Energy allocation trade-offs between life-history traits in the Mediterranean sardine: an ecophysiological approach

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Abstract

Since 2008, the oldest and largest sardines have been disappearing in the Gulf of Lions which strongly affected the regional fisheries. A bottom-up process involving a shift in their diet towards smaller planktonic preys has been suggested as the main driver affecting their decreasing condition. Yet, their reproductive capacities have not been altered, suggesting potential modifications in energy allocation trade-offs. Whether this could also affect maintenance, in particular at the end of the winter reproductive period, and explain the lower adult survival and the disappearance of older individuals remains unclear. We therefore experimentally investigated the consequences of a seasonal modulation of food availability (summer *vs* winter) on sardine life-history traits and energy allocation trade-offs at the individual and population levels. Our results indicate that food resources during summer had a major effect on energy reserves and growth, limiting the maximum size and body condition reached at the end of reproduction. In addition, food restrictions during growth and/or reproduction periods led into physiological costs mediated by increased oxidative damages. Mediterranean sardines did not show any abilities to do compensatory growth and did not appear to be 'capital breeders'. Instead, they displayed differences in individual qualities in dealing with physiological constraints and displayed various life history strategies regardless of the food modulation. We therefore highlighted three main individual energy allocation strategies: (i) favor body condition, (ii) favor growth or (iii) allocate simultaneously in reproduction and growth. Such understanding is key as climate change is expected to favour phytoplankton of smaller size which might amplify the decrease in condition in Mediterranean sardines.

Keywords: compensatory growth, capital breeders, individual quality, oxidative stress, reproduction, maintenance, *Sardina pilchardus*

1. Introduction

How organisms acquire, store and use energy or nutrients throughout their annual cycle is a key component of their life strategy and an important feature defining their fitness (McEwen & Wingfield 2003). If/when resources become limiting (in quantity and/or quality), allocating energy to one specific function will occur at the expense of another (Gadgil and Bossert 1970, Zera, Anthony and Harshman 2001), which implies trade-offs between the organism growth, somatic maintenance and reproduction (Stearns 1989).

In the natural environment, the availability of resources is variable in time and/or space. As such, animals have evolved a range of strategies to face alternation of high and low resource's levels. For instance, under low resources, growth is often slowed down if not stopped (Sumpter et al. 1991). However, some organisms are able to offset and catch up to the predicted size when resources subsequently improve via the so-called "compensatory growth" (Metcalfe & Monaghan 2001, 2003, Mangel & Munch 2005). This accelerated growth period has been observed across a wide range of taxa (Albon et al. 1987, Näslund et al. 2015, Stier et al. 2015) and seems to occur following a period of undernourishment rather than malnutrition (Boersma & Wit 1997).

To further cope with environmental constraints in resource availability, particularly during breeding, two main and opposite reproductive strategies have been proposed: capital breeding (organisms who store energy by anticipation before reproduction) *vs.* income breeding (no anticipation, energy intake occurs during the reproductive period) (Stearns 1989). Income

57 breeding aims to reproduce while resources are abundant, leading to a rapid transfer of
58 productivity from the ecosystem to species reproduction. On the opposite, to face the highly
59 energy demanding period of gamete production and offspring raising, some species mostly rely
60 on reserves previously accumulated as, mainly, body fat reserves (Rijnsdorp et al. 2005, Palstra
61 & van den Thillart 2010). This is referred to as "capital breeding". Although easily described as
62 dichotomous, it is widely acknowledged that breeding patterns are not limited to extreme forms
63 and should be distributed along a range – perhaps a complete continuum – of intermediate types
64 (Stearns 1989).

65 Such growth and reproductive energy allocation patterns have evolved enable individuals to
66 match their energy expenditure with resource availability and maximise their fitness. Yet, how
67 this could affect trade-offs with other functions, especially regarding the potential costs of body
68 maintenance, is an important question. For instance, the oxidative balance (i.e. balance between
69 production of reactive oxygen species (ROS) owing to metabolism and the level of endogenous
70 and exogenous antioxidant defences) plays a recognized role in the deterioration of body
71 functions and has been proposed as one of the mechanistic bases of ageing (Speakman 2005,
72 Metcalfe & Alonso-Alvarez 2010). However, generality or simplicity of this link within
73 mammals or among taxa is not that evident (Vágási et al. 2019, Kramer et al. 2021). Here, we
74 propose that the current study will test for oxidative stress consequences of manipulated trade-
75 offs in European sardines of the NW Mediterranean Sea.

76 While energy allocation trade-offs and the underlying mechanisms are increasingly studied on
77 terrestrial species (Bonnet et al. 2002, Vedder & Bouwhuis 2018), they are much rarer on marine
78 ones where it is particularly difficult to track individuals in the wild over time. Yet, such trade-
79 offs should be exacerbated in most marine species (at least in fish), which maintain a continuous

growth throughout their lives, extending the question of trade-offs from the single somatic maintenance *vs.* reproduction. Moreover fitness generally increases with size, which should put significant selection pressure on growth and thus urge individuals to grow fast, again leading to possibly exacerbated trade-offs.

Often characterized by short lifespan (2 to 7 years) and high reproductive rate, small pelagic fish are key components of marine ecosystems, playing an important role in energetic transfers from lower trophic levels (plankton) to higher ones (*e.g.* humans, tuna, cetaceans, birds, Cury 2000, Frederiksen et al. 2006, Straley et al. 2018). Their population dynamics are known to be greatly affected by environmental fluctuations (bottom-up effects) and predator abundance/human induced changes (top-down effects), causing populations to commonly face variations in abundance (Checkley et al. 2017). Recently, significant changes in life history traits have been observed in the small pelagic fish populations of the Gulf of Lions in the north-western Mediterranean Sea (Saraux et al. 2019). Since 2008, the two dominant small pelagic fish species, *i.e.* sardine (*Sardina pilchardus)* and anchovy (*Engraulis encrasicolus*), have shown a drastic decrease in size and body condition (Van Beveren et al. 2014). This results in lower value on the stalls, which in return has led to the lowest historical landings of small pelagic fish for 150 years and a local fisheries crisis (Van Beveren et al. 2016a). The hypotheses of a top-down control (overfishing, predation) or epizootic diseases have been recently refuted (Van Beveren et al. 2016b, 2017, Queiros et al. 2018), so that the main hypothesis to explain those changes is a bottom-up control, i.e. a modification of either size and/or quantity of sardine and anchovy preys (essentially copepods), thus limiting fish energy resources (Brosset et al. 2016a, Saraux et al. 2019). Moreover competition for food with other species such as sprat is possible but remain

unclear (Pethybridge et al. 2014) and could have changed over the last decade (Brosset et al. 2016a).

Under limited energy resources, the question of how small pelagic fish, especially sardine which was much more impacted than anchovy (Saraux et al. 2019), solve energy allocation trade-offs might be central in understanding the changes observed at the population level. Indeed, the smaller size of sardines has been shown to result from both a slower growth and from the disappearance of older sardines. On the opposite, a recent study conducted on wild populations showed that sardines started reproducing at smaller sizes and maintained high investment in gonads (Brosset et al. 2016a), suggesting a trade-off between growth and reproduction. Besides, whether the decrease in sardine longevity might result from lower energy resources and/or costs associated with growth and reproduction is still an open question. Sardines are usually considered as capital breeders *i.e.* they store energy in spring and summer that can be mobilized later for the reproduction in winter (Ganias 2009). Depleted reserves at the end of the reproductive period might thus not be enough anymore to support maintenance costs in winter when resources are low.

To formally test the hypothesis of change in energy allocation trade-offs in sardines, we experimentally investigated the consequences of a temporal modulation of food resources during two seasons (summer and winter) on life-history traits. Manipulating food size and quantity has previously done by Queiros et al. (2019), our aim was to answer the following three main questions: (i) When feeding conditions improve, do sardines show compensatory growth? We predicted sardines facing poor feeding conditions in summer and then improved conditions in winter to exhibit compensatory body size growth (Mangel & Munch 2005) (ii) How plastic are sardines in terms of reproductive investment? Do they depend exclusively on their stored

energy? We tested the hypothesis considering sardines as a capital breeder. In such situation, feeding conditions prior to reproduction (i.e. in summer) will have a major effect, and therefore individuals poorly fed in summer but well fed in winter should not be favoured in regard to sardines poorly fed throughout the entire experiment ; (iii) What are the costs in terms of maintenance of such growth and reproductive energy allocation strategies? If sardines exhibit compensatory growth or higher reproductive investment, we supposed that it should lead to the accumulation of damage at the cellular level (Metcalfe & Monaghan 2001) and higher oxidative stress (Mangel & Munch 2005).

An extra layer of complexity is added when considering inter-individual differences. Individual heterogeneity within the same population can be observed especially when the environmental conditions are fluctuating or unstable (McNamara 1998, Tuljapurkar et al. 2009). There is indeed a continuum of life history strategies both inter- and intra-specific, with some individuals favouring survival over reproduction and *vice versa* (Reid et al. 2010). In this case, negative correlations between traits should arise, an increase in one trait being conditioned by a decrease in another one. By contrast, if strong heterogeneity in terms of individual quality exists and some individuals of "higher quality" better succeed at facing food limitation, positive correlations among the different life history traits would be expected (*e.g.* some individuals should be able to invest simultaneously in reproduction and growth, Marchand and Boisclair 1998, Wilson and Nussey 2010, Bergeron et al. 2011). We investigated those hypotheses by (i) analysing the inter-individual variance in size and body condition over the different periods of the experiment and (ii) assessing the existence of different strategies or qualities at the end of winter and testing for associated costs through their oxidative status.

2. Material and Methods

2.1.Experimental design

This study aims to investigate energy allocation trade-offs and individual strategies of sardines in the Gulf of Lions in response to energy limitations imposed during two very distinct periods of their life cycle: summer, with high growth rate due to higher water temperatures and planktonic production peak *vs* winter, when reproduction takes place. To do so, an 8-month experimental approach on wild adult sardines acclimatized in tanks (detailed below) was carried out considering the food size and quantity during two periods (summer and winter). Both size and quantity of food were taken into account, as a previous study revealed that sardines feeding on small particles (0.1mm, actually ranging between 80 and 250 µm) had to consume twice as much as those feeding on large ones (1.2mm, ranging between 900 and 1500 µm) to achieve the same body condition and growth (Queiros et al. 2019). The consequences of these feeding treatments were considered on several life history traits further detailed below: morphometric features (body condition, growth), energy resources (muscle lipid contents), somatic maintenance markers (oxidative stress) and reproductive investment (gonadosomatic index).

In May 2017, around 1,000 sardines were captured at sea (see further details of fish biological information at capture Table S1), and brought back to an experimental research facility, where they were held in quarantine in outdoor tanks of 4.5 m^3 for 1 month and a half until confirmation of the absence of pathogens (similarly to Queiros et al. 2019). During that time, sardines were also weaned from live food (*Artemia nauplii*) to a mixture of aquaculture pellets of different sizes: 0.1 mm, 0.3 mm and 0.8 mm at feeding rates between 1 and 2% of the biomass per day. At the end of June sardines were moved into 2 indoor tanks of 3 m^3 each (Figure 1). Prior to

169 transfer, sardines were anaesthetized with benzocaine (140 ppm), their total length (± 0.1 mm)
170 and mass (± 0.01 g) measured so as to distribute them into homogeneous groups (i.e., similar
171 mean and standard error of size and mass between tanks) between the two tanks. Moreover, after
172 the two first months we switched the fish from one tank to the other, in order to buffer any
173 potential tank effect.

174 The experimentation started on June 27, 2017 and ended on March 5, 2018. The first phase (from
175 June 27 to November 16) was considered as the summer period with two possible scenarii that
176 aim to mimic contrasted natural conditions: (i) A "highly productive" year that was
177 experimentally mimicked by high food quantities (between 0.8% and 1.2% of the total fish
178 biomass, according to prevailing temperature) and large pellets size (1.2 mm) and (ii) a "low
179 productive" year characterized by smaller food quantities (between 0.4% and 1% of the total
180 biomass, according to prevailing temperature) and small pellets size (0.1 mm, see Figure 1).
181 These two contrasting pellet sizes are in the range of prey size in their diet (Le Bourg et al.
182 2015).

183 On October 25, each group of sardines was homogeneously divided into 4 sub-groups (following
184 the same procedure as in June), and transferred to 300 L tanks (8 tanks in total; Figure 1) in
185 preparation for the second phase of the experiment (from November 17, 2017 to March 5, 2018).
186 The second phase of the experiment (afterwards 'winter') started the first week when the
187 temperature dropped below 14°C i.e. mid-November (November 17th) which coincided with the
188 entry into reproduction during a natural breeding cycle for northwestern Mediterranean sardines
189 (Brosset et al. 2016a). Similarly, sardines reared in captivity over the last 4 years have initiated
190 spawning event only when the water temperature dropped below 14°C and have stopped
191 reproduction at the end of winter when temperature rose above 15°C. During this second phase,

192 half of the tanks remained in the same food condition as during summer, while the other half
193 switched. To sum-up, our experimental design ended with four treatments: (i) rich diet in
194 summer and winter (referred as Rich Summer/Rich Winter), (ii) rich diet in summer and poor
195 diet in winter (Rich Summer/Poor Winter), (iii) poor diet in summer and rich diet in winter (Poor
196 Summer/Rich Winter), and (iv) poor diet in summer and winter (Poor Summer/Poor Winter),
197 each composed of two tanks. On March 5, 2018 (when the reproductive period was over), the
198 experiment stopped and 120 sardines (30 per feeding treatment) were randomly sampled and
199 sacrificed by benzocaine overdose in order to study in-depth their physiological conditions. Sex
200 and maturity were determined by gonad observation at the end of experience. Mortality during
201 the experiment was very low, on average 4% (further details in Table S2 with mortality rate for
202 each tank).

203 Tanks were supplied with the same seawater (filtered and passing through UV light) at a renewal
204 of 10%/hours during both period ('summer' and 'winter'). All tanks were provided with
205 individual standardised light source mimicking the sunlight spectrum and mimicking natural
206 cycles including progressive dawns and sunrises. The photoperiod was thus weekly adjusted to
207 follow the natural cycle and seawater temperature was not controlled except to maintain a
208 minimum of 10°C and a maximum of 25°C. Finally, temperature and salinity recordings of tanks
209 were closely following the same trend over the entire period (Figure S1).

210

211 ## 2.2. Total length, body condition and growth **(N = 972 individuals)**

212 Each sardine was tagged to allow individual monitoring of body growth. On August 29, 2017, a
213 tiny RFID tag (Biolog-id, Bernay, France, 0.03 g, or < 0.6% of the body mass of the leanest

sardine) was implanted in the dorsal muscle after being anaesthetized with benzocaine (140 ppm). Thereafter, total length (± 0.1 mm) and mass (± 0.01 g) were recorded individually every 4 weeks (later on named "biometry day") until the end of the experiment. Sardines were fasting 24 hours before each biometry so weight would not be biased by stomach content. Relative body condition of each sardine (N = 972) was calculated with the Le Cren index Kn as estimated by Brosset et al. (2015):

$$Kn = \frac{WW}{0.00607 \times TL^{3.057}} \quad (1)$$

where WW is the wet mass in g and TL is the total length in cm. This index compares the actual mass of an individual with the theoretical mass expected for an individual of its size (based on the size-weight relationship of tens of thousands of individuals fished *in situ*). Therefore, a value of Kn > 1 means that the individual has a body condition higher than the average of the population and *vice versa*.

Growth rates and condition rates were then estimated at different time scales. First, instantaneous growth and condition rates were estimated as the change in length and condition from one biometry day to the next one, divided by the number of days between them. Because of relative measurement precisions (1mm) and the some extremely slow growth, it sometimes resulted in negative growth rate $_{t-1 \rightarrow t}$. To overcome this problem, we translated all instantaneous growth rates by the minimum rate ever observed (-0.28 mm.day^{-1}) considering that this should represent a null growth. For each individual, a summer and a winter growth and condition rates were also estimated as the slope of linear models of total length (mm) or body condition over time (day) (1 linear model per individual per period).

Before the start of individual monitoring (August 29), 130 and 108 individuals were measured in June and July, respectively, to adjust food quantity to total tank biomass. Since the individuals were not tagged yet, the data could not be linked to individual size or condition trajectories. The average condition and size measurements at these 2 dates are therefore presented only for information on the graphs and are not used in analyses. Further, between the 29th August and the 26th September 2017 about 40% of individuals lost their tags. These individuals were retagged on September 26 and no tags were lost afterwards. In order to ensure that the lower sample size for this first month (due to tag lost) didn't affect our analysis we compared mean growth rates and condition rates (± SE) through time per treatment considering 3 subsamples (Figures S2 and S3): a) considering all data points available (N=603 in September and then 972 for all other month), b) the 603 individuals over the entire time series and c) only the 120 individuals sacrificed at the end of the experiment. Since results did not differ whatever the subsample considered, we present hereafter results based on all data available.

At the end of the experiment 120 individuals were sacrificed (30/treatment which were representative of their treatment (similar growth and condition rate), see Figure S2 and Figure S3). To obtain a growth rate for the entire experiment (referred as total growth rate), summer and winter growth were averaged weighted by the number of days of each period (equation (2)):

$$total\ growth\ rate = \frac{growth\ rate_{summer} * days_{summer} + growth\ rate_{winter} * days_{winter}}{(days_{summer} + days_{winter})} \quad (2)$$

In order to obtain a trait independent of the reproductive investment, a second body condition index was calculated where gonads mass was removed from the individual's final weight (therefore only available at the end of the experiment for the N=120):

$$Kn_{\ without\ gonad} = \frac{WW - GM}{0.00055 \times TL^{4.0498}} \quad (3)$$

where WW and GM are the final wet mass in g of individuals and gonads respectively and TL is the final total length in cm. The two constants were estimated from our data based (> XXX individuals) on the final size-weight without gonads relationship of the 120 individuals sacrificed in March.

Total condition rate (i.e. over the entire experiment for the N=120) was then assessed based on this second condition index. Equation (4) indicates how we assessed the gain/loss of body condition for the entire experiment independently of the investment in reproduction:

$$Condition\ rate_{\ without\ gonad} = \frac{Kn_{\ without\ gonad} - Kn_i}{(days_{summer} + days_{winter})} \quad (4)$$

where $Kn_{without\ gonad}$ is the individual final body condition as explained previously (equation (3)) and Kn_i is the initial body condition (equation (1)) at the start of the experiment. Because the experiment started in summer, when individuals have not yet started to invest in reproduction, we considered the mass of gonad to be null at that time (see Figure 2 in Brosset et al. 2016)

2.3. Reproduction status at the end of winter **(N=120 individuals)**

For each of the 120 sacrificed individual, sex and gonad mass were recorded. To estimate sardines' reproductive investment, a gonadosomatic index (GSI, Alam and Pathak 2010) was estimated as follows:

$$GSI = \frac{Gonad\ mass}{Individual\ mass} \times 100 \quad (5)$$

Out of the 120 individuals, 6 individuals displayed non-active gonads (and 3 out of the 6 were not sexually differentiated while all the other individuals presented mature gonads. Therefore we had the sex for 117 sardines at the end of the experience.

2.4.Physiological condition at the end of winter **(N = 120 individuals)**

For each of the 120 individuals sacrificed at the end of the experiment, blood was collected from the caudal vein with a heparinized 26G needle and transferred into 1.5 ml Eppendorf tubes. Blood samples were centrifuged at 3000 g for 10 minutes at 4°C to separate plasma from cells, which was collected and stored at -80°C until further oxidative status analyses. Portions of dorsal epaxial muscle were also removed, immediately frozen in liquid nitrogen and stored at -80°C for further lipid analyses.

2.4.1. Individual oxidative status

The physiological consequences of feeding treatment were studied by assessing the oxidative stress status in plasma by measuring two biomarkers for antioxidant defenses (Total antioxidant defenses, OXY and Superoxide dismutase enzyme activity, SOD) and two biomarkers for oxidative damage (Reactive oxygen metabolite, d-ROMs and Thiobarbituric acid reactive substances formed as a byproduct of lipid peroxidation, TBARs).

All sample measurements were performed in duplicate. Samples with a coefficient of variation (CV) higher than 15% were re-run. Assays were performed on all individuals except for some individuals for whom the amount of plasma was not sufficient to perform all tests, explaining the differences in sample sizes among analyses. Sample sizes are reported in the text and figures.

- d-ROMs and OXY :

According to Costantini and Dell'Omo (2006) reactive oxygen metabolites (d-ROMs) and total antioxidant defenses (OXY) were estimated in plasma using the d-ROMs test and the OXY Adsorbent test, respectively (Diacron International©, Grosseto, Italy). After incubation, absorbance was measured at 555 nm with a microplate spectrophotometer. d-ROMs were expressed in mg of equivalent $H_2O_2.L^{-1}$ and the antioxidant defense capacity (OXY) in µmol $HClO.mL^{-1}$. The intra- and inter-plate CV were 4.5% and 3.1% for d-ROMs and 7.3% and 7.7% for OXY, respectively.

- Superoxide dismutase (SOD) :

Superoxide dismutases (SOD) are important endogenous defense systems against free oxygen radicals which catalyze the dismutation of superoxide radicals ($O_2^{\cdot -}$ into hydrogen peroxide (H_2O_2) and oxygen (O_2) ($2O_2^{\cdot -} + 2\ H^+ \longrightarrow O_2 + H_2O_2$, Fridovich 1989). SOD is represented by three isoforms, differing with metal ions in their active centers, Mn-SOD (SOD2) and Cu/Zn-SOD (SOD1 and SOD3). In plasma, only SOD3 is present. Therefore, an increase in this enzyme indicates good circulating neosynthesized antioxidant defense (Barry Halliwell & John M. C. Gutteridge, 2007). Their concentration in plasma was estimated by colorimetry according to Peskin & Winterbourn (2000). To normalize SOD concentration by protein content in plasma, protein concentration in each sample was determined by the BCA method (Pierce, Thermo Fisher Scientific, France). Four plasma samples lacked the required quantity to run duplicates. Nonetheless, the intra- and inter-plate CV being respectively 8.4% and 3.4% for the SOD estimation (always <15% for all duplicates), we considered the four samples that were run only once reliable. After incubation at 37°C for 30 minutes, absorbance was measured at 450 nm with a microplate spectrophotometer. For each plasma sample the SOD concentration was also

corrected by the protein content and expressed in units/µg protein. The intra- and inter-plate CV were 3.7% and 0.7% for the protein estimation.

- Lipid peroxidation (TBARS test) :

Finally, lipid peroxidation in the sardine plasma was estimated from the production of malondialdehyde (MDA), which is one of the final products of lipid peroxidation (Draper & Hadley 1990). The MDA content was determined by the "MDA colorimetric assay kit" (Elabscience Biotechnology Inc.©). This assay measures the thiobarbituric acid (TBA) reactive substances at 532 nm, following the methodology described by Draper & Hadley (1990). The intra- and inter-plate CV for plasma samples were 2.3% and 1.5% respectively.

2.4.2. Energy storage and reserve

The energy storage capacities were examined by analyzing the lipid content of the dorsal muscle. The lipids were extracted according to the method of Folch et al. (1957) and the content of each class of lipids was measured in the muscle by chromatography, using an Iatroscan as detailed in Sardenne et al. (2019). Phospholipids (PL), sterols (ST), acetone-mobile polar lipids (AMPL) and alcohols (CLA) were grouped in structural lipids, while triacylglycerols (TAG), diacylglycerols (DAG as TAG precursors) and free fatty acids (FFA) were grouped in reserve lipids (Zhol et al. 1995, Tocher 2003, Lloret et al. 2013). The proportions of free fatty acids (FFA) were also checked to ensure that the lipids had not been degraded during sample storage. Here, the proportions ranged from 0% to 12%, significantly below the 25% limit recommended by Parrish (1988).

2.5.Data analyses

2.5.1. Effects of feeding treatments on life history traits at the population level

At the end of both periods (summer and winter), the differences in size and body condition between treatments were tested, using linear mixed model (LMM and pairwise post-hoc tests) where tank was added nested in treatment as random factor to account for tank effect in winter. Summer and winter growth rates and condition rates in response to treatments were also investigated, similarly as above (LMM and pairwise post-hoc tests). To test the effect of the individual's size at the beginning of summer and winter on summer and winter growth rate respectively, we modeled the summer or winter growth rate (response variable) in relation to the initial size (at the beginning of summer or winter), feeding treatment as well as their interaction (explanatory variables). These analyses were run on N=972 individuals. We also ran our different models on the subsample for which we have the sex (N = 117 individuals) in order to test its effect. Sex was included in interaction with treatment and removed when non-significant.

Physiological conditions (plasma oxidative stress and muscle lipid content) and reproductive investment differences between treatments for the N=120 individuals sacrificed at the end of the experiment were examined, using parametric (LMM) or non-parametric (Kruskal-Wallis) tests and associated post-hoc (Tukey or Dunn test), depending on residual normality. Sex was included in interaction with treatment and removed when non-significant.

A multivariate Principal Component Analysis (PCA, Abdi and Williams 2010) approach was also performed, using the N=120 individual sardines as objects and the summer growth and condition rates (August to November), the winter growth and condition rates (November to March), as well as the antioxidant defence biomarkers (SOD and OXY), the oxidative damage

biomarkers (TBARS and d-ROMs), the reserve in lipids and the gonadosomatic index at the end of the experiment, as descriptors. The aim of this analysis was to summarize all the information and investigate the relationships between descriptors and to examine the level of inter-individual variability overall and within each feeding treatment.

2.5.2. Investigating inter-individual variability and allocation trade-offs

Van Noordwijk and De Jong (1986) demonstrated that correlations between competing traits (*e.g* growth, maintenance and reproduction) within a species may take any sign. If individuals differ in their strategies, allocation trade-offs should occur and negative relationships between traits would likely be observed (Stearns 1989). Yet, if heterogeneity in individual quality exists, "high-quality" individuals should be able to display higher investment overall into all competing traits than other individuals referred as "low-quality" individuals, resulting in positive relationships among traits. We checked those possibilities first by analysing the inter-individual variance in size and body condition over the different periods of sampling of our experiment with standard deviation (SD) time series. However, those alternative hypotheses are not exclusive and trait covariation could also depend on the environment (e.g. trade-offs appearing only under limiting conditions, Hämäläinen et al. 2021). Therefore, we investigated how growth rate, condition rate and GSI covaried and whether this depended on the feeding treatment, using various types of regression models (see below). Each model was tested with and without the interaction of the feeding treatment with the covariables (either growth rate, condition rate or GSI) and the best models were selected, using the AIC criterion (Burnham & Anderson, 2004). When these interactions were significant, we presented one model for each treatment to facilitate the analysis of the results. The normality of the residuals of each model was analysed visually with a quantile-quantile plot (Q-Q plot, Ghasemi and Zahediasl 2012) or through a Shapiro-Wilk's test,

384 depending on the number of observations. When data were not independent from each other due
385 to repetitions within individuals (e.g. body condition and body size over time), a mixed model
386 was used with the individual effect sets as a random intercept, either through a linear mixed
387 model (LMM, Zuur et al. 2009) or a generalized linear mixed model (GLMM, Zuur et al. 2009),
388 depending on the distribution of the data.

389 ***2.5.2.1 Modelling growth and energy storage***

390 We first tested how sardines allocated energy between growth and body condition at each time
391 step during winter only depending on body condition at the start of this time step, using the
392 initial N=972 individuals. As the interaction with treatment was significant (see section results
393 below), we conducted for each feeding treatment a GLMM (with a gamma link function and with
394 the individual effect set as a random intercept) where individuals growth rates from *t-1* to *t*
395 during winter were dependent on their changes in body conditions over that same period and
396 their body conditions at the beginning of *t-1* as well as their interactions (equation (6) (N = 972).
397 In order to test for sex effect we also ran sub-models on the 120 individuals for which sex was
398 available. Since sex had no effect it was removed from the final model.

399 $$Growth\,rate_{t-1\rightarrow t} = Condition\,rate_{t-1\rightarrow t} \times Condition_{t-1} + (1|\,ID) \quad (6)$$

400 Where "ID" is used here for individual (Individual tag number considered as categorical for
401 repeated measurement).

402 ***2.5.2.2 Modeling growth, energy storage and reproduction***

403 As body condition index includes energy stored for reproduction, we examined more precisely
404 the links between reproduction, growth and maintenance, using the 120 individuals sacrificed at
405 the end of the experiment. Therefore, we assessed whether reproductive investment (GSI) was

406 constrained by energy investment in growth (total growth rate, equation (3)) and in body
407 condition (condition rate$_{\text{without gonad}}$, equation (4)) over the entire experiment, using a generalized
408 linear model (GLM), with a gamma link function, for each feeding treatment. In order to test for
409 sex effect we added sex in interaction. When sex had no effect it was removed from the final
410 model.

411 ***2.5.2.3 Summarizing the different energy allocation strategies***

412 Using the 120 individuals sacrificed at the end of the winter period, we investigated the different
413 energy allocation strategies through a hierarchical clustering analysis (Johnson 1967). This
414 analysis was performed on total growth rate, total condition rate$_{\text{without gonad}}$ and GSI, using
415 Euclidean distances on normalized data (data were first centered by treatment to remove the
416 direct effect of the feeding treatment on the absolute values of GSI, growth rate and condition
417 rate) and the Ward's agglomerative clustering method (Ward 1963). To test for physiological
418 costs associated with the identified strategies (i.e. the different clusters), differences in oxidative
419 damage and antioxidant defense between clusters were investigated using one-way analyses of
420 variance (LM and pairwise post-hoc tests). In order to account for known sex effect on GSI we
421 realized separate analyses for males and females. The best clustering scheme was identified
422 using the function *NbClust* (Charrad et al. 2014) which tests 30 methods that vary the
423 combinations of number of clusters and distance measures for the hierarchical clustering. To
424 evaluate the effect of the individual's size at the beginning of the experiment on their potential
425 strategies, composition of initial size in each cluster for both sexes were assessed.

426 Analyses were performed with the statistical open source R software v.4.1.1 (R Core Team
427 2020) using the FactoMineR (Lê et al. 2008), the nlme (Pinheiro et al. 2021), the lsmeans (Lenth

2016), and the factoextra (Kassambara & Mundt 2020) packages. Values are indicated as mean ± standard error (SE) and all statistical tests were performed at a significance level of 0.05.

3. Results

3.1. Effects of feeding treatments on life history traits at the population level

3.1.1. Compensatory growth

At the end of summer (vertical dotted line in Figure 2a and 2b), rich summer feeding conditions led to individuals of larger size (LM; $F = 225.48$; $P < 0.001$; Table S3) and in better condition (LM; $F = 689.58$; $P < 0.001$; Table S3). Well-fed sardines grew twice as fast as those facing poor summer feeding conditions (0.14 ± 0.004 mm/day and 0.07 ± 0.004 $mm.day^{-1}$ respectively) (LM; $F = 119.29$, $P < 0.001$) and body condition rates increased 5 times more for sardines in rich vs. poor feeding conditions (LM; $F = 439.72$; $P < 0.001$, Figure 2c and 2d, Table S3). In summer, smaller sardines in rich feeding condition grew significantly less than larger ones whereas smaller sardines in poor feeding condition grew significantly more than larger ones, indicating that initial size is important but its effect on growth rate is treatment-dependent (LM; $P < 0.01$, Table S4, Figure S4). In none of our model considering size and growth rate the sex had any effect. However, males poorly fed displayed better body condition (1.02 ± 0.02 and 0.95 ± 0.05 for male and female respectively, Figure S5) and higher body condition rates than females in the same feeding condition which presented body condition rates over summer no significantly different from zero (Student's *t*-test; $t = -0.090386$; $P = 0.93$).At the end of the winter, the four treatments led to four significantly distinct groups in terms of total length and body condition (i.e. Rich Summer/Rich Winter > Rich Summer/Poor Winter > Poor Summer/Rich Winter >

Poor Summer/Poor Winter for both variables, Post-hoc HSD-Tukey; $P < 0.001$; Figure 2a and 2b). Individuals well fed throughout the entire experiment grew 1.5 to 2 times faster during winter than individuals in the intermediate Rich Summer/Poor Winter and Poor Summer/Rich Winter treatments (Post-hoc HSD-Tukey; $P < 0.001$) and 6 times faster than individuals poorly fed all along (Post-hoc HSD-Tukey; $P < 0.001$). For the latter, growth almost stopped, but was still significantly different from zero over winter (Student's *t*-test; $t = 9.2838$; $P < 0.001$). Interestingly, sardines from the Poor Summer/Rich Winter treatment strongly increased their body condition over the winter ($10.7.10^{-4}$ day^{-1}), between 1.5 and 7 times more than extreme treatments ($7.4.10^{-4}$ day^{-1} and $1.5.10^{-4}$ day^{-1} for the Rich Summer/Rich Winter and Poor Summer/Poor Winter treatments respectively, Post-hoc HSD-Tukey; both $P < 0.001$), while sardines experiencing the opposite changes (from rich to poor) decreased in condition ($-4.2.10^{-4}$ day^{-1}, Post-hoc HSD-Tukey; $P < 0.001$). Tank (for a given feeding treatment) had no effect on body condition and length over time and was therefore removed from the analyses. According to the AIC, the better model for the winter growth rate included both the initial size, the treatment and their interactions. Nonetheless, only the feeding treatment effect was significant while the initial size remained non-significant globally and in interactions (Table S5). Sex had no effect in all models including size and growth rate. Males poorly fed all along displayed better body condition than females for the same feeding treatment ($P < 0.01$, Figure S5) while no significant differences between sexes were found for the other treatment. Similarly male and female in the same feeding condition revealed similar body condition rates over winter.

3.1.2. Plasticity in reproduction

Gonadosomatic indices (GSI measured at the end of the experiment) for the Rich Summer/Rich Winter treatment (median: 7.9%) were about twice as high as those for the intermediate

473 treatments (medians: 3.8% and 2.6% for the Rich Summer/Poor Winter and Poor Summer/Rich
474 Winter treatments, respectively) and 12 times higher than for sardines always fed in poor
475 conditions (median: 0.7%, Figure 3). A significant sex effect on the reproductive investment was
476 found ($P < 0.001$), males displaying 2 to 3 times higher GSI than females, which held true in
477 each treatment (Figure S6).

478 ### 3.1.3. Costs in terms of maintenance

479 No significant differences between sex and tanks (for the same feeding treatment) for plasma
480 oxidative state and muscle lipid contents were found.

481 - Individual oxidative status

482 Overall, sardines from the Rich Summer/Rich Winter treatment presented the lowest level of
483 antioxidant defenses in both OXY and SOD (Figure 4a, 4b) although these differences were not
484 always significant with respect to sardines from other treatments. Sardines from the Poor
485 Summer/Poor Winter treatment presented low to average OXY levels, but displayed endogenous
486 antioxidant SOD levels twice as high as those under the intermediate treatments (Post-hoc HSD-
487 Tukey; $P < 0.01$; Figure 4b) and five times as high as those under the Rich Summer/Rich Winter
488 treatment (Post-hoc HSD-Tukey; $P < 0.001$). Furthermore, sardines from the Rich Summer/Rich
489 Winter treatment displayed lower oxidative damages than sardines of other treatments (d-ROMs
490 and TBARS, Figure 4c, 4d). No difference in oxidative damages was observed among the other
491 three treatments.

492 - Lipid content

493 Reserve lipid concentration in muscle gradually increased with the improvement of the feeding
494 conditions. Reserve lipids for Rich Summer/Rich Winter treatment were 2 to 7 times higher than

those of the three other treatments. Sardines from the Poor Summer/Poor Winter treatment presented the lowest concentration of reserve lipids (Post-hoc Dunn's test, $P < 0.001$). On the other hand, structural lipids were similar among all four treatments (Kruskal-Wallis; $H = 2.95$; $P > 0.05$; Figure S7).

3.1.4. Multivariate analysis

The first 2 components of the PCA explained 50.2% of the total variance observed. The main contributing variables to the first axis were winter growth and reserve lipids, whereas d-ROMs and OXY were the two main contributors to the second axis (Figure S8). The PCA tends to disentangle extreme treatments. Individuals from Rich Summer/Rich Winter treatment were mostly characterized by high winter and summer growth, high summer body condition, high GSI (i.e. reproduction investment), high lipid body and low oxidative states (OXY, d-ROMs, TBARS and SOD) while individuals from Poor Summer/Poor Winter treatment generally displayed the opposite (Figure 5). Individuals from intermediate treatments, were in-between, close to the barycenter, although individuals from the Poor Summer/Rich Winter and Rich Summer/Poor Winter treatments were closer to those of the Poor Summer/Poor Winter and Rich Summer/Rich Winter treatments, respectively (Figure 5).

3.2. Diversity of individual life-history strategies

SD in total length from the Rich Summer/Rich Winter and Rich Summer/Poor Winter individuals were higher than those of the two other treatments and increased continuously over the experiment (Kruskal-Wallis; $\chi^2 = 15.923$; $P < 0.001$; Figure S9a).

The SD in body condition of the Rich Summer/Rich Winter and Rich Summer/Poor Winter treatments decreased throughout the experiment, while SD of the Poor Summer/Rich Winter

treatment seemed to stabilize from September and those of the Poor Summer / Poor Winter increased after September. At the end of winter, the sardines from the rich treatment (Rich Summer/Rich Winter) showed less variance than fish reared in poor feeding condition throughout the experience, while intermediate treatments are in-between but still significantly different from one another with Rich Summer/Poor Winter lower than Poor Summer/Rich Winter (Figure S9b).

3.2.1. Trade-off or individual quality between growth and investment in body condition

Because sardines were monitored repeatedly over time, we investigated the allocation trade-off towards growth vs. body condition every month during winter only according to the initial condition and the treatment (see eq.6). As the interaction with the treatment was always significant, we conducted a GLMM for each feeding treatment. In all models, the random effect for individuals contributed to an increase of 7% to 18% of the R^2. For all feeding treatments during winter, sardines having good body condition at time *t-1* invested more in body size growth (positive relationship) except for sardines from the Rich Summer/Rich Winter treatment where no significant effect was detected between these two traits (Tables S5). Results clearly highlighted that whichever the diet, sardines investing in their body condition invested less in their body size growth leading to negative relationships between these two traits (Figure 6, Table S6 to Table S7). Yet, this decrease varied in intensity depending on body condition at *t-1* for sardines of the Poor Summer/Rich Winter feeding treatment (Figure 6b, significant interaction, Table S7). It then appeared that the larger the body condition (*t-1*), the steeper the decrease in the growth rate (t) with the condition rate (t) (Figure 6b).

3.2.2. Trade-off or individual quality between growth, investment in body condition $_{\text{without gonad}}$ and reproduction

We then focused on the 120 individuals sacrificed at the end of the experiment to study possible trade-offs between investment in growth, body condition independently of the reproductive investment (condition rate$_{\text{without gonad}}$) and reproduction. As in the previous analysis, the treatment interaction was significant, so that a model was conducted for each feeding treatment. Generalized linear model suggested that neither energy investment in growth nor in body condition, constrained the reproductive investment in any of our experimental groups (Table S10 to S13). On the contrary, sardines from the Poor Summer/Poor Winter treatment displayed a positive relationship between growth and reproductive investment, suggesting that sardines who grew the most also developed the highest GSI (Tables S11). However this last result must be tempered considering the medium R^2 (R^2 = 0.41).

3.2.3. Energy allocation strategies

To investigate potential differences in energy allocation strategies among the 120 individuals sacrificed at the end of the winter, a clustering analysis on growth, condition rate$_{\text{without gonad}}$ and GSI was performed separately for both sex (in order to account the know effect of sex on GSI). Note that clustering analyses were performed on the 117 individuals for which we had information on sex. The best clustering scheme was with 2 clusters for males (Figure 7a) and 3 clusters for females (Figure 7b). The composition in feeding treatment as well as the size at the beginning of the experiment and the maturity of individuals (at the end of the experience) of each cluster was also assessed.

All four feeding treatments were represented in each cluster for both sex except in the third cluster for females where the Rich Summer/Rich Winter treatment was absent (Figure S10 and

562 S11). No clear maturity-related pattern was identified as only 6 sardines of the 120 sacrified at
563 the end of the experiment were immature. The distributions of initial lengths (measured in
564 August 2017, at the beginning of the experiment) did not display any significant difference
565 between clusters for both sex (Figure S16). For males, the first cluster (56% of individuals)
566 included sardines with an important investment in condition rate (1.4 times higher than in the
567 other cluster; LM, $P < 0.001$, Figure S12) at the detriment of growth rate and GSI. Individuals of
568 the second cluster (44%) are characterized by lowed condition rates, but invested more in the two
569 other traits, especially in GSI, *i.e.* displaying GSI between 2 times higher (7.7 ± 0.4 %) than the
570 first cluster (3.6 ± 0.4%, LM, $P< 0.001$, Figure S12). For females, groups 2 and 3 look quite
571 similar to those identified for males, i.e., a group (39% of the individuals) presenting an
572 important investment in body condition (1.4 times higher than the other cluster; LM, $P < 0.001$,
573 Figure S13) with moderate growth rate and GSI and a group (15% of fish) with low condition
574 rates but higher growth rate and especially GSI (being between 2 to 4 times higher than for the
575 first two clusters, Post-hoc HSD-Tukey, $P < 0.001$, Figure S13). The first cluster (46% of
576 individuals) included sardines favouring investment in growth rate with low GSI and body
577 condition rate, but differences were not significant with the other cluster $P> 0.05$, Figure S13).
578 Sardines appeared to favour one trait over another, in particular for females or even two traits for
579 the second and third cluster for males and females respectively.

580 Finally, no significant differences in antioxidant defence and oxidative damage between clusters
581 for male and female were found except for male where cluster 1 displayed 1.6 times higher
582 endogenous antioxidant SOD level than the second cluster (Kruskal test, $P < 0.05$, Figure S14
583 and S15).

584

4. Discussion

Life history trajectories reflect how animals manage the investment of available energy in competing traits like growth, reproduction and lifespan (McEwen & Wingfield 2003). While such trade-offs are the heart fitness optimization strategies in a given environment, understanding their intimate mechanistic links and plasticity may enable us to assess more precisely the present effects of global change. Our experimental study focuses on the energy allocation trade-offs in the north-western Mediterranean sardines, to shed light on possible mechanisms involved in the unusual decline in fish size and condition (Van Beveren et al. 2014a). Such changes are currently thought to derive from a bottom-up control, i.e., modification of either size and/or quantity of sardine preys (Brosset et al. 2016a, Saraux et al. 2019). Therefore, we investigated how resource temporal variability (in quantity and size) impacted their main life-history traits through a long-lasting experiment on 972 adult sardines. We focused on four questions:

(i) When feeding conditions improve, do sardines exhibit compensatory growth? (Mangel & Munch 2005);

(ii) How plastic are sardines in terms of reproductive investment? Are sardines strictly "capital-breeders" as usually considered (Ganias 2009)?

(iii) What are the costs in terms of maintenance of different energy allocation strategies (Metcalfe & Monaghan 2001, Mangel & Munch 2005)?

(iv) How can we explain inter-individual variability in these traits (reproduction, growth and somatic maintenance)? Do they display different energy allocation strategies

606 (Reid et al. 2010) or does it rely exclusively on individual quality and heredity
607 (Marchand & Boisclair 1998, Wilson & Nussey 2010, Bergeron et al. 2011b)?

608 ## 4.1. Compensatory growth

609 Although compensatory growth has been advocated for some fish (Ali et al. 2003), the present
610 study did not confirm such a process for the Mediterranean sardines, as individuals from the Poor
611 Summer/Rich Winter feeding treatment displayed slower growth rates than sardines fed in rich
612 conditions all along the experiment. Similarly to our results, gilthead seabream (*Sparus aurata*)
613 that were starved for 1 or 2 weeks showed no sign of compensatory growth during the following
614 8-weeks re-feeding period (Peres et al. 2011). Rather, when sardines went from poor to rich
615 conditions, they seem to use this new income of energy to rebuild their reserves by increasing
616 their body condition (Poor Summer/Rich Winter has the highest condition rate in winter).
617 Further, Rich Summer/Poor Winter sardines were the only ones to exhibit a decrease in body
618 condition during winter, confirming energy limitation during winter. However, their growth rates
619 remained higher than those of sardines fed poorly all along the experiment. Surprisingly, growth
620 rates of fish from Rich Summer/Poor Winter treatment appeared higher than those of fish from
621 Poor Summer/Rich Winter, suggesting the importance of a pre-acquired energy capital to derive
622 energy for growth. This is also supported by the fact that growth rates observed over a month
623 were positively correlated with the body condition at the beginning of that month. Still, when
624 comparing sardines with a same capital (i.e. Rich/Rich with Rich/Poor and Poor/Rich with
625 Poor/Poor), growth was still higher for sardines from rich feeding conditions than sardines fed in
626 poor conditions during winter, highlighting the additional importance of income energy
627 resources on growth. Altogether, our results indicate that an increase in energy resources might
628 be immediately allocated toward body condition, a fast-adjusted variable, while the effects of

feeding conditions on growth might be delayed over time as suggested by Peck et al. (2015) who highlighted preferential allocation of food energy to restore body mass in recently re-fed fish. This pattern further agrees with results found in the Gulf of Lions for anchovy and sardine, where both species showed a decrease in body condition before a decrease in growth (Van Beveren et al. 2014).

4.2. Plasticity in reproduction

Some processes, such as reproductive investment, seem to only take place after reaching a critical mass/size/body condition (Asher & Cox 2013). In the Mediterranean Sea, sardines are believed to reproduce in winter based on the energy capital they have built in the previous summer (Ganias 2009). In this study, we indeed confirmed the importance of such a capital, individuals from the rich treatment in summer displaying high GSI. However, such a statement need to be put into perspective since individuals from the same rich treatment in summer differed according to their winter feeding conditions (GSI in Rich/Rich being higher than GSI in Rich/Poor). Similarly, individuals from intermediate treatments (Rich/Poor and Poor/Rich) displayed similar reproductive investment (GSI), which is not in line with the vision of a strict "capital-breeder" usually attributed to the Mediterranean Sardine (Aldebert & Tournier 1971). Thus it appears that sardines reproductive behaviour could be more opportunistic than usually assessed without a defined underlying strategy. This was previously suggested by Nunes et al. (2011) for Atlantic sardine from the Portuguese coast and by Ganias (2009) for Atlantic sardine from the Earstern Mediterranean Sea. Similarly, Hunter & Leong (1981) showed for the northern anchovy, *Engraulis mordax*, another multiple spawning clupeid with indeterminate fecundity that almost 2/3 of reproductive expenditure might be financed from fat reserves accumulated during the preceding feeding season whilst the remaining 1/3 comes from direct feeding. We

652 suggest that this plasticity in the energy allocation in reproduction could help sardines to cope
653 with the recent warming trends. Indeed according to Sommer and Lengfellner (2008) climate
654 change seems to lead to weaker phytoplankton spring bloom and favor planktonic chains of
655 smaller size which would result in poorer feeding condition for sardines at the end of their
656 reproductive period. Moreover, the GSI was systematically higher for males than for females for
657 all feeding treatments at the end of their reproductive period. This difference between sexes has
658 also been reported for Atlantic sardine along the Moroccan coast (Amenzoui et al. 2006). The
659 reserve lipids showed similar pattern for males and females of the same feeding treatment,
660 suggesting the way in which energy was stored was the same for both sexes. Similarly, Caponio
661 et al. (2006) found no significant difference in lipid content between male and female Atlantic
662 sardine in the Ionian Sea.

663 ### 4.3. Cost in term of maintenance

664 We assessed the potential costs of maintenance, as a result of environmental constraints in
665 resource availability, using oxidative balance as integrative markers of metabolic costs. Plasma
666 oxidative state was relatively unaffected by the different feeding treatments. Individuals from the
667 treatment with rich feeding conditions in summer and winter presented the lowest oxidative
668 damage and antioxidant defences. This suggests that when feeding conditions were abundant,
669 sardines could preserve a balanced oxidative stress despite displaying high growth rates. On the
670 contrary, individuals facing poor feeding conditions during summer and/or winter displayed
671 higher levels of oxidative damages (d-ROMs and TBARS), suggesting that dietary restriction
672 during growth and/or reproduction ultimately led to physiological costs (Monaghan et al. 2009).
673 These results are in line with a recent study showing that sardines in poor condition optimize
674 mitochondrial coupling efficiency (consume less oxygen than sardine in rich feeding condition to

675 produce a given amount of ATP) which may result in an increase of ROS production (Thoral et
676 al. 2021). In addition, individuals poorly fed in both summer and winter had high concentrations
677 of antioxidant enzyme SOD at the end of the experiment, which suggests an attempt to
678 compensate for possible deficiencies in exogenous antioxidants by increasing the endogenous
679 (neo-synthetized) antioxidant capacity. These results are consistent with previous work on
680 gilthead seabream, which found significant increases in MDA levels (lipid peroxidation control)
681 and SOD activity (as well as other antioxidant enzymes) as a consequence of food restriction
682 (partial or total, Pascual et al. 2003).

683 Previous studies suggest that oxidative stress may cause physiological trade-offs with
684 reproduction, so that greater investment in reproduction may reduce the resources available for
685 basic maintenance costs (Ilmonen et al. 2000, Alonso-Alvarez et al. 2004). However, our results
686 indicated that individuals seemed to be able to remain at a physiological optimum regardless of
687 resource availability. Thus, the oxidative balance did not necessarily appear as a marker of cost,
688 but rather as a life-history constraint as suggested by Metcalfe and Alonso-Alvarez (2010) and
689 Stier et al. (2012). However, studies focusing on the associations between body size, energy
690 metabolism, oxidative stress and lifespan suggested that results of intra- and interspecific
691 comparisons are difficult to generalise, and highlight the complex links between these life history
692 traits (Speakman 2005).

693 ## 4.4. Individual quality

694 The PCA approach further highlighted a high degree of individual variability within each
695 treatment, in terms of metabolic costs (oxidative damage and antioxidant defences) and life
696 history traits (growth, condition and reproduction investment). Yet, this variability manifested
697 itself differently depending on the feeding treatment. SD of individual size from sardines of the

698 Rich Summer/Rich Winter treatment increased while the SD of their body condition decreased. It
699 appears that they tended towards a common (rather high and not limiting) body condition, but
700 that their structural growth varied greatly from one individual to another due to other factors,
701 such as individual quality (Wilson & Nussey 2010). Conversely, the SD in body condition of
702 individuals poorly fed in summer and winter tended to increase over time (and was higher than
703 the other 3 treatments), indicating that some individuals managed to accumulate more energy
704 reserves over the experiment than others. Nonetheless, the SD in size remained low for this
705 treatment, due to low to null growth. This suggests that when facing poor conditions, individuals
706 could hardly invest in structural growth, whatever their body conditions. Altogether, these results
707 tend to advocate for different individual qualities in the Mediterranean sardine population.
708 Theoretically, individual quality differences in a given environment can be explained by
709 variations in their capacity to acquire, efficiency in processing and using resources (Van
710 Noordwijk & De Jong 1986). Early-life experiences (which we did not control in this study) may
711 also explain differences between individuals. Indeed, it has been suggested that the early
712 environment can help shape a phenotype adapted to the conditions the organism is most likely to
713 experience in its adult environment (Costantini et al. 2012). Variability in fish growth is often
714 interpreted as a result of density-dependent process due to intra-specific competition for a limited
715 resource among individuals of similar age-classes (e.g. Lorenzen and Enberg 2002). Indeed, it is
716 often thought that larger individuals have an advantage over smaller individuals in competition
717 due to their higher swimming capacity and consumption capacity (Lundberg & Persson 1993).
718 This in return should also decrease their probability of being predated, hence the importance of
719 growing fast. Still, numerous other explanations can be proposed to explain differences in energy
720 acquisition: (i) the potential inter-individual competition is not only size-dependent, but also

721 linked with individual behavioural differences ("bolder" individuals may have better access to
722 food than "shy" ones, Réale et al. 2007) and (ii) for indeterminate growing animals, body
723 condition is of greater interest for individual fitness (*i.e.* enhancing the chances of individual
724 survival and/or future reproduction, Bêty et al. 2003). To distinguish between such hypotheses
725 would require further work, possibly through behavioural observations of individuals feeding.

726 Apart from quality, inter-individual differences can also be interpreted as different energy
727 allocation strategies. In particular, one of the hypotheses to characterise these differences
728 between individuals lies in the differences in the energy pool devoted to reproduction. Our GLM
729 outputs suggest that sardines invested in reproduction regardless of their investment in body
730 condition and growth. These results are in accordance with Brosset et al. (2016b) who
731 highlighted that fish can maintain high reproductive investment potentially at the cost of other
732 traits which might explain the present disappearance of old and large individuals in the Gulf of
733 Lions. This preferential allocation of energy to gonad maturation was also observed in Atlantic
734 herring in the Baltic Sea (Rajasilta et al., 2015). Furthermore, we observed between two and
735 three main energy allocation strategies at the individual level in this study depending on sex: (i)
736 favouring body condition displayed for both sexes (56% of males and 39% of females), (ii)
737 favouring growth only for female (46% of females) or (iii) investing in both reproduction and
738 growth for both sexes (44% of males and 15% of females). Our results from the cluster analysis
739 highlighted a trade-off between growth and reserve storage, which was also displayed by the
740 GLMM outputs (negative correlation between growth rate (t) and condition rate (t)). However,
741 some individuals (i.e. those of the second cluster for males and the third cluster for females) were
742 capable of investing in both growth and reproduction whatever the treatment indicating that
743 despite different food limitations, some individuals can maintain simultaneously growth and

744 reproduction independently of their initial size. In this study, temperature seemed to be the main
745 driver of this trade-off. At colder temperatures, sardines may invest in condition and
746 reproduction but not in growth, even if feeding availability increases. Moreover, costs in terms of
747 maintenance and oxidative balance were relatively unaffected between the different strategies.
748 This clearly tends to invalid the hypothesis of a compromise between these two traits at the
749 individual level, as this has already been stressed at the population level on a number of taxa (see
750 Cam et al. 2002, Hamel et al. 2009).

751 # 5. Conclusion

752 Our results highlighted the impact of the seasonal variations in food availability on growth,
753 individual energy reserves and reproduction. Food resources during the summer period had a
754 major effect on energy reserves and growth, thus limiting the maximum size and body condition
755 achieved at the end of winter. The negative effects of a summer food restriction were still visible
756 during winter. These effects, also known as carry-over effects, have been documented in many
757 species and play a major role in energy allocation trade-offs between growth, maintenance and
758 reproduction (Mangel and Munch 2005, Norris & Marra 2007). In addition, food restrictions
759 during growth and/or reproduction period resulted in physiological costs through increased
760 oxidative damage, which sardines attempt to compensate by an overexpression of endogenous
761 antioxidant defenses (SOD). As increasing temperature favors weaker planktonic bloom and
762 phytoplankton of smaller size climate change might actually accelerate and amplify such
763 phenomenon. Mediterranean sardines did not show any compensatory growth, did not appear to
764 be “capital breeders” *sensu stricto* and tended to display different individual qualities in their

765 physiological adaptations. As sardines can live over 7 years in the wild, assessing the long-term
766 costs on individual longevity and subsequent reproductive output remain to be established.

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Figures

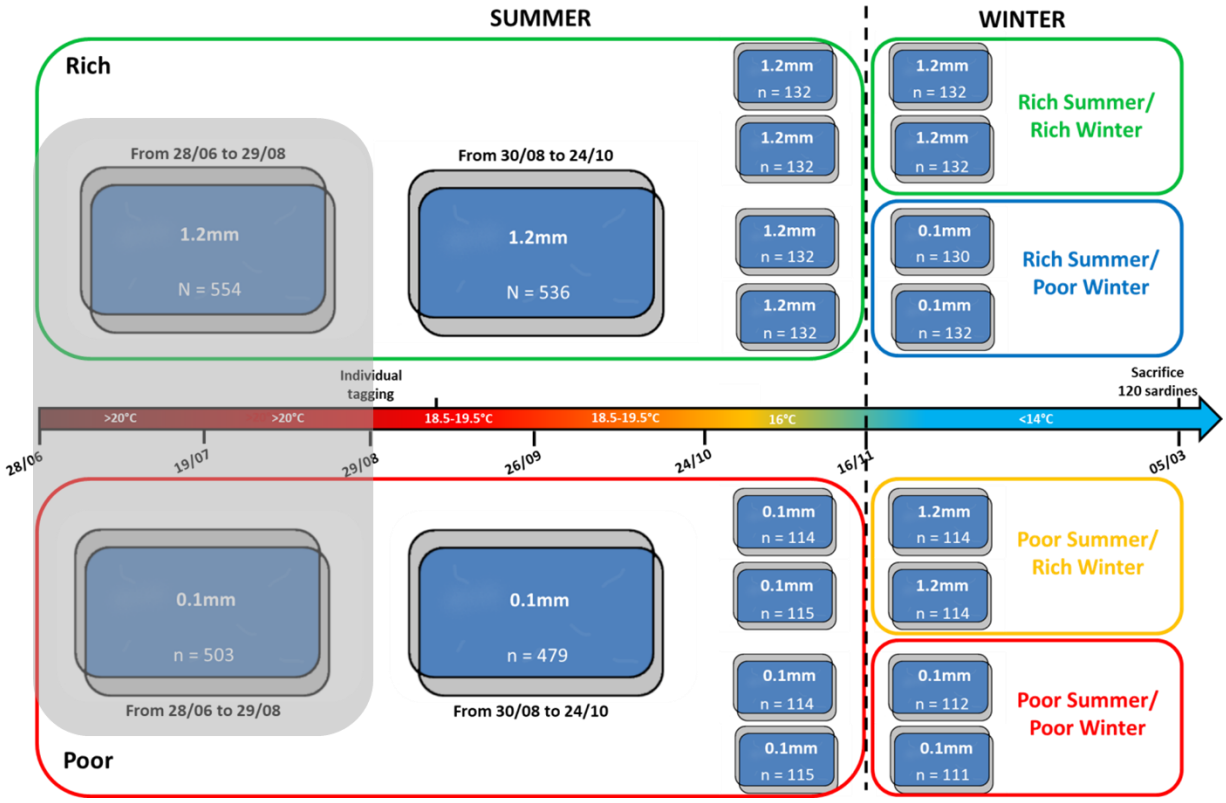


Figure 1: Design of the 8-month experiment. The experiment is divided into two periods separated by the dotted vertical line: summer for 4 and a half months with average to warm temperatures (from 16°C to over 20°C) and winter for 3 and a half months, corresponding to the breeding season of sardines (between 13°C and 14°C). First 2 tanks of 3 m^3, followed by 8 tanks of 0.3 m^3 were used. Pellet sizes (0.1 mm and 1.2 mm) and the quantity of food as a percentage of fish biomass (0.4% to 1.2%) are indicated for each tank. Individual tagging is indicated by the blue arrow on August 29, 2017, before which individual size and body condition could not be

monitored (greyed area). Temperature ranges are indicated for each time step. The end of the experiment and the sacrifice of the 120 individuals randomly sampled for the study of physiological conditions are indicated by the red arrow on March 5, 2018.

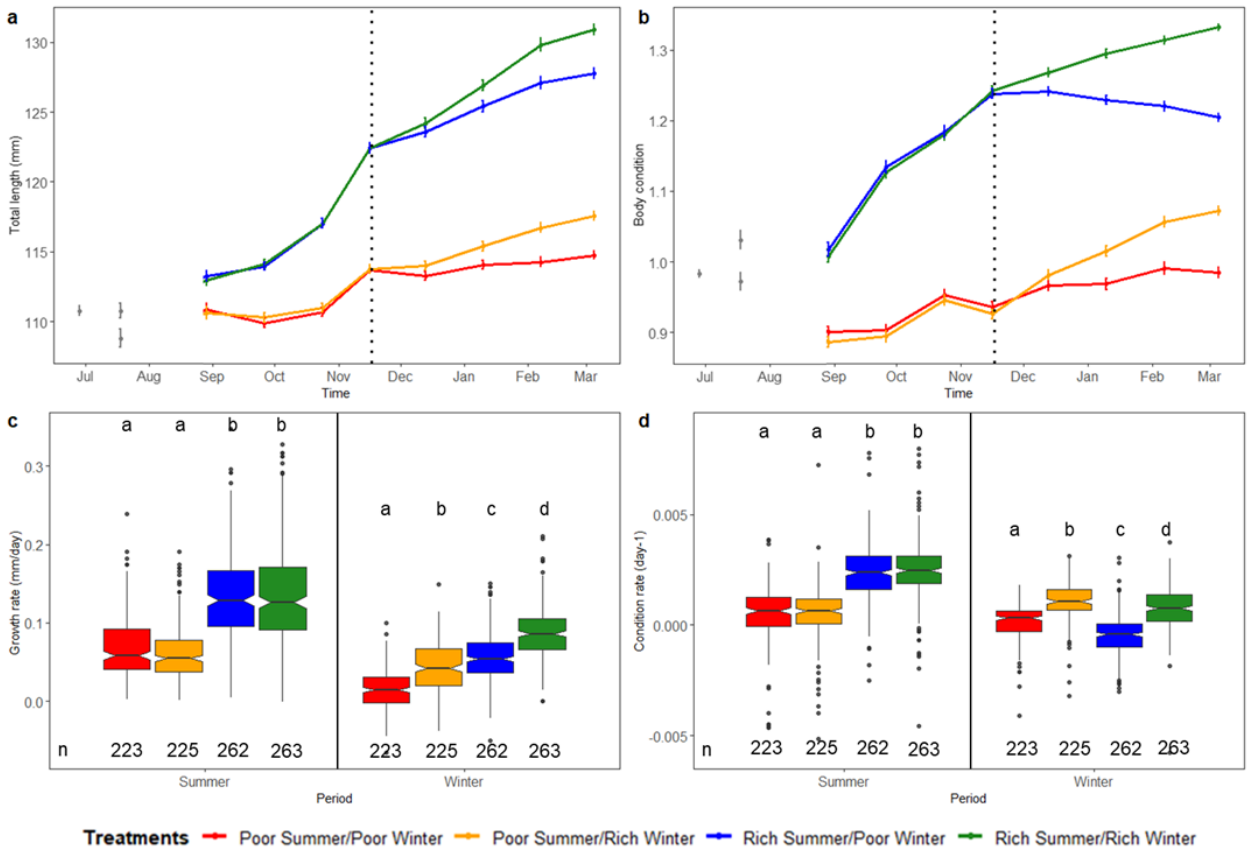


Figure 2: Time series of mean (± SE) total length (a) and body condition (b) per feeding treatment and boxplots of summer and winter growth rates (c) and condition rates (d) for the four treatments. Values in June and July based on a subsample are indicated in grey as individual monitoring started from August 29th, 2017. Sample size for each treatment is given below the boxes. Boxplot with different superscript letters are significantly different ($P < 0.05$). The outliers are represented by black dots.

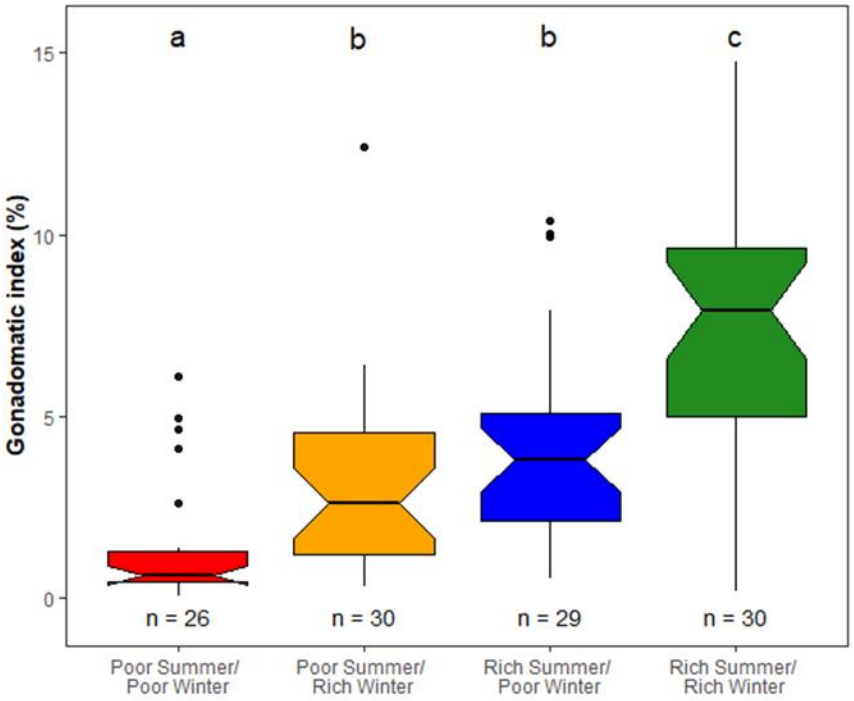


Figure 3: Gonadosomatic indices at the end of the experiment for each treatment. The sample size is indicated under each boxplot. Outliers are represented by black dots. Boxplots with different letters are significantly different ($P < 0.05$).

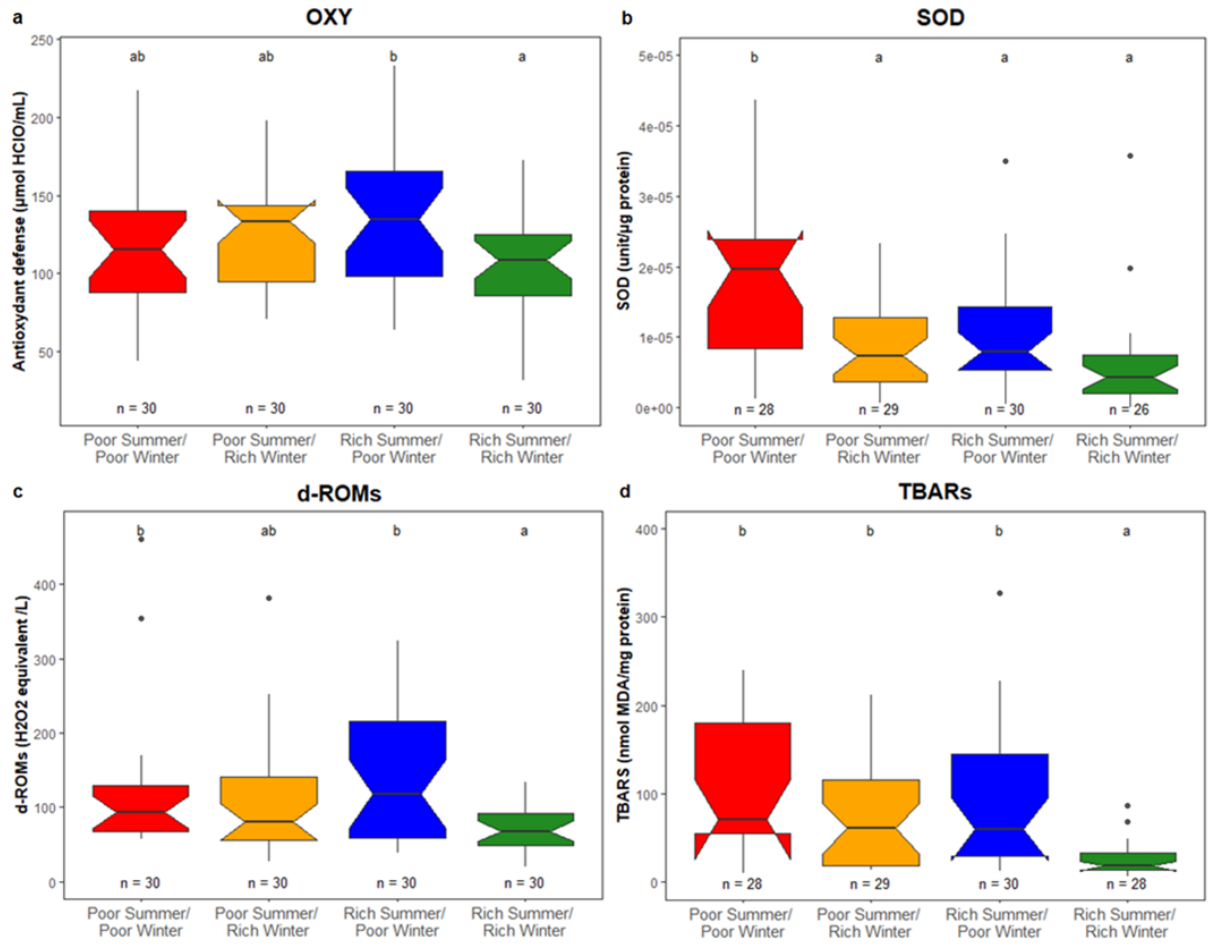
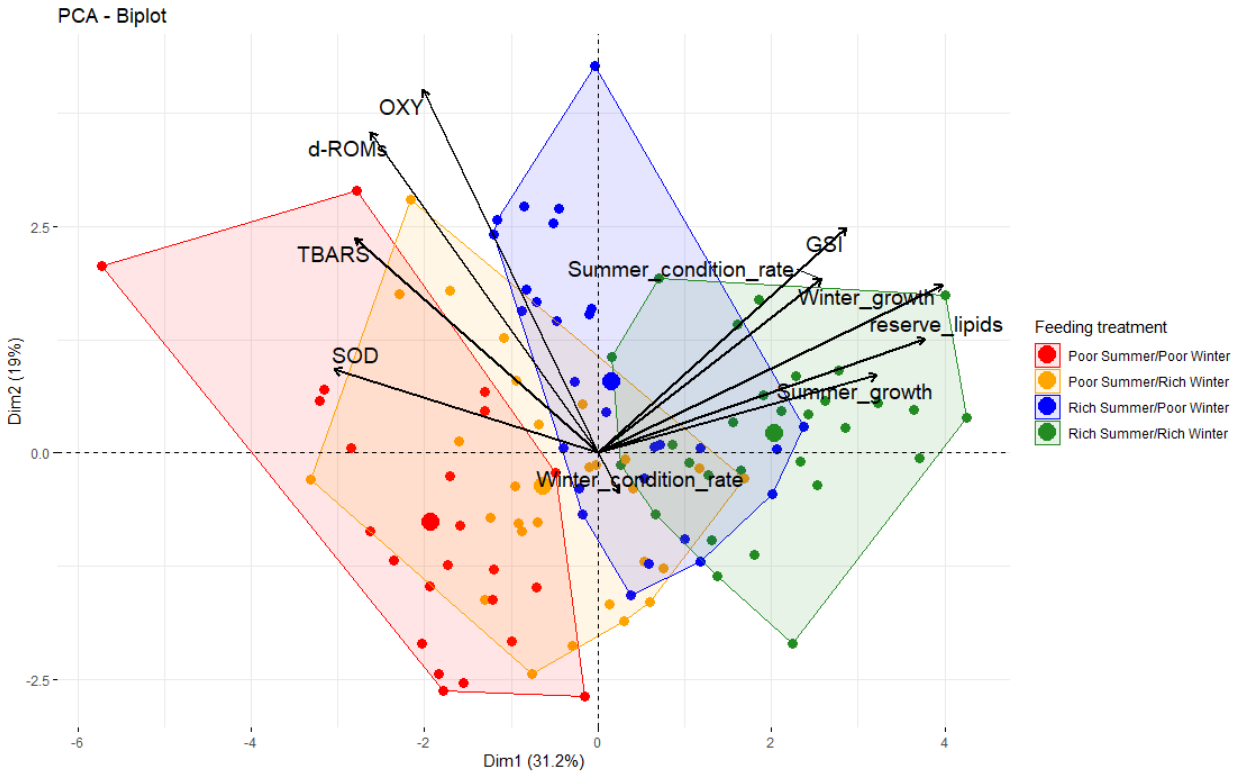


Figure 4: Boxplot of plasma concentrations of OXY (a), SOD (b), d-ROMs (c) and TBARS (d) for each treatment at the end of the experiment. The number of individuals is indicated under each boxplot. The outliers are represented by black dots. Treatments with different letters are significantly different ($P < 0.05$).



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1028 **Figure 5**: Biplot of the PCA built with summer and winter growth and condition rates,
1029 antioxidant defense (OXY and SOD), oxidative damage (TBARS and ROM), reserve lipids, and
1030 GSI. Each point represents an individual. The larger circles represent the barycenter of the
1031 individuals for a given treatment represented using minimum convex polygon. Note that
1032 structural lipids have not been included due to their very low variability.

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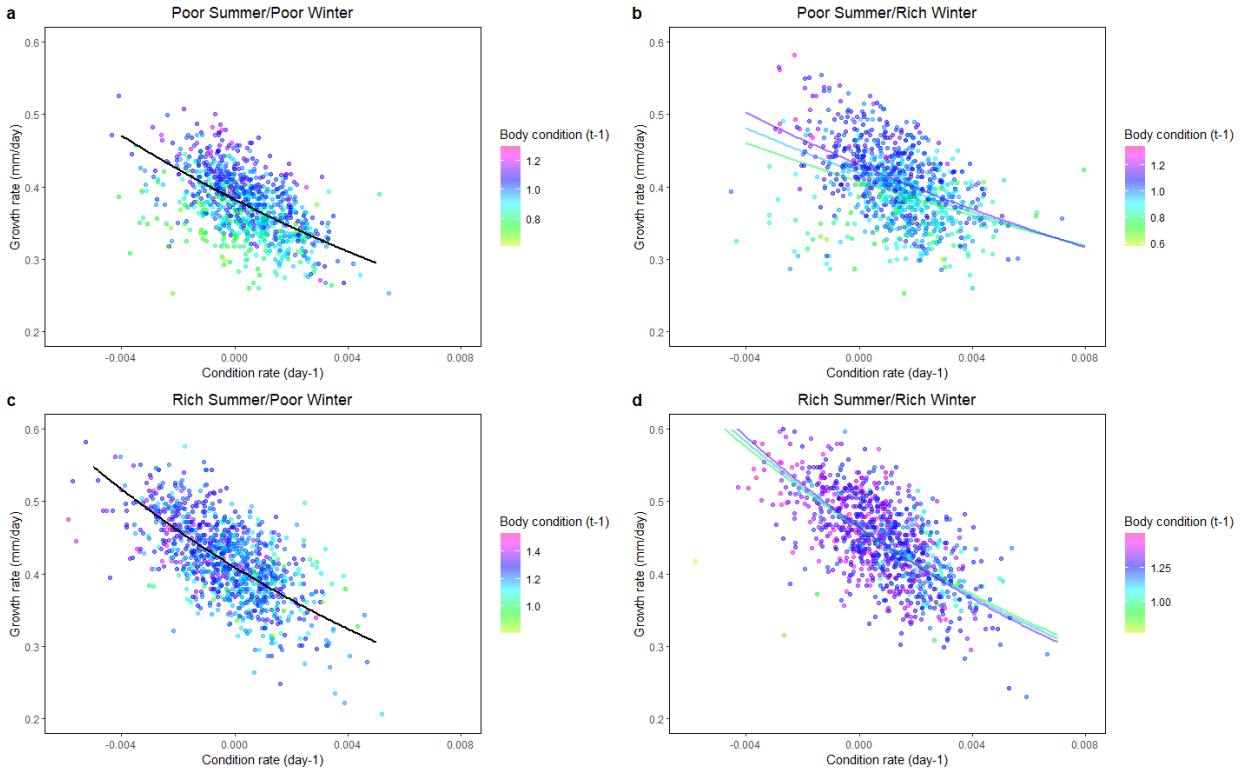

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1035 **Figure 6:** Relationship between growth and body condition rate for the four feeding treatments
1036 during winter only: Poor Summer/Poor Winter (a), Poor Summer/Rich Winter (b), Rich
1037 Summer/Poor Winter (c) and Rich Summer/Rich Winter (d). When the interaction between
1038 condition rate$_{t-1 \rightarrow t}$ and body condition$_{t-1}$ was significant we represented several prediction lines
1039 corresponding to the 25%, 50% and 75% quantile of the body condition$_{t-1}$. If the interaction is
1040 not significant, only one prediction line (black) is represented corresponding to the median body
1041 condition $_{t-1}$.

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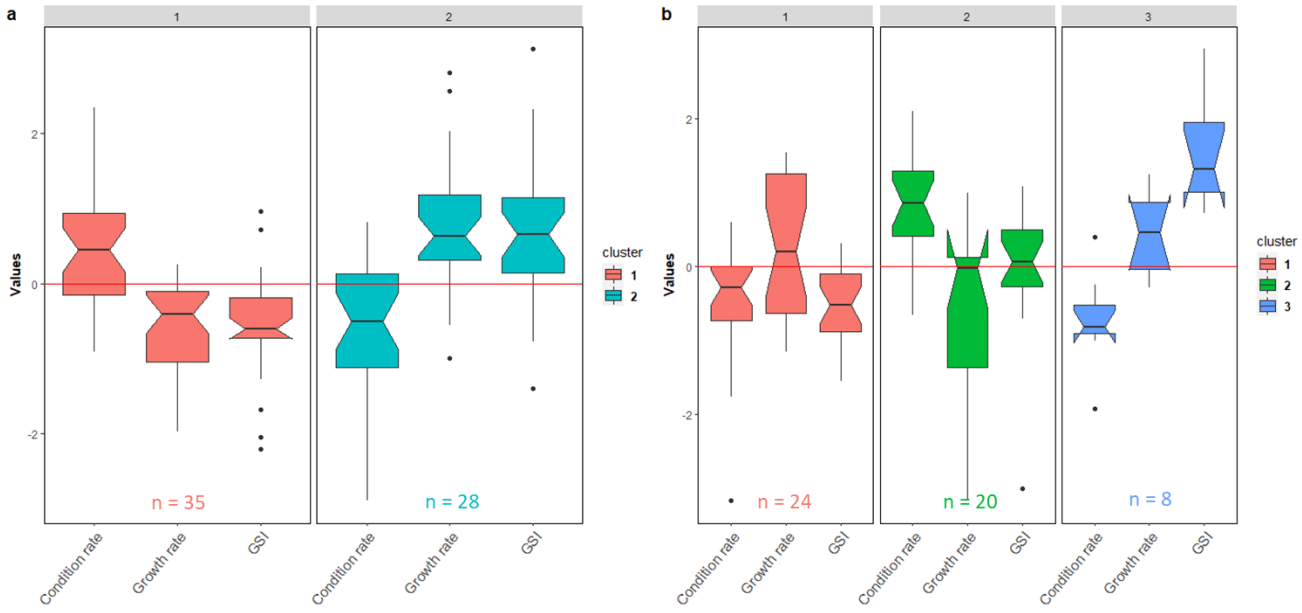

Figure 7: Boxplot of normalized values of body condition rate$_{\text{without gonad}}$, growth rate and GSI for each cluster for males (a) and females (b). The number of individuals is indicated under each boxplot. The outliers are represented by black dots.