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Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions

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Abstract :

Endogenous and environmental variables are fundamental in explaining variations in fish condition. Based on more than 20 yr of fish weight and length data, relative condition indices were computed for anchovy and sardine caught in the Gulf of Lions. Classification and regression trees (CART) were used to identify endogenous factors affecting fish condition, and to group years of similar condition. Both species showed a similar annual cycle with condition being minimal in February and maximal in July. CART identified 3 groups of years where the fish populations generally showed poor, average and good condition and within which condition differed between age classes but not according to sex. In particular, during the period of poor condition (mostly recent years), sardines older than 1 yr appeared to be more strongly affected than younger individuals. Time-series were analyzed using generalized linear models (GLMs) to examine the effects of oceanographic abiotic (temperature, Western Mediterranean Oscillation [WeMO] and Rhone outflow) and biotic (chlorophyll a and 6 plankton classes) factors on fish condition. The selected models explained 48 and 35% of the variance of anchovy and sardine condition, respectively. Sardine condition was negatively related to temperature but positively related to the WeMO and mesozooplankton and diatom concentrations. A positive effect of mesozooplankton and Rhone runoff on anchovy condition was detected. The importance of increasing temperatures and reduced water mixing in the NW Mediterranean Sea, affecting planktonic productivity and thus fish condition by bottom-up control processes, was highlighted by these results. Changes in plankton quality, quantity and phenology could lead to insufficient or inadequate food supply for both species.

Keywords : Anchovy, Sardine, Relative condition factor, NW Mediterranean Sea, Endogenous effect, Environmental effect

1. Introduction

Body condition is widely used in ecological studies to determine the nutritional or physiological status of an individual (Bolger & Connolly 1989, Stevenson & Woods 2006) and is defined as the quantity of nutrient reserves, i.e. the quantity of accumulated energy reserves exceeding that required for daily nutritional demands (Schulte-Hostedde et al. 2001, Schamber et al. 2009). Body condition indices are thus used in order to evaluate the quantity of stored energy, giving an indication of an individual's well-being which can affect its future performances (Stevenson & Woods 2006, Wilson & Nussey 2010). For example, individuals with larger nutritional reserves may have a better chance to survive and a higher reproductive success or growth (Millar & Hickling 1990), which may in turn affect the dynamics of the whole population (Jakob et al. 1996, Adams 1999). Many studies have used fish condition indices to monitor and investigate both pelagic and demersal fish population health and variability (Lambert & Dutil 1997, Lloret et al. 2002, Shulman et al. 2005, Ndjaula et al. 2013). For example, anomalous conditions have been shown to strongly affect spawning and both egg quality and quantity of many fish species (Adams 1999, Óskarsson et al. 2002). Earlier sexual maturation, associated with smaller size as well as higher natural mortality, has also been shown to occur in low condition fish for *Clupea harengus* (Winters & Wheeler 1994, Heino & Godø 2002, Malzahn et al. 2007) while the chances of becoming mature increase with good condition in *Hippoglossoides platessoides* (Morgan 2004).

Fish condition may be linked to several factors, whether endogenous or exogenous (Shulman & Love 1999, Lloret et al. 2013). Reproductive state, sex or age are the main endogenous parameters known to affect condition. Drastic changes in population age/size structure have for instance resulted from differences between individuals of a single species. For example, a higher condition for females and older individuals led to an unbalanced sex-ratio or age distribution and increased population vulnerability to environmental stress (*Pagellus erythrinus*, Lloret et al. 2002, Ballón et al. 2008). Exogenous factors potentially impacting body condition are numerous as well, ranging from parasitism (Lambert & Dutil 1997, Barton et al. 2002) to environmental conditions or food availability (Murphy et al. 1990, Porath & Peters 1997), highlighting the use of fish body condition as a measure of habitat quality and exogenous disturbance.

Anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) populations in the Gulf of Lions supported important fisheries before exhibiting a major decline in the 2000s while the unexploited sprat (*Sprattus sprattus*) increased exponentially (GFCM 2012). The biomass of these small pelagic and their role in the energy transfer from low (plankton communities) to high (e.g. marine mammals, tunas, seabirds) trophic levels underline the importance of these species (Cury et al. 2000, Bănaru et al. 2013). In the Gulf of Lions, where anchovy and sardine biomass decreased, the number of sardines slightly increased and the number of anchovies remained steady due to the high abundance of small and young individuals (Van Beveren et al. 2014). This underlines changes in the size and age-class distribution of both species. In parallel, fish condition started to decrease before the mean length and the mean age in both species, suggesting that condition and nutritional status might be an important factor explaining the currently observed population dynamics. Moreover, overexploitation was not retained as the prime force for this pelagic ecosystem shift, as bottom-up processes are the current major hypothesis for the change in small pelagic fish condition (Van Beveren et al. 2014). Further investigations on the determinants of body condition are thus warranted to better understand the current situation of these stocks.

The aim of the present study was to analyze more precisely the variations in anchovy and sardine condition in the Gulf of Lions using a unique long-term dataset of morphometric (length and weight) and biological (age and sex) variables on more than 43,000 individuals from 1971 to 1978 and from 1993 to 2013. The first objective was to confirm the existence of different groups of years based on fish condition for both species using the largest dataset available in the Gulf of Lions. Secondly, according to the previously defined groups of years of fish condition, we investigated the potential effect of sex and age on condition of each species. Finally, we related the fluctuations in fish condition to environmental variables in order to determine potential exogenous drivers of the dynamics of small pelagic fish in the Gulf of Lions.

2. Material and Methods

2.1. Study area and data collection

This study took place in the Gulf of Lions located in the North Western part of the Mediterranean Sea (42°26'N, 3°00'E; 43°40'N, 5°28'E) and covering about 10,000 km². This area is composed by a wide continental margin (>60 km), bordered by numerous canyons (Millot 1990). The Gulf of Lions is one of the most productive Mediterranean areas, dependent of Rhodanian inputs and strong mixing events induced by NW and N winds and local upwellings (Palomera et al. 2007). A nutrients gradient exists from East to West due to the Rhodanian input located at the East of the area (Darnaude et al. 2004).

Samples were collected from both scientific and commercial pelagic trawls. PELMED scientific surveys have been conducted each month of July on board the research vessel l'*Europe* to assess small pelagic fish biomass through acoustic methods from 1993 to 2013. Nine parallell fixed transects perpendicular to the coastline were carried out each year. Acoustic data allowed to detect fish occurrence and pelagic trawls were deployed to determine fish school composition when records of the presence of fish were long enough (> 2 nm). A random sample of fish in each trawl was collected and morphometric parameters, i.e. size (to the nearest millimetre) and body mass (to the nearest 0.1 gram), as well as age (otoliths reading), sex (by visual assessment) and maturity stage (by visual assessment according to (ICES 2008) were determined for each fish. Maturity stages were described from 1 to 6, with an increasing development of gonads from stages 2 to 4, spawning period during stage 5 and resting period during stages 6 and 1. To investigate the seasonality of fish condition, samples were collected on other periods of the year from commercial fisheries, and brought back to the lab for analyses. These samples were collected randomly in the Gulf of Lions from 1999 to 2013 (more regularly since 2005) during the different months of the year except months covered by the scientific survey (July). Samples consisted of one crate of fish randomly taken out of a pelagic trawl, before any sorting. Once in the lab, the same parameters as previously described for the scientific survey were collected. Data for sardine between 1971 and 1978 were also collected monthly by the commercial fleet and analyzed in the lab with the same accuracy. Thus, both periods (i.e 1971-1978 and 1993-2013) were judged comparable. In all fish sampling date, the length range was kept as large as possible to allow subsequent comparisons between periods and avoid bias in length-weight relationships computing.

2.2. Morphometric index of condition

As recommended by Froese in 2006 to compare condition within a given sample and as the two studied species exhibited an allometric growth pattern (Van Beveren et al. 2014), we used for this study the relative condition index K_n, (Le Cren 1951, Bolger & Connolly 1989, Blackwell et al. 2000):

$$K_n = W/W_r$$

where W_r is the predicted weight of an individual of a given length TL (W_r=αTL$^{\beta}$). Length-weight relationships were calculated separately for each month from each year (when the number of individuals was superior to 10) and the parameters α_m and β_m were then computed as geometric mean of all the α and β obtained. As no difference in weight-length relationship was found between sex and between juveniles versus adults (tested as interaction with fish length in separate linear models, e.g *lnW~lnLT*Sex* for sex effect), no distinction was made between males, females, juveniles and adults and a single length-weight relationship computed. Based on a 30-year dataset including more than 43,000 individuals (Table 1.), the following values were obtained: α_m=3.7.10^{-3}±2.1.10^{-4} and β_m=3.3±2.3.10^{-2}, α_m=9.1.10^{-3}±9.2.10^{-4} and β_m=3.1±4.2.10^{-2} for anchovy and sardine, respectively. Fitted β values were in the usual range of 2.5 to 4 (Mendes et al. 2004, Froese 2006, Sinovčić et al. 2008). By definition, the higher the index, the better the condition. As recommended by several authors (Schulte-Hostedde et al. 2005, Stevenson & Woods 2006, McPherson et al. 2011), this morphometric index was comparable with direct assessment of total lipid content but outside the reproductive periods (Brosset et al. 2015). During the reproductive period, (Brosset et al. 2015) found that this index could reflect a more integrative measure of condition (such as lipids and proteins).

2.3. Environmental parameters in the Gulf of Lions

Small pelagic populations are subject to considerable fluctuations caused by environmental variability (Bakun 1996), mainly due to their relatively short life span (3-5 years). Satellite-derived sea surface temperature (°C SST) and surface chlorophyll *a* (Chl-*a* mg.m^{-3}) were extracted from MODIS-aqua data (http://oceancolor.gsfc.nasa.gov). The Rhône outflow was computed with the daily inputs of the Grand Rhône, measured at the Beaucaire station, and provided by the Compagnie Nationale du Rhône (CNR). The Western Mediterranean Oscillation index (WeMO; Martin-Vide & Lopez-Bustins 2006) was computed as the daily differences in standardized surface atmospheric pressure values between San Fernando (Spain) and Padua (Italy) (López-Bustins, pers. comm). This index integrates fluctuations of temperature, rainfall and wind mixing. Positive values reflect low temperature and high river runoff and wind mixing while negative values reflect the opposite. As environmental variability also affects primary and secondary production, the planktonic community was included in our analyses. Daily plankton concentrations estimates were extracted from the coupled physical-biogeochemical model SYMPHONIE-Eco3m-S. The physical model SYMPHONIE (Marsaleix et al. 2009, 2011, 2012) is based on a 3-D primitive equation, free surface model, with hydrostatic and Boussinesq approximations. The biogeochemical model Eco3m-S (Baklouti, Diaz, et al. 2006, Baklouti, Faure, et al. 2006, Auger et al. 2011) is a multi-nutrient and multi-plankton functional type model that simulates the dynamics of several biogeochemical elements (carbon, nitrogen, phosphorus, silica and chlorophyll) and plankton groups (picophytoplankton (0.7-2µm); nanophytoplankton (2-20µm, high taxonomic heterogeneity); microphytoplankton (20-200µm, dominated by diatoms); nanozooplankton (5-20µm, small ciliates and flagellates bacteriophage); microzooplankton (20-200µm, ciliates and large flagellates) and mesozooplankton (>200µm, mainly copepods species)). The coupled model was previously used to study the dynamics of plankton communities impacted by freshwater discharge and their role in carbon export on the Gulf of Lions (Auger et al. 2011), as well as the interannual biogeochemical variability linked to atmospheric and hydrodynamic forcing in the Gulf of Lions from climatological (Herrmann et al. 2013) and statistical (Auger et al. 2014) points of view. In this study, we used a horizontal curvilinear mesh, giving a resolution smaller than 1 km on the Catalan and western Gulf of Lions shelf and ~2 km near the eastern coast of the Gulf of Lions. Initialization and boundary conditions were provided by the NEMOMED8 model (Herrmann et al. 2010). The coupled model was forced by the atmospheric ARPERA model outputs (Herrmann & Somot 2008). MODIS chlorophyll-a monitoring started in 2002, and the biogeochemical simulation that provided 6-classes plankton concentrations was produced over the period 2001-2011. Therefore, we extracted morphometric data for the Gulf of Lions from January 2002 to December 2011 with the advantage that this decade covered all the different types of years (i.e good, average or low) of both anchovy and sardine conditions in the Gulf of Lions. All these variables were averaged per month over the entire Gulf of Lions from January 2002 to December 2011.

2.4. Data analyses

Two components of the large time-series dataset were studied in this paper. On the one hand, we described the seasonal cycle of anchovy and sardine condition. On the other hand, linking fish condition and environmental drivers allowed understanding fish condition fluctuations in the Gulf of Lions. Therefore, the time series was decomposed into:

$$\text{Series} = \text{Trend} + \text{Seasonality} + \text{Residuals}$$

First, we studied the seasonal signal. A seasonal cycle of fish condition was computed for anchovy over the whole studied period (1993-2013). Because of a big temporal gap of 14 years in the dataset (from 1979 to 1992), sardine data were divided into two periods (1971-1978 and 1993-2013). Seasonal cycles were then estimated by period and compared using a Generalized Linear Model (GLM) including a period effect and the interaction between month and period.

The dataset showed irregularities in the sampling scheme (e.g. different monthly sample sizes, missing data for some months, Table 1). To avoid any influence of the sampling month on the endogenous and exogenous factors possibly affecting fish condition, we deseasonalized and scaled the fish condition data. Deseasonalized values were obtained by removing median values estimated with the seasonal cycle of condition for each species. All values were then scaled by dividing each value by the standard deviation (SD) of the corresponding month. To investigate the potential effect of endogenous factors (sex and age), we then used the Classification And Regression Tree (CART) approach of (Breiman et al. 1984)). Decision trees were built by recursively partitioning our dataset into increasingly homogeneous subgroups based on fish condition values. Each split is defined by a simple rule based on a single explanatory variable, and each final group is characterized by mean values of fish condition. Two separate CARTs were applied for the two fish species. Year was also added as an explanatory categorical variable in order to define precisely groups of years according to fish condition.

In addition, we evaluated the link between environmental variables and fish condition over a decade using data available from January 2002 to December 2011. As we were interested in the origin of the trend in fish condition, we deseasonalized environmental data to reduce risks of spurious correlation which could be due to a seasonal cycle. Following the same procedure applied for fish condition, environmental variables were (i) deseasonalized by removing median values of the raw data and (ii) scaled by dividing by the SD. The standardized environmental time series were implemented as explanatory variables in a GLM approach.

Because the present paper concentrated on the factors influencing fish condition, we did not consider interactions between the explanatory variables. Model residuals were visually assessed for normality and an untransformed response with a normal error structure was found to be appropriate. As the sample size (n) was small compared to the number of predictor variables (K) ($n/K < 40$), the Akaike's Information Criterion (AIC) was corrected for small sample sizes and the best model was selected according to the AICc (Hurvich & Tsai 1989). GLMs were used to detect potential effects of environmental parameters on fish condition as follows:

$$\text{Condition} = \mu + \alpha\text{SST} + \beta\text{Chl } a + \gamma\text{Rhone runoff} + \delta\text{WeMO} + \theta\text{Zoomeso} + \lambda\text{Zoomicro} + \nu\text{Zoonano} + \xi\text{Syn} + o\text{Diatom} + \pi\text{Nano} + \varepsilon \qquad (1)$$

where μ is the intercept and ε the error relative to a normal distribution.

Variance inflation factors (VIF) were calculated between all the environmental parameters to detect high-dimensional collinearity. When collinearity was identified between covariates, the covariates with the highest VIF were sequentially removed from the model until the highest VIF value was less than 5 (Zuur et al. 2007). The same model was run for both anchovy and sardine.

All statistical analyses were performed with R version 3.0.2 (R Development Core Team, 2013). Values are indicated as mean ± standard error (SE) and all statistical tests were performed at a significance level of 0.05. As autocorrelation has been recognized as inflating the probability of a type I error in hypotheses tests, causing biases in variable selection, and violating the assumption of independence of error terms in regression models, we also checked for temporal autocorrelation in both anchovy and sardine condition time series; but this was not significant.

3. Results

3.1. Annual cycle of fish condition

The period and the interaction between period and month were significant for sardine (GLM, d.f =1, P <0.001 and GLM, d.f.=11, P <0.001, respectively), indicating changes in the phenology of the condition and the need to run separate analyses for each period.The condition values of each month (excluding April) were significantly higher for the 1971-1978 years (Fig 1). Anchovy showed a minimal condition in winter, i.e. during January (0.89±0.002) and February (0.89±0.003), and a peak in the beginning of the summer, i.e. in June (1.05±0.002) and July (1.05±0.001). Sardine exhibited a similar pattern to that of anchovy for the minimum (0.85±0.006) and the maximum (1.08±0.002) of condition during the 1993-2013 years, while the maximum value of condition occurred later (e.g. 1.15±0.005 in September and 1.16±0.005 in October) during the earlier years (1971-1978).

3.2. Fish condition partition and endogenous factor

Regression trees (CART analyses) were used to partition fish condition data in relation to year, age and sex. They revealed year and age as explanatory variables for both species while sex did not show any significant effect (Fig 2 & 3). Year had the greatest effect on anchovy condition with the highest values for years from 1995 to 2007 (except 2003) (Fig 2). In this group, a secondary partition separated the highest values (for years 2005 and 2006) from the others. Three groups of years were thus identified for anchovy (Fig 2). Within these groups of years, condition was then partitioned according to age. While no effect of age was demonstrated in the low condition years, anchovy condition tended to slightly decrease with age during the years of average and high condition (Fig 2 & 4).

Year was also the most important variable explaining sardine condition. Indeed, three groups of years were identified: years of low condition composed by 1993, 1996, 2003 and 2008-2013, years of high condition (2005-2006, as for anchovy) and years of intermediate condition values (1994, 1995, 1997-2002, 2004 and 2007) (Fig 3). Age then determined the following nodes. In the years of good condition, sardine condition increased from age 0 to 1 and was higher and steady in individuals older than 2 (Fig 3 & 4). Even if age did not affect condition in the intermediate years (except for individuals older than 5 which had a low condition, although this was based on 11 individuals only), a similar pattern of sardine condition with age was found during years of average condition (Fig 3 & 4). On the contrary, in the years of low condition, which comprised the last 6 years, condition seemed to decrease sharply with increasing age after 1 year old. Sardine of age 3, 4 or 5 exhibited the worse condition observed in the dataset (Fig 4).

3.3. Fish condition and environmental parameters

Variance inflation factors were calculated to determine the variables with high collinearity. As the picophytoplankton showed a value of 8.42, this variable was removed from the model for each species. Other variables showed a maximum VIF of 4.58 and did not introduce a major bias in our analyses. The AICc selected models including mesozooplankton and Rhône runoff for anchovy, and mesozooplankton, temperature, WeMO and diatoms concentration for sardine.

Anchovy condition was significantly and positively influenced by the concentration of mesozooplankton, and the Rhône Runoff (Table 2). For sardine, the GLM revealed a significant positive relationship of condition with the mesozooplankton concentration, the WeMO and the diatom concentration while there was a negative effect of temperature (Table 2). Final models selected with AICc explained 48% and 35% of the variance for anchovy and sardine (r^2_{adj}), respectively.

4. Discussion

4.1. Annual cycle of anchovy and sardine condition

Monthly variations of fish condition showed similar patterns for anchovy and sardine. Condition was maximal in summer and minimal in winter, as has been described in other Mediterranean areas (Basilone et al. 2006, Zlatanos & Laskaridis 2007, Simat & Bogdanović 2012) and in the Gulf of Lions by lipid analysis (Pethybridge et al. 2014). However, while sardine exhibited a strong difference in condition between winter and summer, seasonal variations in condition were lower for anchovy. Such differences between species might be explained by different spawning strategies and the seasonality of prey abundance. Summer vs. winter represent periods of high vs. low energy intake for both species due to increased food (Lefevre et al. 1997) determined by prey availability and quality in spring/summer. However, expenses differ greatly between the 2 species. Indeed, anchovies are income breeders (i.e they acquire energy concurrently to spawning period) while sardines are capital breeders (i.e they store energy before spawning period, see Ganias et al. 2007, Pethybridge et al. 2014, McBride et al. 2015). At the beginning of spring, fish condition of both species increase because of higher prey availability, but a part of that energy storage is then directly allocated to the gonads during summer for anchovies. On the contrary, energy storage of sardine, and thus its condition, continues to increase during summer because no spawning event happens during that season. Similarly, the progressive decline in food quantity at the end of summer (Lefevre et al. 1997) induced a reduction in condition for both species. The seasonal difference in body condition is thus stronger for sardines, which alternate a season of high intake and low expenses (summer) with a season of low intake and high expenses (winter), than anchovies, which alternate high intake and expenses with low intake and expenses. As a result, the decrease in condition is more drastic in sardines and one can wonder if a delayed increase in food abundance might affect sardines to the point of impairing their survival. We hypothesized that after February, in both the 70's and recent decades, sardines were able to recover their fat reserves as they stopped the lipid allocation to gonads (Lefevre et al. 1997). However, we highlighted differences for sardine between periods (we also investigated another methodology using two different LW relationships, one per period, and direct comparison between their parameters gave similar conclusions than the comparison of body condition based on a single LW relationship for both periods). First, the condition of this species was always higher in the 70's (excluding April). Secondly, while their maximal condition was in autumn during the first period, it occurred at the beginning of summer during the recent years. As the breeding season is likely to be the same over time (Lee 1961, Palomera et al. 2007), this suggests a potential change in feeding condition. In particular, a change in the phenology of the primary and secondary production, usually marked by a second bloom of phytoplankton in September in the Gulf of Lions (Lefevre et al. 1997), might explain the change in small pelagic fish condition.

4.2. Fish condition and endogenous characteristics

For the two species, different clusters of condition values were clearly separated in accordance with the general pattern of condition variability previously found (Van Beveren et al. 2014), highlighting the low anchovy and sardine condition since 2008.

Another study in the same area pointed out differences in condition between sexes for some demersal species like *Mullus barbatus* or *Pagellus erythrinus* (Lloret et al. 2002). However, no variation between sexes was found in our study or according to previous study on lipid content (Pethybridge et al. 2014). Thus, for anchovy and sardine of the Gulf of Lions, a high or low fish condition cannot be due to one of the two sexes.

Significant variations between age classes depended upon years. Sardine condition always increased similarly from age-0 to age-1 and either increased afterwards (years of high condition), remained steady (years of average condition) or decreased dramatically (years of low condition). These results might provide some explanation about the current changes in size and age structure of sardine, with recent dominance of small and young individuals in the Gulf of Lions (Van Beveren et al. 2014). Sardine condition decreases after July, possibly because of a lack of food followed by the start of the breeding season later on, which mobilizes a high quantity of lipid reserves. The lack of sufficient fat reserves for old sardines could lead to a higher mortality at the end of the winter. Although anchovy also exhibited a pattern of condition changing with age and according to groups of years, the trend was not as pronounced. This could be both because of a smaller number of age classes and a lower parameter variability than sardine due to measurements to the nearest millimeter (Brosset et al. 2015). A shift in quantity and/or availability of zooplanktonic prey species between years could have affected the condition of older and larger adults.

4.3. Fish condition and environmental parameters

The relation between fish condition and environmental data was investigated from 2002 to 2011, a period where environmental data were available and encompassed years of both high and low condition for anchovy and sardine. High sardine condition was linked with high WeMO values, corresponding with low temperature and strong Rhône runoff and wind mixing, i.e. a regime of enhanced primary and secondary productivity. As the statistical model also confirmed this negative effect of temperature on sardine condition, the positive effect of WeMO is likely to be mostly related to planktonic productivity. Variations in sea temperature may affect the fish directly (by physiological stress) or indirectly (through changes on the ecosystem production and prey availability) (Brett 1979, Lloret et al. 2013). Indeed, temperature is a proxy of planktonic productivity. Warmer temperatures can reduce upwelling and water mixing and may therefore reduce and move earlier the late summer energy peak (Vidussi et al. 2011, Calvo et al. 2011), preventing sardine and anchovy to find sufficient food resources before entering the prolonged winter season. Moreover, the development of cold water copepods during the winter could also be affected by warmer water (Halsband-Lenk et al. 2002, Hinder et al. 2014) leading to low copepod abundance as demonstrated in the Balearic Sea (Puelles et al. 2004). A similar case has already been observed along the Portuguese coast for sardine (Rosa et al. 2010), where temperature explained a sharp decline in their condition as it changed prey availability and phenology during the year. Similarly, anchovy condition was positively affected by the Rhône river outflow. The Rhône is the main source of runoff in the Gulf of Lions (and the Western Mediterranean) and enhances planktonic production by strongly increasing nutrients inputs (Lefevre et al. 1997). Its positive effect can thus be explained by favoring feeding conditions for both species, increasing energy reserves and improving fish condition.

Our results on the significant effect of mesozooplankton support the close relationship between food supply and fish condition. As expected, the mesozooplankton estimated from a coupled model outputs showed a significant positive relationship with fish condition. This could be explained by the fact that small pelagic fish derive the bulk of their dietary carbon mainly from copepods and euphausiids (Plounevez & Champalbert 2000, Garrido et al. 2008, Nikolioudakis et al. 2014, Costalago & Palomera 2014). Sardine condition was also affected by a variation in diatom concentration. The consumption of phytoplankton and especially diatoms was already underlined in the Gulf of Lions (Plounevez & Champalbert 2000). Furthermore, fish condition is a function of food quality and/or food quantity. Food quantity is important, as demonstrated by the decreased food supply during different invasions of jellyfish, which were associated with a sharp decline in condition of different species of small pelagic fish (Shulman et al. 2005, Daskalov & Mamedov 2007, Sabatés et al. 2010). In our study, local (temperature, river runoff, wind mixing and surface chlorophyll a) and regional (Western Mediterranean Oscillation) environmental conditions could have such an impact on the trophic web and thus on fish condition. Additionally, prey quality in term of species composition can also have an important effect on fish condition. For example, differences in lipid content of fish according to copepod diversity were found in other sardine populations (Garrido et al. 2008) and also in populations of capelin (Orlova et al. 2010) in the Atlantic Ocean. In the case of the Gulf of Lions, there is currently insufficient knowledge on potential variations in the planktonic communities to be able to establish a clear link with the observed changes in fish condition. However, several authors pointed out changes in the composition and phenology of zooplankton associated with environmental fluctuations in Mediterranean areas surrounding the Gulf of Lions, especially the Ligurian and the Balearic Sea (see Molinero et al. 2005, 2008, Puelles & Molinero 2008, Calvo et al. 2011, Auger et al. 2014). The overall trend in the North Western Mediterranean Sea is characterized by an increasing temperature, decreasing wind stress and water mixing (Calvo et al. 2011). Such changes induce a longer stratification period, which leads to a reduced nutrient supply to the upper layers and results in changes in the phytoplanktonic and zooplanktonic compositions as demonstrated by (Auger et al. 2014) in the Gulf of Lions. In such cases, small-sized phytoplankton should dominate, decreasing diatom concentration, affecting grazing efficiency of copepods and ultimately copepod size and egg production (Halsband-Lenk et al. 2002, Ianora et al. 2003). As anchovy mainly feeds on large copepods and sardine on large copepods and diatoms, fish condition should benefit more from diatom-based food chains (Lloret et al. 2013) than from the more heterotrophic food chains occurring in summer and early fall (small-sized phytoplankton composed out of e.g. flagellates and ciliates). In this way, the prevalence of small copepods may be insufficient to satisfy the entire energetic demand of the fish. The differences in the annual cycle of the condition of sardine between 1971-1978 and 1993-2013 also support possible changes in environmental conditions. A change in the phenology of the primary and secondary production, usually marked by a second bloom of phytoplankton in September in the Gulf of Lions (Lefevre et al. 1997), might explain the observed changes in sardine condition. (Bosc et al. 2004) evidenced changes in the timing and magnitude of the blooms in the north-western Mediterranean using satellite images. In particular they showed a quasi-absence of an autumnal bloom over the Seawifs images period (1998-2001) while it was clearly marked over the CZCS images period (1978-1986). They ascribed these differences to environmental changes. Warmer water during the period 1993-2013 could reduce or delay the second bloom of phyto and zooplankton, and prevent sardine to remain in good condition until September or October. This strong dependency of condition upon mesozooplankton may be the explanation of the observed shift in the phenology of the sardine condition between the two periods (1971-1978 vs 1993-2011). However, the lack of historical data on chlorophyll *a* and plankton composition for the period 1971-1978 prevented us from comparing with current seasonal signals of plankton production. Further studies are needed in the Gulf of Lions to investigate the evolution of the planktonic community and to evaluate the link between the different mesozooplankton components and fish condition.

5. Conclusion

This long term study allowed us to assess the main drivers of the condition of the two main small pelagic fish in the Gulf of Lions. Our results are in agreement with previous studies which highlighted the importance of bottom-up processes for anchovy and sardine condition (Shulman et al. 2005, Rosa et al. 2010, Nikolioudakis et al. 2012). Sardine clearly exhibited differences in condition between groups of years, with decreasing and very low values for individuals of two years old or more during the low condition years of 1993, 1996, 2003 and from 2008 to 2013. Differences were less evident for anchovy which showed only small dissimilarities between age classes for the different groups of years. Thus, the low condition of older individuals, mainly for sardine remains one of the main hypotheses for the current disappearance of old individuals in the Gulf of Lions. Environmental factors, such as temperature and Rhône runoff, were essential to explain small pelagic fish condition, probably through their indirect impact on primary production and thus on food availability. Furthermore, mesozooplankton was the major parameter driving significant fluctuations in condition for both species. Also, there was a positive effect of diatom concentration on sardine. Therefore, mesozooplankton appears to be an essential aspect for understanding small pelagic fish condition and further studies are needed to investigate the impact of this plankton compartment on small pelagic fish condition more precisely. The recent increase in sprat abundance and biomass (Van Beveren et al. 2014) may lead to an increase in trophic competition, which would also need to be investigated to completely understand the current and prolonged poor condition of anchovy and sardine.

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Tables

Table 1. Summary of dataset characteristics used in the study. For both species, number of individuals and size range under parenthesis were showed for each month of the different groups of years identified.

Species	Period	Group of years	January	February	March	April	May	June	July	August	September	October	November	December
Sardine	1971-1978		434, (118-201)	468, (134-208)	230, (137-203)	347, (142-210)	381, (129-213)	272, (135-212)	321, (118-215)	206, (150-207)	546, (133-216)	524, (126-210)	369, (131-210)	347, (138-206)
	1993-2013	Good condition			192, (127-181)		118, (142-182)	51, (136-200)	997, (80-205)	20, (150-205)				
		Average condition		143, (140-200)					2909, (70-205)	65, (110-180)				
		Low condition	722, (90-187)	1055, (79-200)	872, (75-190)	1583, (95-193)	555, (109-194)	1149, (74-190)	4675, (70-210)	715, (76-183)	521, (96-189)	692, (91-181)	1702, (81-193)	868, (93-194)
Anchovy	1993-2013	Good condition			282, (105-175)	101, (105-135)	91, (125-165)	112, (120-170)	973, (70-185)					60, (143-182)
		Average condition		60, (135-180)		11, (155-180)	24, (100-175)		2785, (55-185)			220, (70-170)	5, (120-125)	
		Low condition	779, (67-168)	799, (68-159)	1227, (79-173)	1101, (70-171)	853, (90-158)	1659, (86-167)	5407, (40-180)	1323, (93-155)	1220, (78-166)	663, (72-148)	1469, (71-162)	536, (96-160)

Table 2. Results of the AICc selected GLMs performed on anchovy and sardine. The relative condition index was taken as a function of Sea surface temperature (SST), Chlorophyll *a* concentration (Chl *a*), Rhone runoff, Western Mediterranean Oscillation (WeMO), Mesozooplankton concentration (Mesozoo), Nanozooplankton concentration (Nanozoo), Microzooplankton concentrations (Microzoo), Nanophytoplankton concentration (Nanophyto) and Microphytoplankton concentration (Diat). All data were standardized and GLMs were performed with a Gaussian distribution and identity link.

	Anchovy				**Sardine**			
Parameter	**Estimate**	**s.e**	***t***	***p*-value**	**Estimate**	**s.e**	***t***	***p*-value**
Intercept	0.168	0.146	1.179	0.235	-1.215	0.388	-3.348	0.005
Mesozoo	0.273	0.056	4.871	<0.001	0.646	0.142	3.369	<0.001
SST	-	-	-	-	-0.749	0.261	-3.004	0.005
Rhone runoff	0.306	0.109	2.903	0.006	-	-	-	-
WeMO	-	-	-	-	0.601	0.226	2.921	0.007
Chl *a*	-	-	-	-	-	-	-	-
Nanophyto	-	-	-	-	-	-	-	-
Diat	-	-	-	-	0.396	0.112	3.620	<0.001
Nanozoo	-	-	-	-	-	-	-	-
Microzoo	-	-	-	-	-	-	-	-

Figures

Figure 1. Seasonal cycle of the relative condition for anchovy and sardine. For sardine, the condition was significantly higher during 1971-1978 years for all month (except April). The number of individuals sampled during each month is included at the bottom of the boxplot.

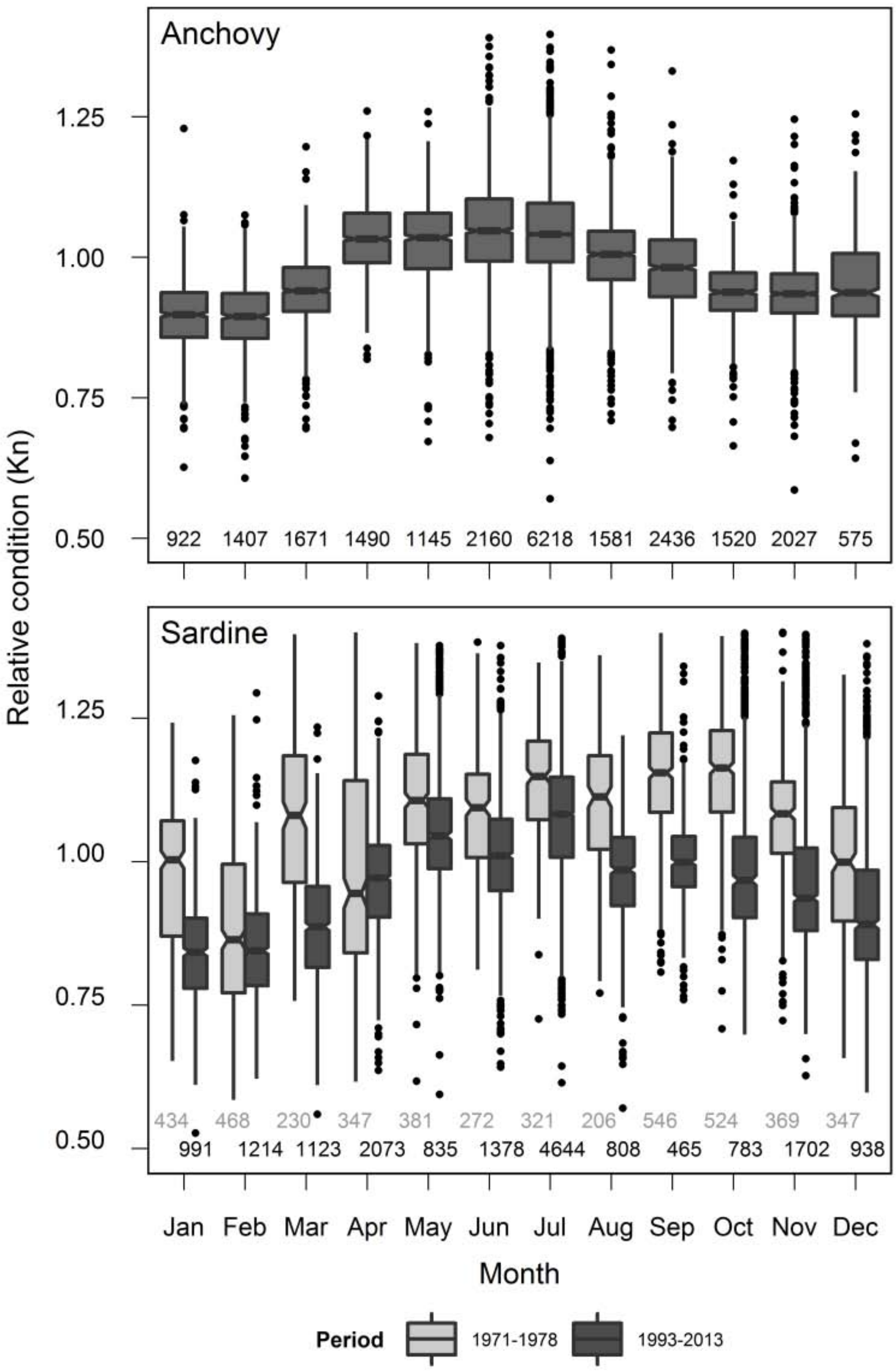

Figure 2. Results of the classification and regression tree assessing the importance of years, age and sex to anchovy condition values. The tree is split off on the values of one covariate at a time such that the overall variance in the dependent variable is minimized at each split. Terminal nodes indicate the value of anchovy standardized condition assigned to the node. The different groups of years identified according to the anchovy condition were highlighted in boxes.

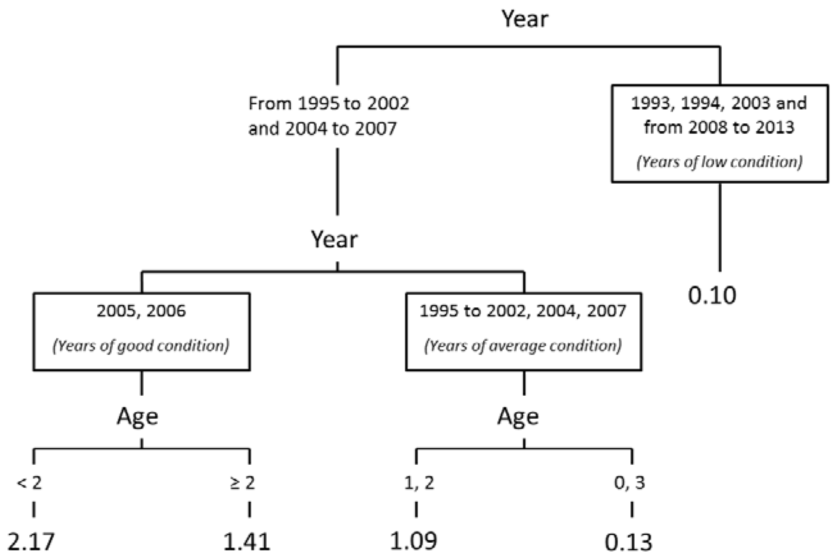

Figure 3. Results of the classification and regression tree assessing the importance of year, age and sex to sardine condition values. The tree is split off on the values of one covariate at a time such that the overall variance in the dependent variable is minimized at each split. Terminal nodes indicate the value of sardine standardized condition assigned to the node. The different groups of years identified according to the sardine condition were highlighted in boxes.

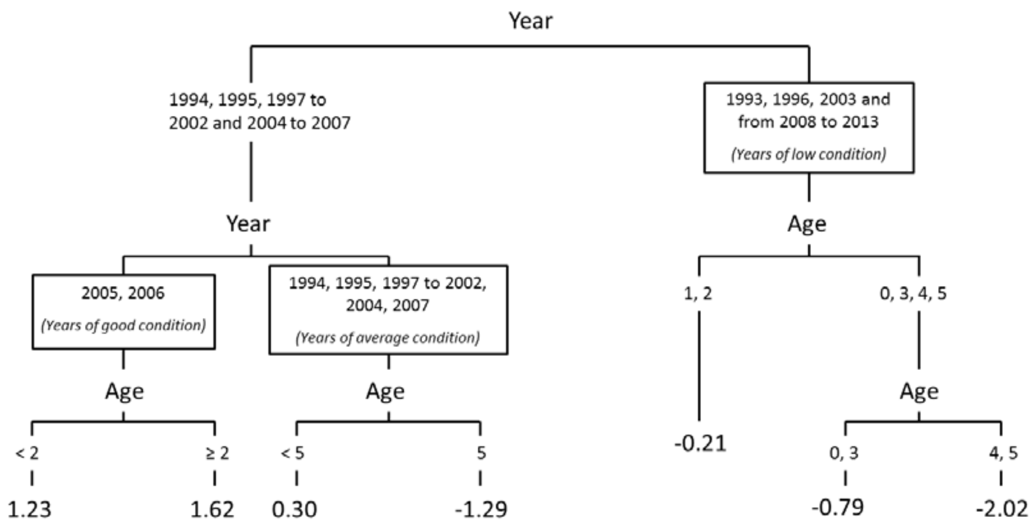

Figure 4. Boxplot of the standardized relative condition in function of age for anchovy and sardine. The number of individuals of each age class is included below each boxplot and letters indicate box age-classes that are statistically different for each group of years.