
Fish shrinking, energy balance and climate change

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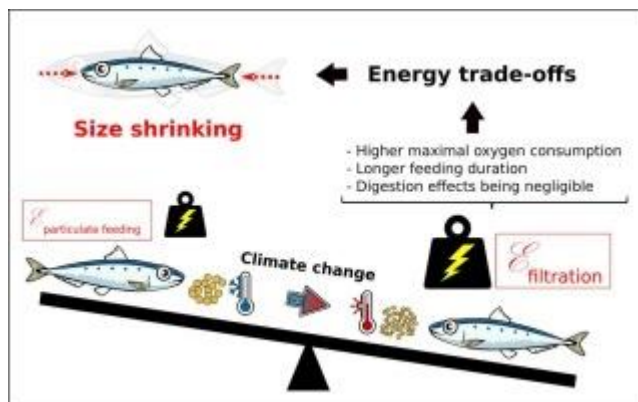
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Abstract :

A decline in size is increasingly recognised as a major response by ectothermic species to global warming. Mechanisms underlying this phenomenon are poorly understood but could include changes in energy balance of consumers, driven by declines in prey size coupled with increased energy demands due to warming. The sardine *Sardina pilchardus* is a prime example of animal shrinking, European populations of this planktivorous fish are undergoing profound decreases in body condition and adult size. This is apparently a bottom-up effect coincident with a shift towards increased reliance on smaller planktonic prey. We investigated the hypothesis that foraging on smaller prey would lead to increased rates of energy expenditure by sardines, and that such expenditures would be exacerbated by warming temperature. Using group respirometry we measured rates of energy expenditure indirectly, as oxygen uptake, by captive adult sardines offered food of two different sizes (0.2 or 1.2 mm items) when acclimated to two temperatures (16 °C or 21 °C). Energy expenditure during feeding on small items was tripled at 16 °C and doubled at 21 °C compared to large items, linked to a change in foraging mode between filter feeding on small or direct capture of large. This caused daily energy expenditure to increase by ~10 % at 16 °C and ~40 % at 21 °C on small items, compared to large items at 16 °C. These results support that declines in prey size coupled with warming could influence energy allocation towards life-history traits in wild populations. This bottom-up effect could partially explain the shrinking and declining condition of many small pelagic fish populations and may be contributing to the shrinking of other fish species throughout the marine food web. Understanding how declines in prey size can couple with warming to affect consumers is a crucial element of projecting the consequences for marine fauna of ongoing anthropogenic global change.

Graphical abstract



Highlights

► Size decline in fish may be a universal response to global change. ► Global change can disturb energy balance of consumers feeding at low trophic levels. ► Prey shrinking raised the energetic costs of feeding and daily energy expenditure. ► Warmer waters with smaller prey dramatically increase energy expenditure.

Keywords : size decline, energy expenditure, feeding behaviour, temperature, small pelagic fish, respirometry, experiments

1. Introduction

Ongoing global warming constitutes a major threat for biodiversity, especially in marine ecosystems, with some scenarios of future temperature increases reaching +5°C in 2100 (IPCC, 2013, 2014; Orr et al., 2005). For ectotherms such as fishes, warming results in large increases in their physiological rates (Clarke & Fraser, 2004; Seebacher et al., 2015). While ongoing global warming might therefore be expected to boost growth rates in ectotherms (Morrongiello et al., 2019; Seebacher et al., 2015), it has in fact been correlated with a progressive decline in adult body size of many fish species in the wild (e.g. in Baudron et al., 2014; Gardner et al., 2011; Sheridan & Bickford, 2011, but see Audzijonyte et al., 2020). The factors that contribute to this shrinking of fishes are poorly understood; it is coherent with how warming might affect macroecological phenomena such as Bergmann's rule and James' rule, and is associated with a significantly higher proportion of younger age classes and a generalised decline in individual size-at-age in populations (Daufresne et al., 2009). Shrinking of fishes may also be linked to the Temperature-Size rule (TSR), the phenomenon whereby warm temperatures cause more rapid early growth of ectotherms but a decline in their final adult size, when compared to conspecifics reared in a cooler regime (Atkinson, 1994). The mechanisms involved in the TSR remain to be elucidated, it is observed in wild populations but can also be reproduced under controlled conditions in the laboratory (Forster et al., 2012; Horne et al., 2015).

Although there has been recent theoretical focus on whether the TSR relates to respiratory physiology (Verberk et al., 2021), early work focussed upon whether changes in energy budget and allocation may be a major driver of fish shrinking with warming (Gardner et al., 2011; Pauly et al., 2010). The availability and quality of food resources can affect individual growth rates and adult body size through energy trade-offs among growth, survival and reproduction (Stearns, 1989, 1992), and such effects may be exacerbated if energy requirements are increased by warming. That is, it is unlikely that temperature per se is the only variable involved in the size decline in wild populations, since few exceptions to this rule are spreading across years, in particular studies that investigated food resources as a driver explaining the TSR (e.g. in Diamond & Kingsolver, 2010; Lee et al., 2015; Ljungström et al., 2020; Millien et al., 2006).

Temperature and food resources are both environmental variables whose variations can challenge an individual's energy balance and that can drive fish life-history traits through physiological processes. Thus, while the higher physiological rates due to warming cause an increase in energy demands, energy availability for marine fishes is predicted to decline due to climatic stressors that affect primary production and marine animal biomass (Ariza et al., 2022; Bopp et al., 2005; Daufresne et al., 2009; Lotze et al., 2019). Ocean warming can amplify vertical stratification and limit nutrient mixing (Roemmich & McGowan, 1995) which causes declines in plankton abundance at the base of the food web and leads to communities dominated by smaller-sized species and individuals (Bopp et al., 2005, 2013; Daufresne et al., 2009; Richardson & Schoeman, 2004; Ward et al., 2012).

The first impacts of such changes at low trophic levels could be observed on planktivorous species, such as small pelagic fishes (e.g. Brosset et al., 2017; van Beveren et al., 2014).

These species represent about 25 % of worldwide fishery landings by weight (FAO, 2018), supporting the economy of several countries (Alheit et al., 2009; Fréon et al., 2005). Fluctuations of their populations can have critical economic and social consequences, as observed following the collapse of the Peruvian anchovy in the early 1970s (Alheit et al., 2009; Allison et al., 2009; Schwartzlose et al., 1999). Population fluctuations of small pelagics are being exacerbated by ongoing global change (Brochier et al., 2013; Shannon et al., 2009), so these species represent key models to evaluate energetic mechanisms underlying shrinking of adult fish size.

In fact, small pelagic planktivorous fishes in the Mediterranean Sea are a major example of shrinking (Albo-Puigserver et al., 2021; Brosset et al., 2017). There is an ongoing and profound decrease in individual body size and condition of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*), which appears to be a consequence of bottom-up control mediated by changes in plankton composition and abundance (Brosset et al., 2016; Saraux et al., 2019). This was associated with a major regime change in the mid-2000s, with shifts of nutrient inputs, water mixing and plankton production (Feuilloley et al., 2020). Since 2008, these species' diet was shifted progressively from large prey (> 1 mm, especially cladocerans) to increased reliance on smaller prey (< 1 mm, especially copepods), which indicates changes in the plankton community towards smaller species (Brosset et al., 2016). Smaller zooplankton can be less nutritious (Zarubin et al., 2014), so a decline in zooplankton size could entrain a decrease in rates of energy acquisition by their predators. Identifying a clear mechanistic link between a decrease in plankton size and fish growth, and ultimately population dynamics, is crucial since fish shrinking is spreading to new ecosystems and species (see Bensebaini et al., 2022; Véron et al., 2020).

Challenges to energy balance when prey become smaller could be further exacerbated in fishes if prey size also influences foraging behaviour. Here, the sardine is also an interesting model species. Sardines spontaneously modify their feeding behaviour according to the size of their prey, using diffuse filter-feeding when prey is small but direct capture when prey is large (Garrido et al., 2007, 2008). A recent long-term experiment on captive sardines showed that, for the same food ration, a reduction in food size could significantly impair growth and body condition (Queiros et al., 2019). Sardines filter feeding on small particles had to consume twice as much as those capturing large particles to achieve the same growth and body condition (Queiros et al., 2019). We suspected that the two foraging modes had different energetic costs for the same degree of resource acquisition, with costs being higher for sustained aerobic swimming during filter-feeding compared to brief bursts of swimming to capture prey (Costalago & Palomera, 2014; Queiros et al., 2019). At the same time, food availability could be highly significant in the wild, filtration could be effective in very rich areas such as upwellings whereas particulate feeding might be more advantageous in areas with lower prey density (Costalago et al., 2015).

The current study focused on this complex predator-prey interaction in a captive population of adult sardines. We investigated the hypothesis that foraging on smaller prey would lead to increased rates of energy expenditure by sardines, and that these energy requirements would be exacerbated with warming temperature. To assess the energetic consequences of feeding sardines on prey of different sizes and at different abundances, we used group respirometry to measure rates of oxygen uptake and provided prey as commercial pellets of two different sizes at a range of ration levels. We compared animals acclimated to two temperatures within the species' thermal range, either a cool 16°C or warm 21°C. Thus, the

effects on oxygen consumption of particle size and temperature were investigated according to 5 scenarios: (1) change from large to small particles at cool temperature; (2) change from large to small particles at warm temperature; (3) rise in temperature with fish fed on large particles; (4) rise in temperature with fish fed on small particles, and (5) change from large to small particles while also increasing temperature. To that end, we focussed on overall daily energetic costs but also a careful comparison of energetic costs incurred during and after feeding for each scenario.

2. Material and methods

2.1. Animal capture and husbandry

Sardines were captured by commercial purse-seiner and transferred to the IFREMER Palavas-les-Flots research station, with the same fishing and husbandry procedures as described in Queiros et al. (2019). Over the first week, sardines were acclimated to tanks and weaned onto commercial aquaculture pellets. They were fed with a mixture of *Artemia nauplii* and commercial aquaculture pellets (mix of 0.2 and 1.2 mm diameter), with increasing proportions of pellets and decreasing proportions of *Artemia* throughout the week, concluding exclusively with pellets. After 2-3 weeks, sardines were transferred into indoor 1m³ holding tanks, until experimentation. Water temperature was not set during this period but followed natural fluctuations from 15 to 20°C (SST at the time of capture was 14°C).

2.2. Experimental design

Eighty sardines were distributed among 8 experimental tanks in groups of 10 animals (volume 50 L), to ensure similar distributions of body mass and condition among tanks (Fig. S1), and fish densities comparable to those of Queiros et al. (2019). Fish were acclimated to the new tanks while temperature was gradually changed from 19°C to either 16°C or 21°C over one week. Before the experiments began, fish were fed with commercial pellets twice a day, a mix of 0.2 and 1.2 mm to avoid preference bias for pellet size. These eighty sardines were used for both experiments 1 and 2, described below, and these two experiments were performed sequentially in the same setup.

The tanks were modified to function as open automated respirometers (McKenzie et al., 2007, 2012; Queiros et al., 2021) using the principles of cyclical intermittent stopped flow (Steffensen, 1989), as described below. Four tanks were held at each of the two temperatures, each set of four was supplied by water from a single reservoir where water temperature was regulated by an Ice 3000 (Aquavie) at 16°C or by a Red Line heater (Zodiac) at 21°C. Water in the reservoir was vigorously aerated, to maintain oxygen saturation and ensure thorough mixing. Water was delivered to tank respirometers by submersible pumps (Eheim 3400); within each respirometer the water was also gently but thoroughly mixed by a submersible pump (Nawa Maxi 500) to avoid any thermal or oxygen gradients (see Supplementary Material and Fig. S2).

All respirometers were exposed to a 12L:12D photoperiod (L: light, D: darkness) with a natural sunlight spectrum and 30 minute progressive dawns and sunsets. Individual total length and body mass was measured every two weeks under anaesthesia (140 mg L⁻¹ benzocaine). To estimate total tank biomass each day, body mass gain (or loss) was assumed to be linear between successive bi-weekly measures. Total biomass was then used to adjust

rations and to calculate oxygen consumption. No mortality was observed during the experiments.

2.3. Protocols

2.3.1. *Experiment 1: Effects of prey size, prey abundance and temperature on daily energy expenditure.*

To investigate effects of prey size, we offered sardines one of two commercial pellets that had similar composition in terms of lipids and proteins but differed in size, being either 0.2 mm or 1.2 mm in diameter, for a period of six weeks. These sizes fall within the natural range of sardine prey (Nikolioudakis et al., 2012), but elicit two markedly different foraging modes, being either filtering on 0.2 mm pellets or particulate capture of 1.2 mm pellets (Queiros et al., 2019). Eight prey abundances were studied, as pellet rations ranging from 0.1 to 1.8 % of the total fish mass per tank: 0.1%, 0.2%, 0.3%, 0.4%, 0.6%, 1.0%, 1.4%, 1.8%. The combination of two sizes and eight rations resulted in 16 feeding treatments for each of the 2 temperatures (Figure 1). Sardines were fed once a day at 09:00 in the morning. Daily feeding treatment for a tank was randomly assigned but comprised 2 replicates of each feeding treatment per tank over the entire experiment (i.e. 8 replicates per feeding treatment x temperature).

The cyclical measures of oxygen uptake rate (MO_2 in $mg\ kg^{-1}\ h^{-1}$) provided an indirect estimate of metabolic rate and, therefore, energy use, while the sardines fed, digested and exhibited diurnal patterns of spontaneous activity. Methodological details are provided below. A continual cycle of 15 min stopped flow to measure MO_2 alternated with 15 min flush with aerated water was used, except at feeding when flow was stopped for 30 min (at rations of 0.1%, 0.2%, 0.3% and 0.4%) or 60 min (at rations of 0.6%, 1.0%, 1.4% and 1.8%), to

ensure the entire ration was consumed before flushing. Food was distributed 5 minutes after flow was stopped, when water level had stabilized in all respirometers.

Bias due to behavioural responses to the act of feeding (e.g. anticipation caused by human presence near tanks at the typical feeding time) was controlled for by sham-feeding events, where the typical feeding gestures were performed but no food was provided. These shams were performed twice a day (9:00 am and 2:00 pm) for 2 days in all tanks, in the middle and at the end of experiment 1.

2.3.2. Experiment 2: Effects of prey size, prey abundance and temperature on features of foraging behaviour.

In this experiment we studied features of the foraging modes, filtration or particulate capture, in more detail, considering duration and maximum intensity (Figure 1). To this end, sardines were fed twice a day (9:00 am and 2:00 pm) for 3 weeks with 8 treatments: one of two food sizes (0.2 and 1.2 mm) at four rations (0.1, 0.2, 0.3 and 0.4% of tank biomass). The combination of two sizes and four rations resulted in 8 feeding treatments for each of the 2 temperatures (16°C and 21°C). Based on the results of Experiment 1, rations were chosen not to cause satiety. Similar to Experiment 1, MO₂ was measured throughout and for 30 min during feeding (food distributed after 5 min). Combining these data with those of Experiment 1 (Fig. S3), we obtained a total of 24 replicates per feeding treatment x temperature for food rations between 0.1% and 0.4%. Any bias due to behavioural responses to the act of feeding were assessed by two sham events, as described above.

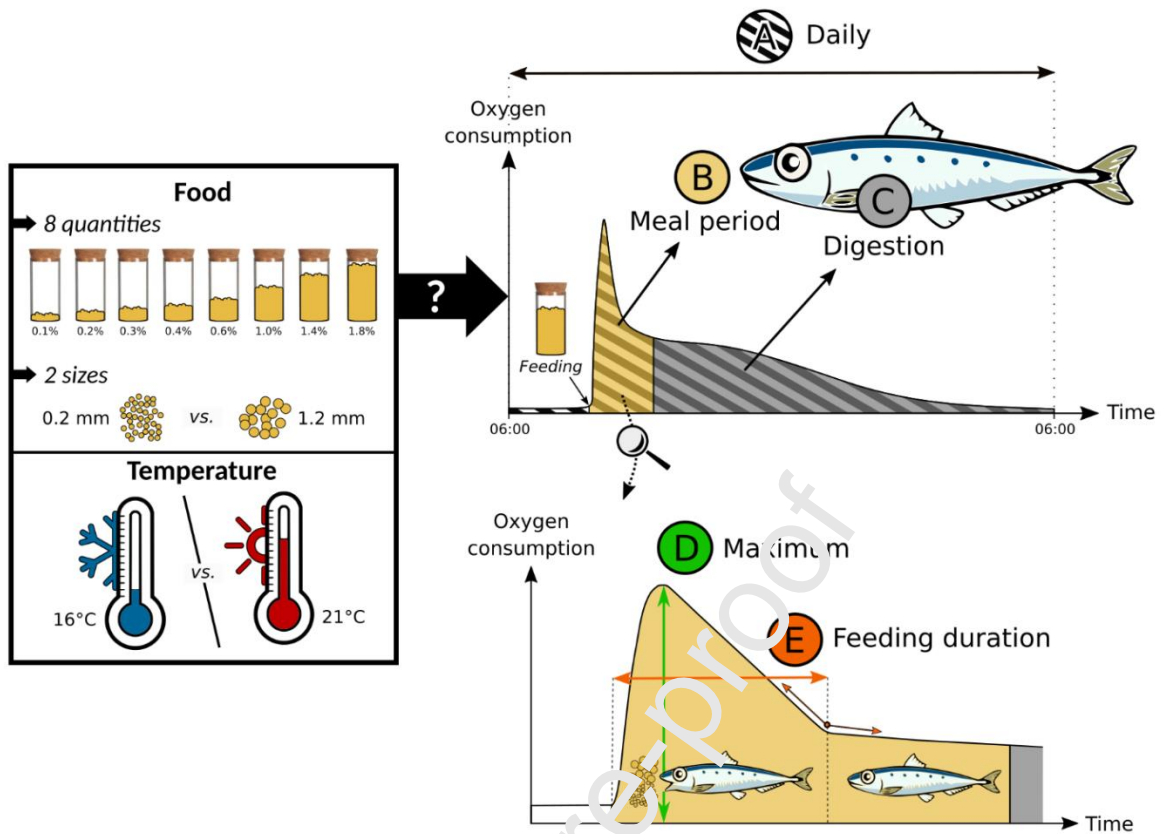


Figure 1: Conceptual framework of the two experiments on cocktail effects of food size (0.2 and 1.2 mm), food ratios (between 0.1% and 1.8% of the total biomass in tank) and temperature (16°C and 21°C) on energy expenditure of sardines (daily [A], during the meal period [B], during digestion [C], on the maximal intensity during feeding [D]) and on the duration of the feeding activity [E].

2.4. Respirometry

Water oxygen levels were recorded every 5 seconds in the tank respirometers, with an O₂ optode (Oxy-10 mini; PreSens Precision Sensing GmbH, /www.presens.de) and associated software (Pre-Sens Oxy 4v2). Water O₂ saturation never fell below 70% during the 15 min of stopped flow and never below 60% after feeding. Saturation was rapidly restored when the tanks were flushed with a flow of aerated water from the reservoir.

Oxygen uptake by the sardines caused a linear decline in water O₂ concentration over time during each stopped flow phase ('closed phase'). The MO₂ was calculated in mg O₂ kg⁻¹ h⁻¹, using least-square regression of the slope, considering oxygen solubility at the appropriate temperature (measured continuously) and salinity (measured daily); tank volume (50 L), and fish biomass (McKenzie et al., 2007). Only slopes with $R^2 \geq 0.95$ were kept for further analyses (<5% of slopes were removed from analyses). Gas exchange across the water surface being negligible, no correction was applied when estimating sardine oxygen consumption (McKenzie et al., 2007; Queiros et al., 2021).

2.5. Respirometry data analyses

2.5.1. Basal and daily oxygen consumption

Basal O₂ uptake rate of day_i was expressed as the lowest 15%-quantile (Chabot et al., 2016a) of the daily O₂ consumption of the previous day (from 06:00 a.m. day_{i-1} to 06:00 a.m. day_i). This rate of oxygen uptake was then used as a baseline for calculating daily oxygen consumption on day_i, expressed in mg O₂ kg⁻¹ d⁻¹, as an increase from this basal rate. This normalisation avoided bias linked to a change in fish biomass during experiments, short-term effects of a previous meal, or a small change in temperature, salinity, minor human disturbance, etc. Daily MO₂ was calculated as the area under the curve (AUC) of MO₂ over time, from 06:00 a.m. and for 24 hours (Figure 1, point A) using the 'DescTools' package in R (Andri Signorell 2021). The AUC was calculated over two periods: (i) raw data from 06:00 a.m. until noon, to catch the peak of oxygen consumption observed during the meal period and (ii) smoothed values of the oxygen consumption after 12:00 a.m. (oxygen consumption smoothed using *lowess* function) to avoid outliers due to, for example, minor disturbance in the room, that might distort daily estimations (Fig. S3).

2.5.2. Oxygen consumption during feeding

When focusing on effects of a meal on MO_2 , these were calculated relative to a control baseline that was estimated as the mean of the preceding 2.5 hours. This was done to avoid bias when either lights were turned on 1.5 hour before the 1st daily meal, or there were remnant effects of digestion of that 1st meal for the 2nd meal period. Since it took up to 2 minutes to feed all tanks (i.e. between 5 and 7 minutes after the beginning of the closed phase), we first needed to establish the start of the feeding event for each tank. To do so, we identified a break in the rate of oxygen decline in the water during the initial minutes of the 'closed phase', using the 'segmented' package (Mugge, 2008). Once this was identified, oxygen consumption was calculated, in $mg\ O_2\ kg^{-1}\ h^{-1}$, as the linear decline of oxygen concentration from there until 2 min before the end of the 'closed phase' (Figure 1, point B).

2.5.3. Oxygen consumption during digestion

The start of the digestion period was considered to begin 90 min after the start of the meal period, this being the maximal duration of the feeding and then flush periods across the different rations. Thus, with feeding at 09:00, the oxygen consumption during digestion was calculated, in $mg\ O_2\ kg^{-1}\ d^{-1}$, as the AUC of the oxygen consumption over time between 10:30 a.m. of day_i and 06:00 a.m. of day_{i+1} (Figure 1, point C). This oxygen consumption was expressed as an increase from the basal O_2 uptake of day_i as estimated above.

2.5.4. Maximal oxygen consumption during feeding

To reveal dynamics of metabolic rate after feeding (Fig. S5), MO_2 was estimated as a moving average at 30 second intervals during the closed feeding period, using linear regressions over 1 minute on smoothed data for 12 measures of tank oxygen concentration. This

revealed the maximum oxygen consumption, in $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, achieved during each meal period (Figure 1, point D).

2.5.5. Duration of the feeding period

To estimate feeding duration, in minutes, we identified the end of the meal as the breakpoint when oxygen concentration stopped decreasing severely after feeding, taken to indicate the end of feeding-related activity (Figure 1, point E). That is, a broken-line regression was performed on oxygen consumption values calculated every 30 seconds (also every 30 seconds over 1 minute), starting at the peak of oxygen consumption as estimated above.

2.6. Statistical analyses

Effects of food rations, prey (particle) size and temperature, on oxygen consumption and feeding duration, were assessed using linear mixed-effects models. We built a series of models including three fixed effects (food size, food ration and temperature), as well as their interactions. Because of variability among tanks within each food ration x food size x temperature treatment, we also introduced a random tank intercept effect. The best-fitting model was selected based on the lowest AIC_c values (Burnham and Anderson, 2002) following Zuur et al. (2009). When the difference between these models in AIC_c (ΔAIC_c) was lower than two, the most parsimonious model was selected (Burnham and Anderson, 2002). Food ration was log-transformed for models of MO_2 during feeding and maximal MO_2 during feeding. Then, food ration was second order polynomial transformed to model feeding activity.

Finally, the effects of prey (particle) size and temperature on oxygen consumption were investigated according to 5 scenarios: (1) a change from large to small particles at cool

temperature; (2) a change from large to small particles at warm temperature; (3) a rise in temperature with fish fed on large particles; (4) a rise in temperature with fish fed on small particles, and (5) a change from large to small particles while also increasing temperature (see arrows in Figure 2). As such effects also depend on the food ration when the interaction with food ration was significant, we performed pairwise comparison to test significance of scenarios using selected best-fitting models as previously described. Results of scenarios over food ration are expressed as absolute and relative increases. Results are indicated as mean [95% CI]. Upper and lower 95% CI values of relative differences over food ration were calculated following Kohavi et al. (2009).

All data analyses were performed under R (R Core Team, 2020) and linear mixed-effects models were built using the 'lme4' package (Bates et al. 2015). All statistical tests were considered significant at p-values < 0.05.

3. Results

When fasted, MO₂ was low and statistically similar throughout the day (black curve in Figure 2). When sardines were fed, MO₂ peaked during the feeding period after 09:00, then decreased for the rest of the day for all feeding treatments and both temperatures. Oxygen consumption increased with food ration and rearing temperature but, during feeding at both temperatures, MO₂ was higher when feeding on the small particles (Figure 2).

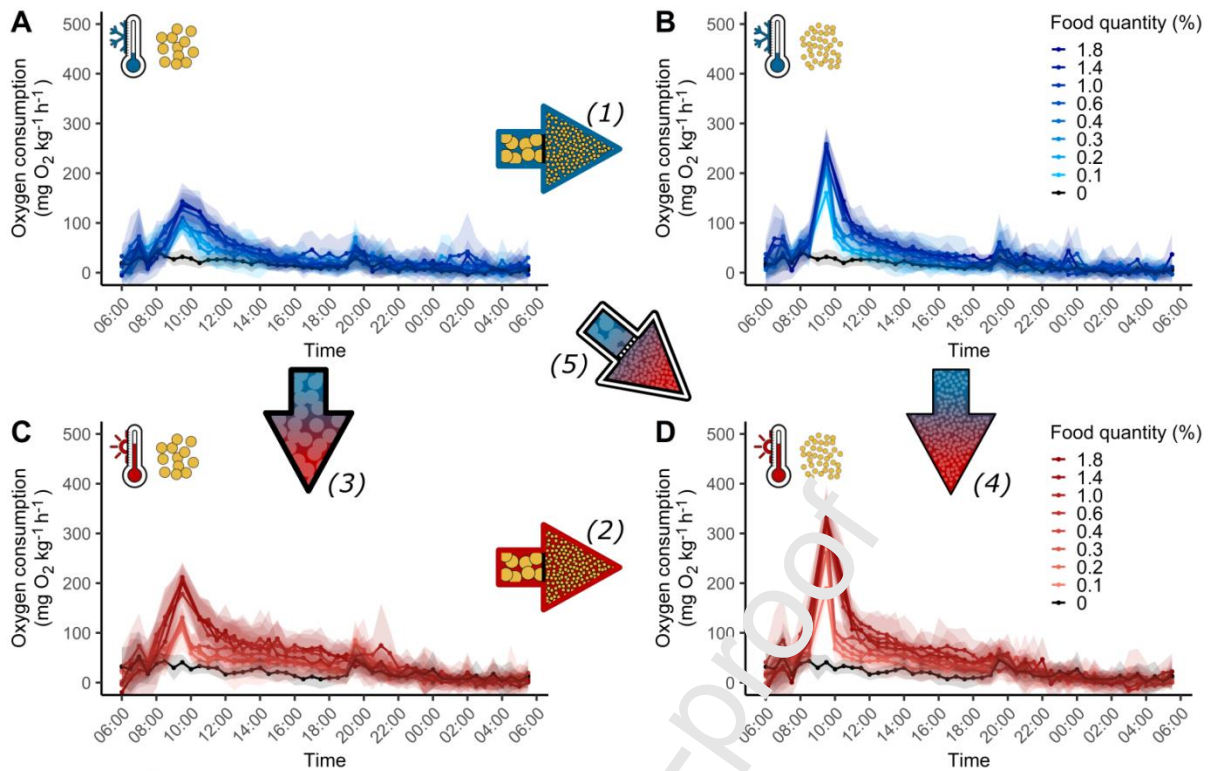


Figure 2: Median oxygen consumption over time according to food ration for the 4 experimental treatments: cool temperature and large particles (A), cool temperature and small particles (B), warm temperature and large particles (C) warm temperature and small particles (D). Black lines are for days of fasting, blue and red represent cool (16°C) and warm (21°C) temperatures, respectively. Darker lines represent higher rations of food. Arrows represent the 5 scenarios for which oxygen consumption were compared: (1) change from large particles to small particles at cool temperature; (2) change from large particles to small particles at warm temperature; (3) rise in temperature for fish fed on large particles; (4) rise in temperature for fish fed on small particles, and (5) change from large particles to small particles while also increasing temperature.

3.1. Daily oxygen consumption

During fasting days, median daily MO₂ (i.e. the AUC relative to basal daily oxygen consumption) was the lowest, demonstrating the clear effects that feeding and/or digestion exerted on daily energy expenditure (Figure 2, Fig. S6).

The best linear mixed-effect model included double interactions between food ration and food size and between food ration and temperature (Tables S1 and S2, Fig. S6, S7). An increase in ration consistently caused a significant increase in daily oxygen consumption when considering either food size or temperature. When considering only food size effects, slopes were significantly different ($p < 0.001$) and the increase was smaller for large particles (slope [95% CI]; 420 [324;515] mg of O₂ kg⁻¹ d⁻¹) than for small particles (714 [618;810] mg of O₂/kg/d, graph *Daily* in Figure 3, Table S3).

When comparing large to small particles over all food rations, scenarios (1) and (2) were not significant since food size x temperature interaction was not retained during model selection. Daily MO₂ exhibited a mean [95% CI] relative increase of 13 [1;37]% for small particles at 16°C, while this increase was 10 [3;22]% at 21°C (graph *Daily* in Figure 3, Table 1).

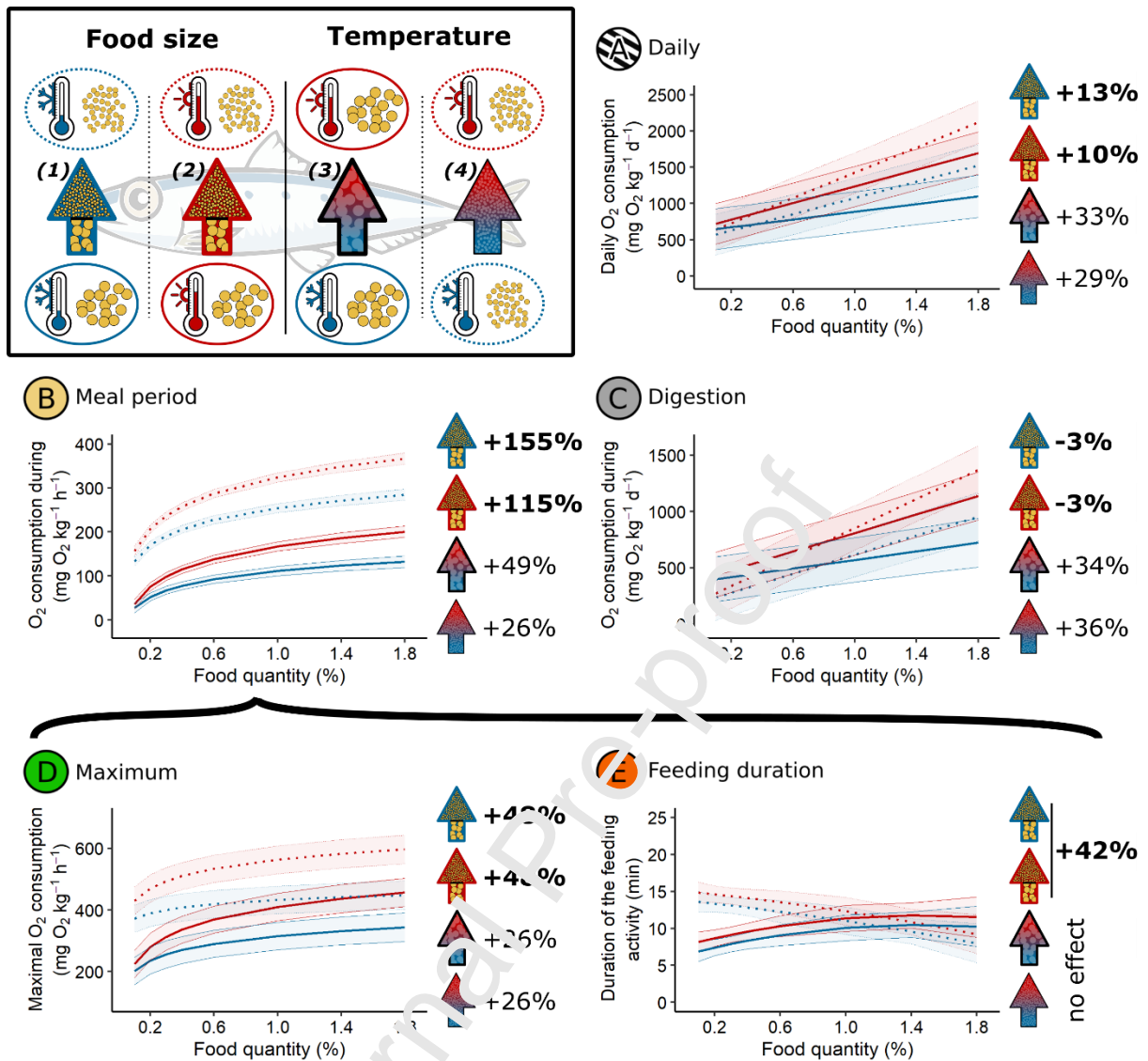
























Figure 3: Smooth functions of [A] daily, [B] while feeding, [C] while digesting, [D] maximal oxygen consumptions (relative to basal oxygen consumption, see details in Material and Methods) and [E] feeding duration according to the food ration for the 4 experimental treatments: cool temperature and large particles (solid blue lines), cool temperature and small particles (dotted blue lines), warm temperature and large particles (solid red lines) and warm temperature and small particles (dotted red lines). Arrows represent the mean relative increase of the oxygen consumption/feeding duration according to 4 scenarios summarized in top-left panel: scenario 1 = meal modification from large particles to small particles at cool temperature, (2) meal modification from large particles to small particles at warm

temperature, (3) increasing temperature when fish fed on large particles and (4) increasing temperature when fish fed on small particles. Only food size x food ration had a significant effect on feeding duration.

Table 1: Absolute and relative differences (estimates and 95% confidence intervals) for the 5 scenarios for which oxygen consumption were compared: (1) change from large particles to small particles at cool temperature; (2) change from large particles to small particles at warm temperature; (3) rise in temperature for fish fed on large particles; (4) rise in temperature for fish fed on small particles, and (5) change from large particles to small particles while also increasing temperature. Scenarios were tested using pairwise comparisons. Both differences were calculated by pairwise comparisons and 95% CI of relative differences were estimated following Kohavi et al. 2009. Absolute differences are given in mg of O₂ kg⁻¹ d⁻¹ for daily and during digestion, in mg of O₂ kg⁻¹ h⁻¹ for maximal and during feeding, and in minutes for feeding duration.

| Period | | Scenario | Relative change (%) | Absolute change |
|-------------|---|--|---------------------|-----------------|
| Daily |  | Scenario (1): 16°C Large ⇌ Small | 13 [1;37] | 108 [6;211] |
| |  | Scenario (2): 21°C Large ⇌ Small | 10 [3;22] | 108 [6;211] |
| |  | Scenario (3): Large 16°C ⇌ 21°C | 33 [6;87] | 265 [-290;821] |
| |  | Scenario (4): Small 16°C ⇌ 21°C | 29 [8;68] | 265 [-265;821] |
| |  | Scenario (5): 16°C + Large ⇌ 21°C + Small | 46 [10;121] | 373 [-179;926] |
| Meal period |  | Scenario (1): 16°C Large ⇌ Small | 155 [45;398] | 131 [120;143] |
| |  | Scenario (2): 21°C Large ⇌ Small | 115 [59;208] | 145 [134;157] |
| |  | Scenario (3): Large 16°C ⇌ 21°C | 49 [11;129] | 41 [24;59] |
| |  | Scenario (4): Small 16°C ⇌ 21°C | 26 [16;37] | 55 [38;73] |
| |  | Scenario (5): 16°C + Large ⇌ 21°C + Small | 220 [68;562] | 187 [169;204] |
| Digestion |  | Scenario (1): 16°C Large ⇌ Small | -3 [-13;-1] | -18 [-112;76] |
| |  | Scenario (2): 21°C Large ⇌ Small | -3 [-6;-1] | -18 [-112;76] |
| |  | Scenario (3): Large 16°C ⇌ 21°C | 34 [-4;183] | 178 [-212;569] |
| |  | Scenario (4): Small 16°C ⇌ 21°C | 36 [-5;214] | 178 [-212;569] |
| |  | Scenario (5): 16°C + Large ⇌ 21°C + Small | 31 [-3;164] | 160 [-228;548] |
| Maximal |  | Scenario (1): 16°C Large ⇌ Small | 48 [24;84] | 134 [111;156] |
| |  | Scenario (2): 21°C Large ⇌ Small | 48 [29;75] | 170 [147;192] |

| | | | | |
|----------|--|--|--------------|---------------|
| |  | Scenario (3): Large 16°C ⇔ 21°C | 26 [12;46] | 72 [-15;159] |
| |  | Scenario (4): Small 16°C ⇔ 21°C | 26 [16;39] | 108 [21;195] |
| |  | Scenario (5): 16°C + Large ⇔ 21°C + Small | 86 [47;148] | 242 [154;329] |
| Duration |   | Large ⇔ Small | 42 [-11;339] | 4 [2;6] |

3.2. Oxygen consumption during feeding

During fasting days, median MO₂ at the time of sham feeding was centered on zero (Fig. S8), indicating that the increase in MO₂ observed during all true feeding events resulted from actual energy expenditure to feed and not from behavioural responses by the sardines to feeding gestures.

The MO₂ during feeding was significantly related to the three double interactions (food ration x food size, food ration x temperature and food size x temperature, Tables S4 and S5, Fig. S8, S9). When considering only food size effects, slopes were significantly different ($p < 0.001$) and the increase was smaller for large particles (slope [95% CI]; 96 [86;106] mg of O₂ kg⁻¹ h⁻¹) than for small particles (128 [118;138] mg of O₂ kg⁻¹ h⁻¹, Table S3).

Food size had a strong and significant effect on MO₂ during feeding. When sardines fed on small particles at 16°C, their mean [95% CI] MO₂ was almost multiplied by 2.5 by comparison to large particles (p -value < 0.001), rising by 155 [465;398]%, while it doubled in sardines feeding on small particles, rising by 115 [59;208]% compared to large particles at 21°C (p -value < 0.001 , graph *Meal period* in Figures 3, Table 1).

3.3. Oxygen consumption during digestion

Similar to the daily MO₂, best linear mixed-effect model for MO₂ during digestion included double interactions between food ration and food size and between food ration and

temperature (Tables S6 and S7, Fig. S10, S11). Slopes differed significantly ($p < 0.001$); the lowest slope was estimated for sardines on large particles (slope [95% CI]; 300 [213;388] mg of $O_2 \text{ kg}^{-1} \text{ d}^{-1}$) while the highest slope was obtained for sardines on small particles (533 [445;621] mg of $O_2 \text{ kg}^{-1} \text{ d}^{-1}$, graph *Digestion* in Figure 3).

When comparing large to small particles averaged over all food rations, scenarios (1) and (2) were not significant since interaction between food size and temperature was not retained in the selected model. Indeed, mean [95% CI] MO_2 during digestion decreased by 3 [-13,-1]% at 16°C, while this decrease was 3 [-6;-1]% at 21°C (graph *Digestion* in Figure 3, Table 1).

3.4. Maximal consumption during feeding

Similar to the MO_2 during feeding, maximal MO_2 during feeding was significantly correlated with the three double interactions (Tables S8 and S9, Fig. S12, S13). Slopes differed significantly ($p = 0.001$); the lowest slope was estimated for sardines on small particles (slope [95% CI]; 86 [67;106] mg of $O_2 \text{ kg}^{-1} \text{ h}^{-1}$) while the highest slope was obtained for sardines on large particles (133 [113;152] mg of $O_2 \text{ kg}^{-1} \text{ h}^{-1}$, graph *Maximum* in Figure 3, Table S3).

Food size had a strong and significant effect on maximal MO_2 during feeding since food size x temperature interaction was retained during model processing. When sardines fed on small particles at 16°C, their mean [95% CI] maximal MO_2 rose by 48 [24;84]% by comparison to large particles, while such increase was 48 [29;75]% at 21°C (graph *Maximum* in Figure 3, Table 1).

3.5. Feeding duration

Contrary to the previous MO₂ features, the selected model for the feeding duration included interaction between food ration and food size but not with temperature since food ration x temperature and food size x temperature interaction were not retained (Tables S10 and S11, Fig. S14, S15). Slopes differed significantly between the two food sizes ($p = 0.004$). Indeed, the feeding duration decreased with increasing food ration when sardines fed on small particles (slope [95% CI]; -3 [-6;0] min) while it increased when sardines fed on large particles (4 [1;7] min, Table S3).

When comparing large to small particles averaged over all food rations, scenarios (1) and (2) were not significant since interaction between food size and temperature was not retained in the selected model. Mean [95% CI] feeding duration increased by 42 [-11;339]% (graph *Feeding duration* in Figure 3, Table 1).

3.6. Temperature effects

Temperature had significant effects on all oxygen consumptions and on the feeding duration (Tables S1 to S11). Indeed, food ration x temperature interaction was included in all selected models on MO₂ and food size x temperature interaction was included in models on MO₂ during feeding and maximal MO₂ during feeding. Moreover, in the model on feeding duration, temperature was retained without its interactions (Tables S10).

When studying interaction of food ration and temperature, slopes were significant different between the two temperatures in all MO₂ models and they were always smaller at cool than at warm temperature. Thus, slopes were smaller at 16°C than at 21°C for daily MO₂, MO₂ during digestion, MO₂ during feeding, and maximal MO₂ during feeding (Table S3). Surprisingly, slopes were very similar when considering either large particles or cool temperature effects (e.g. slopes [95% CI] for daily MO₂, 420 [324;515] and 413 [317;509],

respectively) and either small particles or warm temperature effects (for daily MO₂, 714 [618;810] and 721 [626;817], respectively, suggesting similar effects of prey shrinking and temperature warming over food ration on MO₂ (see Table S3).

When comparing cool to warm conditions, in scenarios (3) and (4) there was no significant effect of temperature on daily MO₂, MO₂ during digestion or on feeding duration, because food size x temperature interaction was not retained within selected models. On the other hand, warming effects were significant on MO₂ during feeding (p-values < 0.001) but only scenario (4) was significant on maximal MO₂ during feeding (p-value = 0.02). Thus, the temperature change from 16°C to 21°C caused mean MO₂ during feeding to increase by 26 [16;37]% in fish fed on small particles, and by 49 [11;123]% in fish fed on large particles. This temperature change caused mean maximal MO₂ during feeding to increase by 26 [16;39]% in sardines fed with small particles (Figure 3, Table 1).

3.7. Cocktail effects of the global warming

Smaller particle size and higher temperature resulted in a mean [95% CI] daily MO₂ increase of 46 [10;121]%, representing an increase of 373 [-179;926] mg of O₂ kg⁻¹ d⁻¹. This increase was caused by the significant multiplication by 3 of the MO₂ during the meal period (220 [68;562]%, representing 187 [169;204] mg of O₂ kg⁻¹ h⁻¹) and higher MO₂ during the digestion (31 [-3;163]%, representing 160 [-228;548] mg of O₂ kg⁻¹ d⁻¹). Moreover, such change caused an increase of the maximal MO₂ during feeding by 86 [47;148]%, representing an increase of 242 [154;329] mg of O₂ kg⁻¹ h⁻¹, and a longer feeding period (42 [-11;339]%, representing 4 [2;6] min without temperature effect, Figure 4, Table 1).

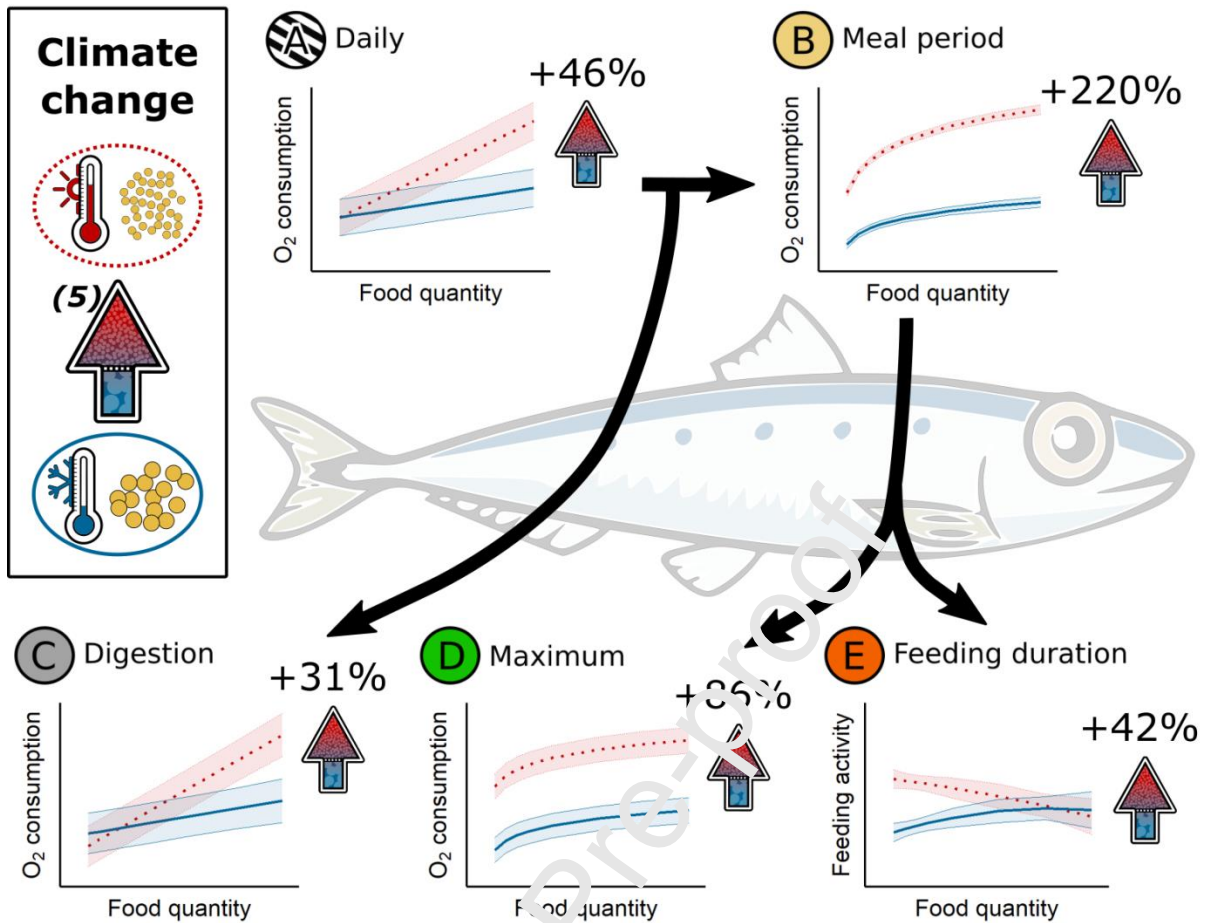


Figure 4: Smooth functions of [A] daily, [B] while feeding, [C] while digesting, [D] maximal oxygen consumptions and [E] feeding duration according to the food ration for the 2 experimental treatments representing past and future environmental conditions, i.e. cool temperature and large particles (solid blue lines) and warm temperature and small particles (dotted red lines), respectively. Arrows represent the mean relative increase of the oxygen consumption/feeding duration according to the global warming (scenario 5), i.e. meal modification from large particles to small particles with increasing temperature, and summarized in top-left panel (feeding duration is not significantly affected by temperature increase, see Results).

4. Discussion

This study investigated how a modification of food resources under climate warming might jeopardize energy balance of small pelagic species, using sardines in the Mediterranean Sea as a case study. To do so, we used in-vivo group respirometry to investigate the effects of prey (food) size and availability (ration) on sardine energy expenditure, and how this was influenced by temperature. Our results demonstrate that both food size and temperature had significant effects on multiple measures of energy expenditures, over daily and hourly timescales. While temperature significantly increased expenditures overall, food size had a major impact on energy expenditure for activity during feeding itself. That is, the results indicate that food resources and temperature are major environmental drivers that can dramatically increase energy expenditures of fishes and disturb their energy balance in a scenario of future climate change, in warmer waters with smaller prey. As such, the results also provide experimental evidence that such challenges to energy balance may contribute to the ongoing shrinking of fish populations.

Daily oxygen consumption measured in this study was corrected against a baseline of standard metabolism (Chabot et al., 2016a), so represents daily energy expenditure on activity. The results suggested greater expenditure for days where sardines fed on small particles, due to higher oxygen consumption during either feeding and/or digestion. The very marked increase in oxygen consumption during actual feeding on small items must reflect different costs of foraging mode, with filtering being more expensive than particulate feeding. While this confirms our hypothesis and helps explain the decreased growth and body condition of sardines fed for an extended period on small items (Queiros et al., 2019), the magnitude of the effect is quite remarkable. Both MO_2 and duration of the meals

provide a more detailed understanding of the widely different energy costs of the two foraging modes. First, the higher maximal MO₂ when fish fed on small particles indicates greater energy requirements for the continuous aerobic swimming in filter-feeding compared to rapid bursts to capture large particles (Costalago & Palomera, 2014). Queiros et al. (2019) had already noted that the duration of feeding activity was longer when sardines fed on small particles, it presumably represents the time needed to filter the entire tank volume and, therefore, might not be expected to change much with ration. It is interesting therefore that feeding duration on small particles was in fact lower at low or high rations than at intermediate ones. Low duration at low ration might suggest rapid loss of interest if food acquisition was very poor, while at high ration it might indicate satiation. For particulate feeding, more particles to catch should translate into longer duration, which was observed until a ration threshold where a plateau would indicate satiation. Overall, we expected feeding duration to be longer on small particles at low ration but longer on large particles, but this was only true for rations below 0.6 %, after which duration was similar for both particle sizes. Finally, all these results indicate that higher energy expenditure by sardines filter feeding on small particles can explain why they would have to eat twice as much as when feeding on large pellets to achieve similar growth or body condition (Queiros et al. 2019).

Our finding that oxygen consumption during the digestion increased with the food ration, for both particle sizes, presumably reflects the so-called specific dynamic action of feeding (SDA) response (McCue, 2006). This reflects the energy needed for the digestion, absorption and assimilation of a meal (Chabot et al., 2016b), hence the energetic 'costs of growth'. Therefore, larger meals require greater energy investment but then provide a great return

in terms of tissue accretion and growth (Fu et al., 2005a, 2005b; Jordan & Steffensen, 2007; Norin & Clark, 2017). The fact that a doubling of ration from 0.4% to 0.8% only caused a 17% or 55% increase in apparent SDA (based on estimated slopes), in fish fed large items at 16 °C or small items at 21°C, respectively, might seem limited. This increase with doubling of ration is low compared to other fish species (see Secor, 2009). Furthermore, the high surface area to volume ratio of small particles should speed up digestion by promoting enzymatic processes and, thereby, reduce a part of digestion costs (discussed in Legler et al., 2010). On the other hand, a large SDA response can indicate that lots of nutrients were assimilated, notably amino acids for protein synthesis, with high costs of turning these into tissues but that reflect robust growth (Fraser & Rogers 2007; McCue, 2006; Secor, 2009). That is, a large SDA would imply good growth, which is coherent with the fact that sardines fed on large particles exhibited higher growth and greater condition in previous studies (see Queiros et al. 2019).

There is another mechanism that might increase energy expenditure during 'digestion' of large particles, being the costs of recovery from rapid bursts of anaerobic swimming used for prey capture. The metabolic cost of such recovery, so-called 'excess post-exercise oxygen consumption' (EPOC) can be divided into 3 phases in fishes: rapid, plateau, slow (Zhang et al., 2018). While the rapid phase is very short (< 1 hour), both plateau and slow phases can require several hours to return to standard metabolism. This can be more than 10 hours for salmon although the duration is certainly species dependent (C. G. Lee et al., 2003; Li et al., 2020; Plambech et al., 2013; Svendsen et al., 2012; Zhang et al., 2018). Considering that we estimated energy expenditure of digestion starting at 1.5 hours after providing the meal, this would omit the rapid phase of EPOC, although the phenomenon

may have contributed to the final phases of metabolic costs of feeding. A potential role for EPOC in costs of feeding on large prey remains to be proven, since studies on individual sardines are technically extremely challenging. Overall, oxygen consumption due to digestion was lower for small compared to large particles, but the magnitude of the difference was much less than for the activity costs of feeding. Therefore, daily energy expenditure was mostly affected by what happened during the meal. The benefit of digesting small prey (in terms of energy expenditure for a same food ration) remained too weak to counterbalance the increased energy to capture striking plankton in the wild. Furthermore, the warm temperature also significantly increased metabolic rates, leading to overall higher energy expenditure during both meals and digestion (Clarke & Fraser, 2004; Seebacher et al., 2015), whatever the food size or ration. Higher energetic cost for digestion at warm temperatures has been reported for tunas, another species that swims continuously (Klinger et al., 2016) although relationships between costs of digestion and temperature are not necessarily linear (McKenzie et al., 2013; Tirsgaard et al., 2015).

Our study applied relatively short thermal acclimation times, which might tend to overestimate temperature effects. When natural populations are allowed to acclimatise over generations, baseline metabolism may show a much less marked effect of temperature (e.g. Wootton et al. 2022). Such intergenerational experiments are not feasible for the Mediterranean sardine because their life cycle cannot be completed in captivity. Our experimental temperatures (16°C and 21°C) were well within the range that sardines have experienced in the Gulf of Lions over the last 40 years (12 - 24°C ; Feuilleley et al. 2020) and our rate of temperature change was slow (< 0.5°C/day) allowing acclimation at an ecologically realistic pace. Furthermore, by expressing oxygen consumption as a relative

increase from MO₂ baseline (the baseline was estimated daily as the lowest 15%-quantile rate for daily MO₂ and MO₂ during digestion, and as the mean of the preceding 2.5 hours for MO₂ while feeding), effects of temperature on baseline metabolism were been taken into account in our study. Finally, although the effects of temperature were significant, potential acclimation across a few generations leading to similar baseline metabolism between generations would reinforce our results on the effects of food size.

Although food size had only quite minor effects on daily energy use, increasing it by 10 [3;22]% in fish fed on small particles at 21°C, long-term effects may be significant. Furthermore, sardines may feed continuously in the wild, not only once or twice a day, which would increase consequences of differences in energy expenditure during feeding. In the wild, sardines face predation and pathogens that require energy expenditure. Therefore, higher daily energy expenditure for feeding may well impair energy balance in the wild, resulting in less energy allocated towards survival and growth. For instance, lower swimming performance due to low energy reserves (e.g. swimming endurance (Martínez et al., 2003, 2004)) could isolate leaner individuals from schools, leading to a vicious circle, with lower food foraging and thus reinforcing lower energy reserves. Nonetheless, calorie-restricted sardines display better phenotypic plasticity to face fasting, which improves their ability to reduce their metabolic energy expenditures during long-term fasting (Queiros et al., 2021). Further, mitochondria from sardines fed with small particles exhibited lower basal oxidative activity but higher efficiency of ATP production than those fed with large particles, a mechanism that should help them spare energy (Thoral et al., 2021). Nevertheless, although sardines may display plasticity or adaptation that ameliorates the energetic

consequences of smaller prey and warmer temperatures, the situation of sardine populations in the Gulf of Lions remains very concerning.

Conclusion

This study supports the hypothesis of bottom-up control to explain the profound shrinking of small pelagic fish communities in the Gulf of Lions and is a hypothesis worth exploring to explain the spread of this phenomenon throughout the Mediterranean (Albo-Puigserver et al., 2021; Brosset et al., 2017) to new ecosystems, and to species higher in the food web (Bensebaini et al., 2022; Véron et al., 2020). Altogether, the results indicate that energy balance can be a major mechanism explaining shrinking of fish populations globally. Declines in prey size could impact the energy balance of individuals when their energy expenditures are increased by warmer temperatures, with future projections of prey resources predicting a decline of prey biomass and quality.

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Quentin Queiros: Conceptualization, Formal analysis, Investigation, Writing - Original Draft, Visualization; David J. McKenzie: Conceptualization, Investigation, Resources, Writing - Review & Editing, Supervision; Shaun Killen: Conceptualization, Funding acquisition; Gilbert Dutto: Conceptualization, Investigation, Writing - Review & Editing; Claire Saraux: Conceptualization, Writing - Review & Editing; Quentin Schull: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition

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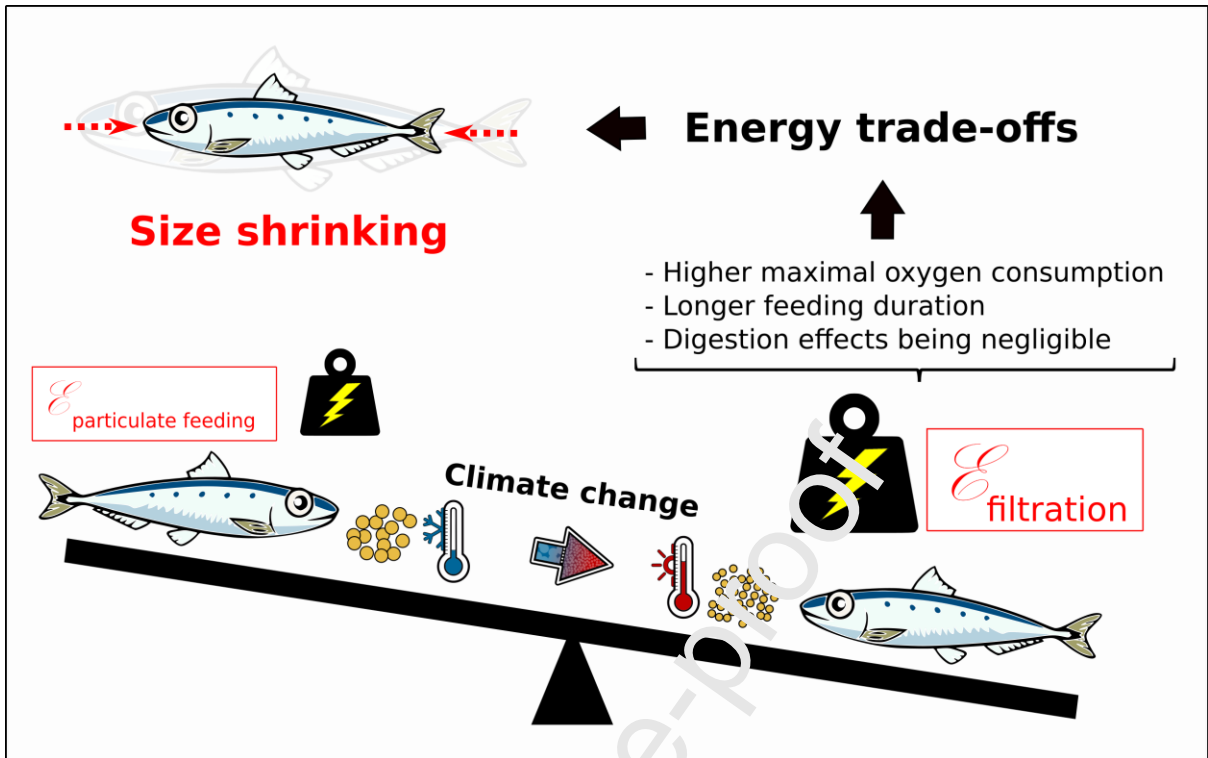
Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Graphical abstract



Highlights:

- Size decline in fish may be a universal response to global change
- Global change can disturb energy balance of consumers feeding at low trophic levels
- Prey shrinking raised the energetic costs of feeding and daily energy expenditure
- Warmer waters with smaller prey dramatically increase energy expenditure

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