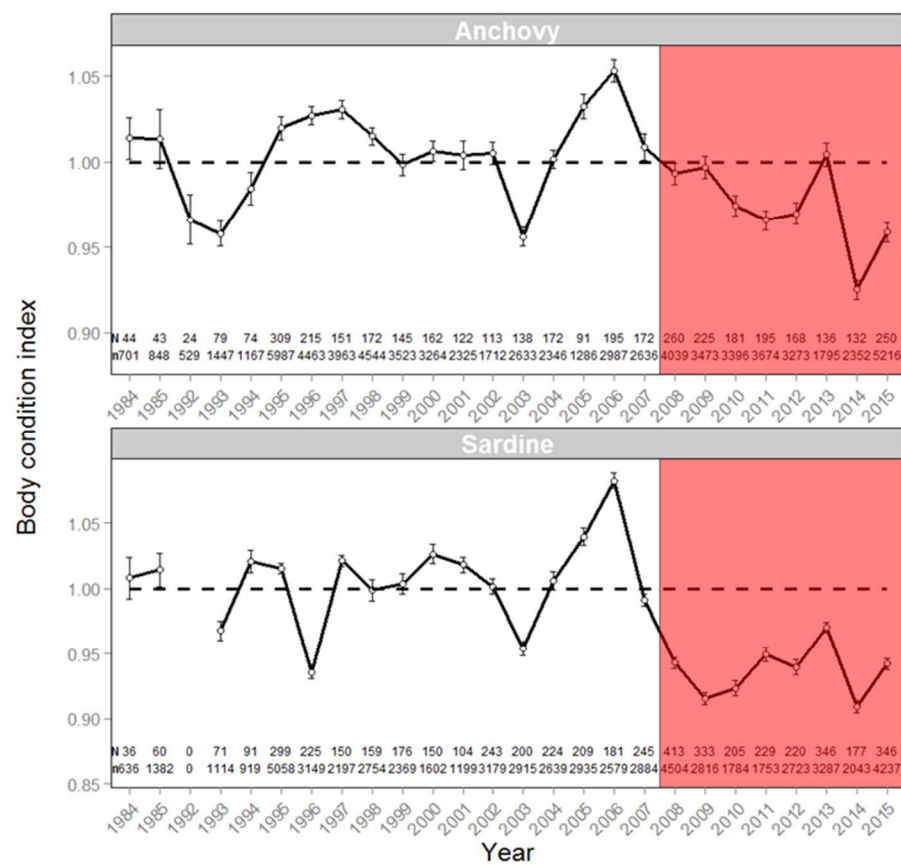
695 Fig 2

696
697



698
699

Fig 3



700

701 Fig. 4

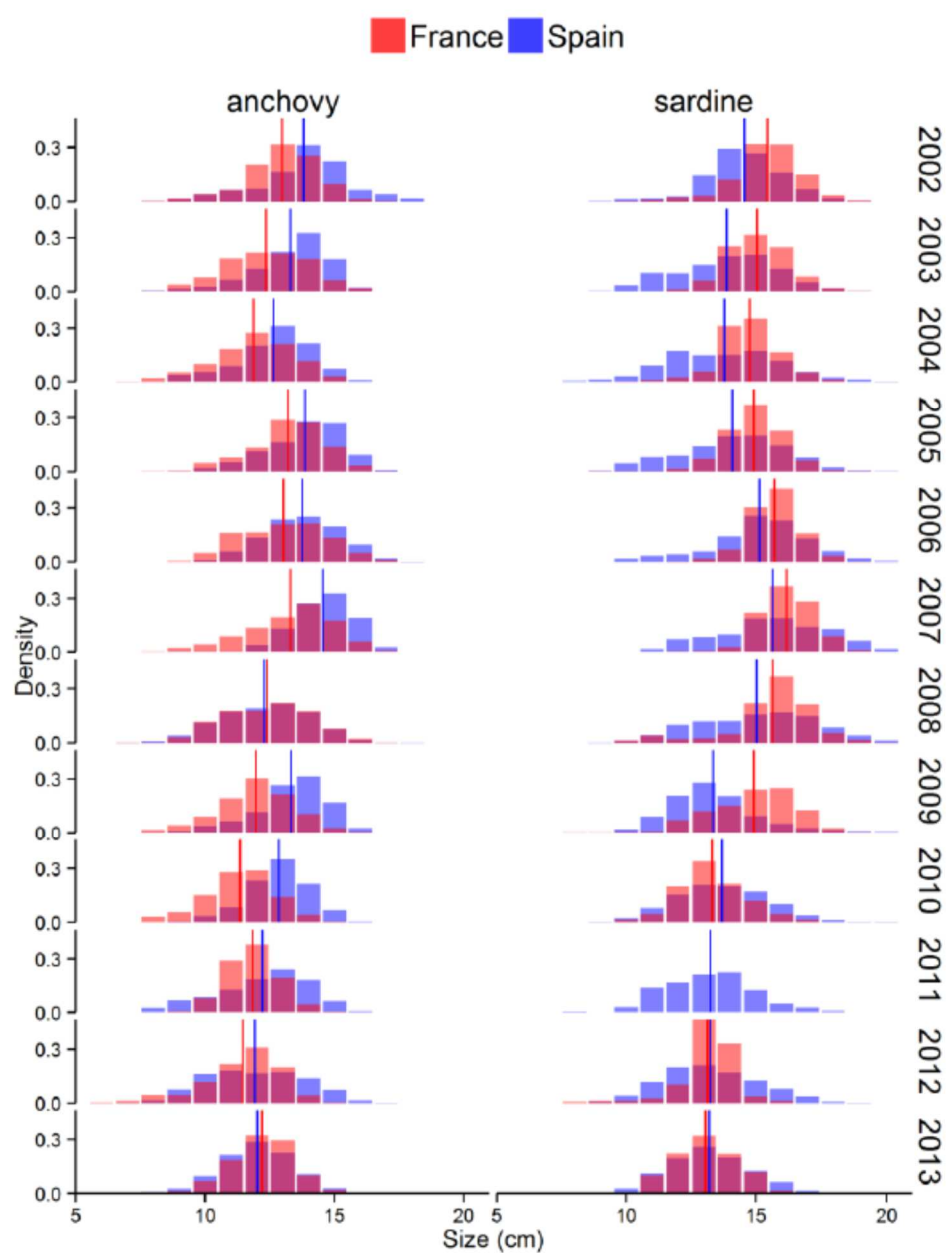
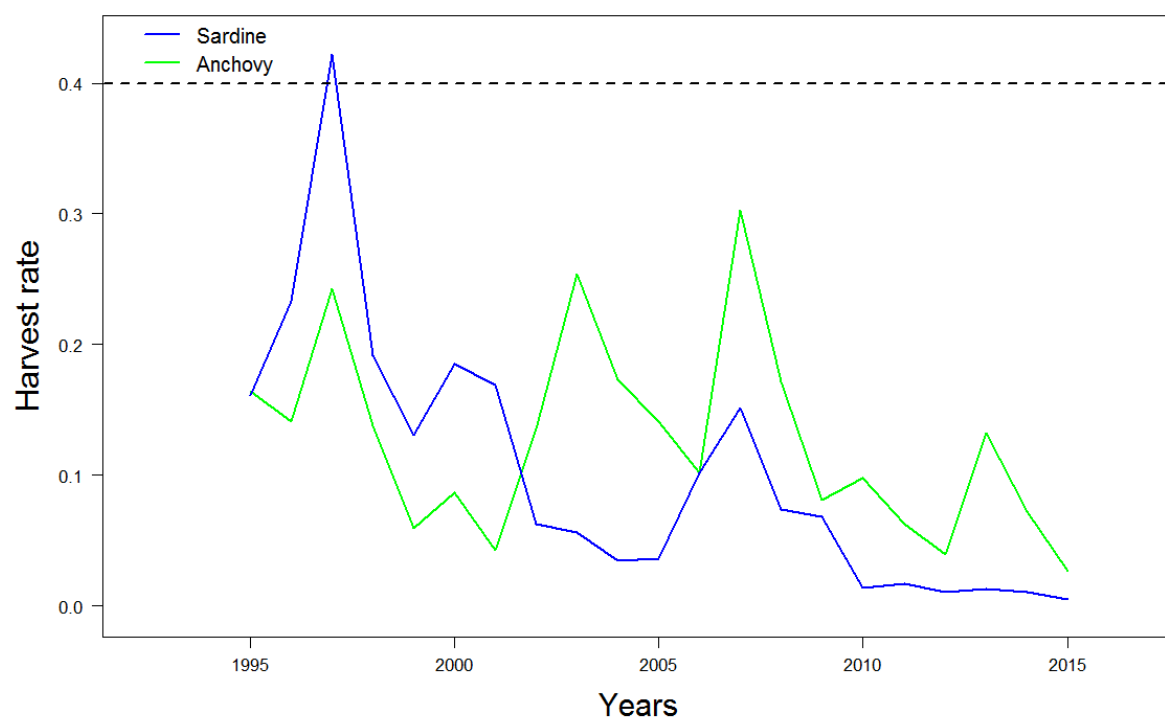


Figure 5.

708

709



710

711 Fig 6

712

713

714

715