



# Linking growth patterns to sea temperature and oxygen levels across European sardine (*Sardina pilchardus*) populations

Donna Dimarchopoulou ·  
Athanasios C. Tsikliras 

Received: 3 November 2021 / Accepted: 3 February 2022 / Published online: 16 February 2022  
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

**Abstract** The previously studied geographic variability in the growth patterns of different European sardine or European pilchard (*Sardina pilchardus*) populations has been attributed to the trophic status and productivity of the various ecosystems, as well as the genetic distance among populations. However, in the face of ocean warming and its multifaceted effects on marine populations and fisheries, it is interesting to explore growth patterns through the prism of sea temperature and dissolved oxygen. Here, data on the asymptotic length, growth coefficient, and maximum reported age of 47 Atlantic and Mediterranean sardine populations, covering the entire geographical range of its distribution, were extracted from published sources and were correlated with regional sea surface temperature and dissolved oxygen. Asymptotic length was negatively related to sea temperature and more strongly positively related to oxygen levels, indicating that sardines grow to larger body size in cooler waters that are more oxygenated. Within the context of climate change, the link of intraspecific

growth variability with temperature and oxygen draws attention to the adverse effects this might have on many fish biological characteristics in a warming future.

**Keywords** Body size · Fish growth · Oxygen limitation · GOLT · Climate change · Atlantic · Mediterranean

## Introduction

Climate change combined with fishing pressure and other environmental and anthropogenic stresses affects the life-history characteristics (Olsen et al. 2004; Pankhurst & Munday 2011) and geographical distribution of marine populations (Harley et al. 2006). This should result in changes in the catches of exploited marine species and likely economic losses (Sumaila et al. 2011) as the fisheries catch potential is expected to decline in many areas around the world, including the Mediterranean Sea (Cheung et al. 2010). Sea warming and deoxygenation were initially perceived to affect mainly the geographical distribution of marine species (Hughes 2000) and, for exploited populations, to cause changes in catch composition and somatic sizes (Tsikliras 2008). Indeed, sea warming has been shown to cause shifts in species distribution ranges towards higher latitudes (Lenoir & Svenning 2015) as species follow their thermal preferences at local and broader scales (Cheung et al.

---

D. Dimarchopoulou (✉)  
Department of Fisheries, Animal and Veterinary Sciences,  
College of the Environment and Life Sciences, University  
of Rhode Island, Kingston, RI, USA  
e-mail: ddimarch@uri.edu

D. Dimarchopoulou · A. C. Tsikliras (✉)  
School of Biology, Department of Zoology,  
Aristotle University of Thessaloniki, UP Box 134,  
541 24 Thessaloniki, Greece  
e-mail: atsik@bio.auth.gr

2009; Sunday et al 2012). Thus, increasing sea temperatures are driving the poleward spread of thermophilous (= warm-water) species (Sabatés et al. 2006) and have facilitated the invasion and spread of non-indigenous species such as the silver-cheeked toadfish *Lagocephalus sceleratus* in the Mediterranean Sea (Coro et al. 2018; Ulman et al. 2021). In contrast, species that prefer lower temperatures ranges (= psychrophilous or cold-water species) experience shrinking habitable ranges (Sabatés et al. 2006).

An increasing number of warm-water species of Indo-Pacific origin have entered the Mediterranean Sea through the Suez Canal (Golani et al. 2021) and are spreading towards northern areas (Vergés et al. 2014) leading to the tropicalisation of the Mediterranean fauna (Bianchi & Morri 2003). The semi-enclosed Mediterranean Sea is among the areas where local species extinctions and range shifts were predicted to be more common (Cheung et al. 2009). Besides distribution shifts and local declines in fish biomass, future projection scenarios suggest that marine resources in the Mediterranean Sea will suffer increasing stress if sea temperature rises more than 2 °C above preindustrial levels (Gattuso et al. 2015). The mean temperature of the catch (MTC), a new index that assesses the effect of ocean warming on marine populations, at the community level, through fisheries catches or abundance/biomass (Cheung et al. 2013a), has been increasing across the Mediterranean showing that the ratio of thermophilous to psychrophilous marine species has been changing in favour of the former, indicating either an increase in the relative proportion of thermophilous species or a decrease in the relative proportion of the psychrophilous ones (Tsikliras & Stergiou 2014). Similar community response and tropicalisation has been reported in other sub-tropical and temperate areas of the world, while the response of tropical communities differs (Dimarchopoulou et al. 2021).

Although the effect of sea warming on species geographical range is well studied, even with future projections according to climate change scenarios (Coro et al. 2018), the effect of climate change on life-history characteristics and the underlying ecological mechanisms remain rather limited (Daufrès et al. 2009). The gill-oxygen limitation theory (GOLT) predicts that fish individuals are expected to shrink in size due to their inability to compensate, via their gill surface area, for the increased metabolic

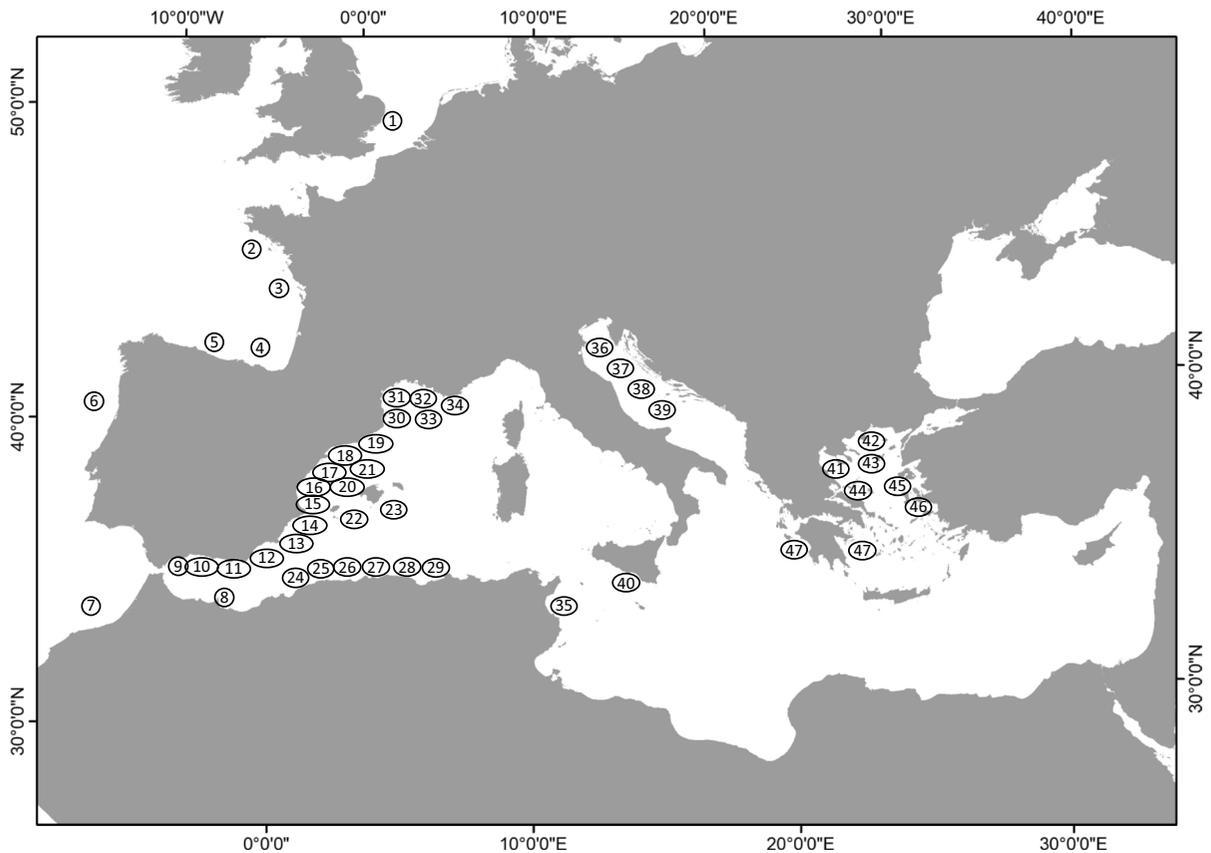
rate that results from higher sea temperatures and lower dissolved oxygen levels (Cheung et al. 2013b; Pauly 2021). The GOLT may also explain the poleward shift of marine organisms (Cheung et al. 2013b) and their bathymetric expansion to deeper, colder waters (Perry et al. 2005) both of which occur in the Mediterranean Sea (Tsikliras & Stergiou 2014). The GOLT also provides the underlying mechanism to the James' Rule (James 1970), according to which within a species, populations with smaller body size are generally found in warmer environments (see Fig. 3 in Pauly 1998).

Natural populations of the European sardine (*Sardina pilchardus*), also known as European pilchard, provide a model system for studying the effect of climate change as they are extended throughout the sub-tropical and temperate zone of the Atlantic Ocean and the entire Mediterranean Sea (Froese & Pauly 2021). The geographical range of the species extends to ecosystems with different temperature and oxygen levels from the warm eastern Mediterranean Sea to the cool waters of the NE Atlantic Ocean. European sardine is a small pelagic species, mainly exploited by purse-seine fleets and accounts for around 15–20% of the total marine catch in the Mediterranean Sea (Tsikliras & Koutrakis 2013).

The aim of the present work was to compare the body size of the European sardine populations in several areas of its distribution and to examine whether intraspecific variation in growth can be linked to oxygen limitation in warmer waters (i.e., smaller body size in higher temperature/lower oxygen level populations vs. larger body size in lower temperature/higher oxygen level populations).

## Materials and methods

The von Bertalanffy growth parameters asymptotic total length  $L_{\infty}$  (the length a population would reach if they were to grow infinitely, in cm) and growth coefficient  $K$  (the rate at which  $L_{\infty}$  is approached, in year<sup>-1</sup>) and the maximum reported age of 47 European sardine populations from various Atlantic and Mediterranean locations were extracted from published sources. These populations represent the entire geographical range of sardine's distribution (Fig. 1), which includes ecosystems with variable environmental characteristics ranging from the warmer eastern



**Fig. 1** Map of the NE Atlantic and Mediterranean Sea showing the location of the European sardine populations listed in Table 1

Mediterranean Sea (average annual sea surface temperature of 19.4 °C) to the cooler North Sea (average annual sea surface temperature of 16.1 °C).

The growth parameters extracted from the literature were converted to the same unit using the growth equations reported by the authors and length-length and length-weight relationships for each area or for neighbouring populations. The growth curves of each population were re-constructed based on the growth parameters and the corresponding lifespan reported in the original study (Table 1).

The growth parameters of all sardine populations were used to construct an auximetric double logarithmic plot (Pauly 1994) of the growth coefficient (logK) against the corresponding asymptotic length (logL<sub>∞</sub>). The auximetric plot was used to compare intra-specific growth performances (Cury & Pauly 2000) and group the sardine populations into clusters based on their growth pattern. The relationships

between the growth coefficient (logK) and asymptotic length (logL<sub>∞</sub>) were tested for differences among clusters by comparing the intercepts of the corresponding regression lines using analysis of covariance. The slope of populations belonging into the same group pattern is expected to be close to -2 (Cury & Pauly 2000); hence the comparison among slopes is meaningless.

Mean present sea surface temperature (°C) and dissolved molecular oxygen (mol/m<sup>3</sup>) data were acquired from the global environmental dataset for marine species distribution modelling, Bio-ORACLE (Tyberghien et al. 2012; Assis et al. 2017) for all locations where the growth of sardine populations was studied. The Pearson’s product moment correlation coefficient was used to measure the degree of linear dependence of the asymptotic total length (L<sub>∞</sub>) and the growth coefficient (K) on temperature and dissolved oxygen.

**Table 1** Growth parameters of European sardine populations across its Atlantic Ocean and Mediterranean Sea distribution ( $L_{\infty}$ : asymptotic length, cm; K: growth coefficient,  $y^{-1}$ ). EA: eastern Atlantic, WM: western Mediterranean, CM: central Mediterranean, EM: eastern Mediterranean

No	Area	Subarea	Country	$L_{\infty}$	K	Reference
1	Atlantic	EA	UK	25.0	0.50	Bougis (1952)
2	Atlantic	EA	France	25.0	0.25	D’Ancona (1937)
3	Atlantic	EA	France	22.0	0.40	Bougis (1952)
4	Atlantic	EA	Spain	24.1	0.34	Perez et al. (1985)
5	Atlantic	EA	Spain	24.3	0.43	Porteiro & Alvarez (1985)
6	Atlantic	EA	Portugal	22.4	0.67	Barraca & Pestana (1985)
7	Atlantic	EA	Morocco	21.6	0.82	Delgado et al. (1981)
<b>Atlantic mean values</b>				<b>23.5</b>	<b>0.48</b>	
8	Mediterranean	WM	Morocco	21.8	0.27	Idrissi (1987)
9	Mediterranean	WM	Spain	16.6	0.56	Andreu et al. (1950)
10	Mediterranean	WM	Spain	17.0	0.60	Bougis (1952)
11	Mediterranean	WM	Spain	17.4	0.84	Alemaný & Álvarez (1993)
12	Mediterranean	WM	Spain	18.0	0.65	Alemaný & Álvarez (1993)
13	Mediterranean	WM	Spain	19.1	0.35	Bouchereau et al. (1985)
14	Mediterranean	WM	Spain	19.4	0.31	Penas Lado (1978)
15	Mediterranean	WM	Spain	19.6	0.31	Larrañeta & Lopez (1958)
16	Mediterranean	WM	Spain	19.9	0.93	Alemaný & Álvarez (1993)
17	Mediterranean	WM	Spain	20.1	0.41	Rodriguez-Roda & Larrañeta (1955)
18	Mediterranean	WM	Spain	20.3	0.31	Larrañeta (1965)
19	Mediterranean	WM	Spain	20.4	0.27	Lopez (1963)
20	Mediterranean	WM	Spain	20.7	0.69	Alemaný & Álvarez (1993)
21	Mediterranean	WM	Spain	20.9	0.53	Rodriguez-Roda & Larrañeta (1955)
22	Mediterranean	WM	Spain	21.2	0.39	GFCM (1981)
23	Mediterranean	WM	Spain	22.1	0.26	Bouchereau et al. (1985)
24	Mediterranean	WM	France	16.4	0.56	Apostolidis & Stergiou (2014)
25	Mediterranean	WM	France	18.2	0.70	Bouchereau et al. (1985)
26	Mediterranean	WM	France	18.9	0.34	Bouchereau et al. (1985)
27	Mediterranean	WM	France	19.9	0.36	Mouhoub (1986)
28	Mediterranean	WM	France	20.4	0.31	Brahmi et al. (1998)
29	Mediterranean	WM	Algeria	16.1	0.71	Djabali et al. (1990)
30	Mediterranean	WM	Algeria	17.6	0.26	Fage (1920)
31	Mediterranean	WM	Algeria	18.3	0.38	Alemaný & Álvarez (1993)
32	Mediterranean	WM	Algeria	18.7	0.28	Campillo (1992)
33	Mediterranean	WM	Algeria	18.9	0.46	Lee (1961)
34	Mediterranean	WM	Algeria	19.2	0.28	Campillo (1992)
35	Mediterranean	WM	Tunisia	19.4	0.43	Kartas (1981)
36	Mediterranean	CM	Italy	17.0	0.70	Mozzi & Duo (1958)
37	Mediterranean	CM	Italy	18.8	0.38	Colloca et al. (2013)
38	Mediterranean	CM	Italy	20.5	0.46	Sinovic (1983)
39	Mediterranean	CM	Croatia	17.0	0.40	Muzinic (1957)
40	Mediterranean	CM	Italy	21.4	0.40	STECF (2013)
41	Mediterranean	EM	Greece	20.8	0.86	Voulgaridou & Stergiou (2003)
42	Mediterranean	EM	Greece	19.5	0.39	Antonakakis et al. (2011)
43	Mediterranean	EM	Greece	16.9	0.59	Tsikliras & Koutrakis (2013)
44	Mediterranean	EM	Greece	16.6	0.40	Laskaridis (1948)
45	Mediterranean	EM	Greece	16.7	0.48	Laskaridis (1948)
46	Mediterranean	EM	Turkey	15.0	0.59	Akyol et al. (1996)

**Table 1** (continued)

No	Area	Subarea	Country	$L_{\infty}$	K	Reference
47	Mediterranean	EM	Greece	18.1	0.30	Tserpes & Tsimenides (1991)
<b>Mediterranean mean values</b>				<b>18.9</b>	<b>0.47</b>	

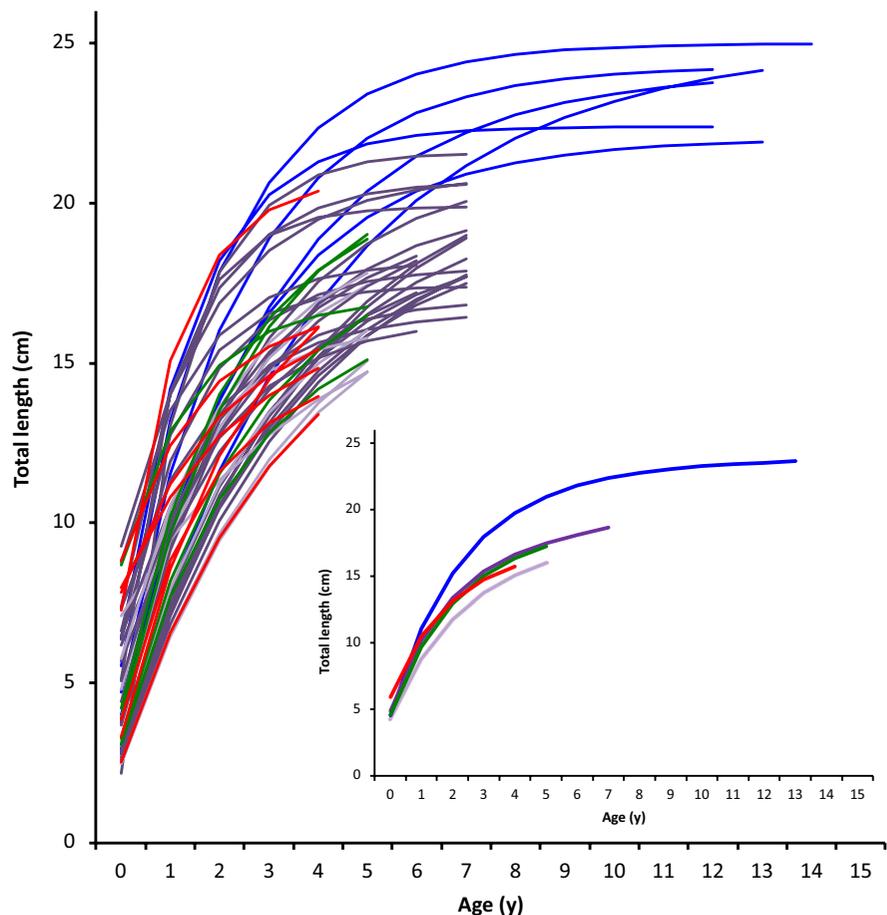
**Results**

Overall, 47 sardine populations were included in the analysis ranging from the North Sea to the NW African coasts in the Atlantic and covering the entire Mediterranean Sea (Table 1, Fig. 1). Their asymptotic length ( $L_{\infty}$ ) ranged between 21.6 and 25.0 cm for the Atlantic populations (mean=23.5 cm) and between 15.0 and 22.1 for the Mediterranean ones (mean=18.9 cm), while their growth coefficient (K) ranged between 0.25 and 0.82  $y^{-1}$  (mean=0.48  $year^{-1}$ ) for the Atlantic populations and between 0.27 and 0.84  $year^{-1}$  (mean=0.47  $year^{-1}$ ) for the Mediterranean ones (Table 1). Maximum

reported age ( $t_{max}$ ) reached 14 years in the Atlantic and ranged between 4 (eastern Mediterranean) and 7 (western Mediterranean) for the Mediterranean populations (Fig. 2).

A clear Atlantic to Mediterranean gradient was apparent with larger body sizes and longer lifespans observed in the NE Atlantic but also a western to eastern intra-Mediterranean gradient with the western Mediterranean populations being generally larger and longer-lived, suggesting that there is at least one intermediate growth pattern between the two extremes. These differences and gradients were very clearly visible when the growth curves of all populations were plotted together (Fig. 2).

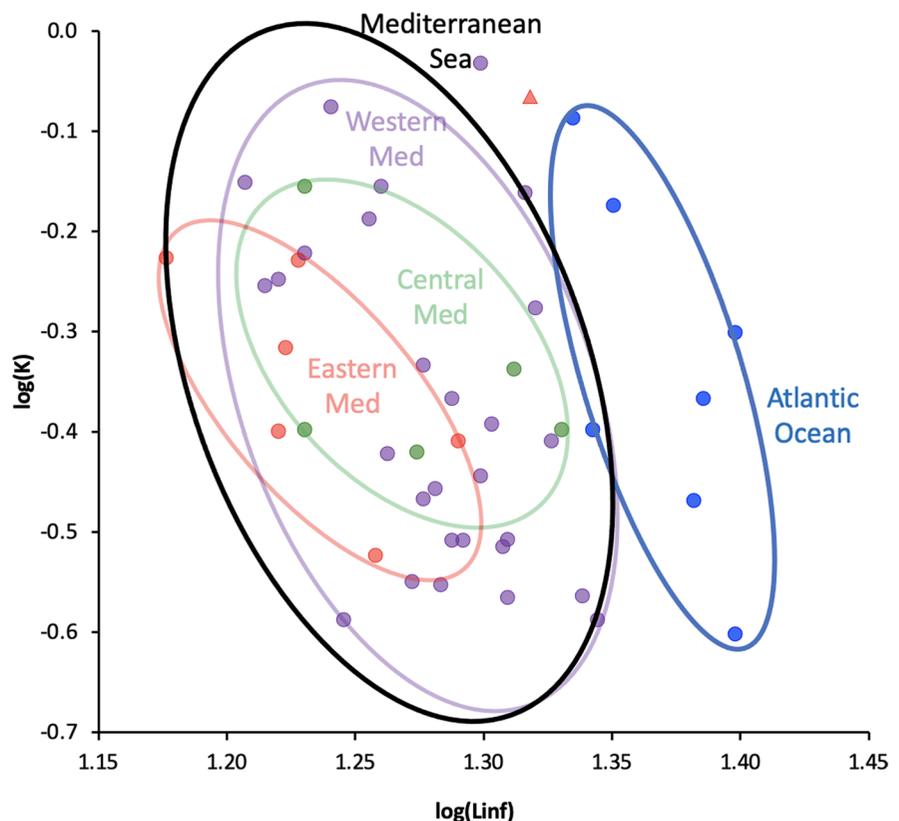
**Fig. 2** Growth curves of the European sardine populations listed in Table 1. The growth curves are marked with different colours on an area basis (Atlantic Ocean: blue; eastern Mediterranean: red; central Mediterranean: green; western Mediterranean: dark purple for northern coastline, light purple for southern coastline). The inside panel shows the averaged growth curves per area

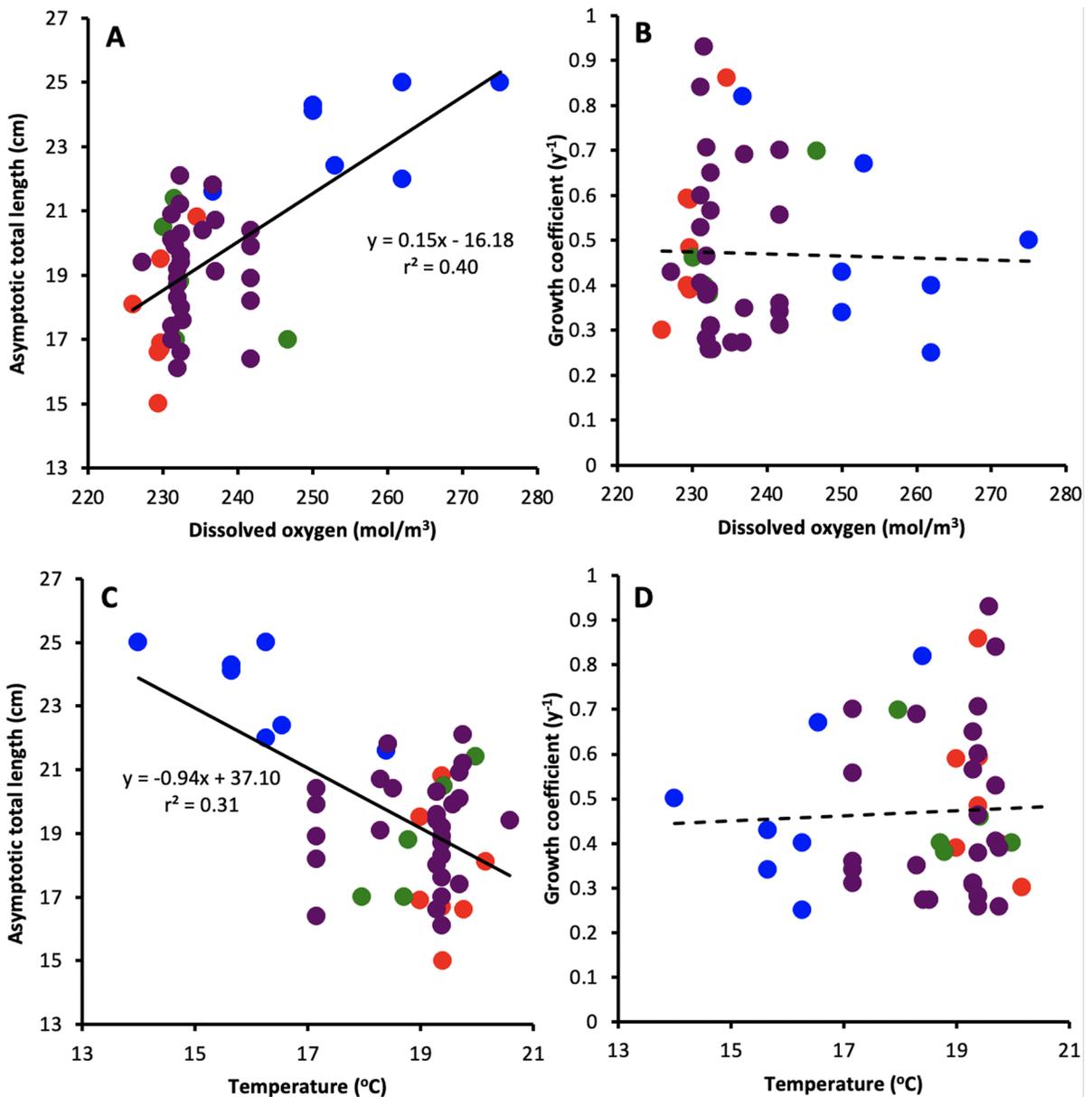


The sardine populations were grouped into two separate clusters based on their asymptotic length and growth coefficient using an auximetric plot (Fig. 3): the Atlantic cluster (large-sized and long-lived) and the Mediterranean cluster (small-sized and short-lived). The intercepts of the two regression lines that correspond to the populations included in the two ellipses (black and blue: Fig. 3) were statistically different (ANCOVA,  $F=6.89$ ,  $P=0.012$ ). The Mediterranean cluster included populations from the eastern Mediterranean, which were the smallest and shorter-lived, as well as from the central and the western Mediterranean with intermediate body size and lifespan (Figs. 2 and 3). Within the western Mediterranean, the populations of the southern and the northern coastline also exhibited differences in growth with the southern populations reaching smaller sizes and lower lifespan (Figs. 2 and 3). However, none of the differences among Mediterranean populations were statistically significant (ANCOVA,  $P>0.05$  in all cases).

Asymptotic length was positively related to oxygen levels (Pearson's product-moment correlation = 0.63,  $P<0.001$ ,  $n=47$ ) indicating that sardines grow to larger body size in higher oxygen levels (Fig. 4a) and negatively related to sea temperature (Pearson's product-moment correlation =  $-0.56$ ,  $P<0.001$ ,  $n=47$ ) indicating that sardines grow to larger body size at lower temperature (Fig. 4c). The relationship of asymptotic length with oxygen was stronger than with to temperature and became even stronger (Pearson's product-moment correlation = 0.67,  $P<0.001$ ,  $n=46$ ) when the single outlier of eastern Mediterranean was removed from the analysis. Growth coefficient ( $K$ ) was not related to oxygen (Pearson's product-moment correlation =  $-0.17$ ,  $P=0.86$ ,  $n=45$ ) or temperature (Pearson's product-moment correlation = 0.30,  $P=0.76$ ,  $n=45$ ) indicating that the rate at which asymptotic length is approached is not oxygen (Fig. 4b) or temperature (Fig. 4d) driven.

**Fig. 3** Auximetric plot of the growth coefficient  $K$  ( $\text{year}^{-1}$ , log) with asymptotic total length (cm, log) showing the growth clusters of the European sardine populations listed in Table 1. The growth cluster ellipses are marked with different colours (Atlantic Ocean cluster: blue; Mediterranean Sea cluster: black; the Mediterranean cluster includes eastern Mediterranean: red; central Mediterranean: green; western Mediterranean: purple). A single outlier of eastern Mediterranean is marked with a red triangle





**Fig. 4** The relationship of the asymptotic total length (a) and the growth coefficient (b) with the dissolved oxygen concentration (mol/m<sup>3</sup>) and the relationship of the asymptotic total

length (c) and the growth coefficient (d) with the sea surface temperature (°C) for the European sardine populations in the Atlantic Ocean and the Mediterranean Sea

### Discussion

Because of their fast life history strategy (rapid growth, short lifespan, early maturation) and their relatively high resilience to overexploitation, small pelagic fishes have been widely used to examine

environmental forcing on their biological characteristics (spawning: Sabatés et al. 2006; early life stages: Pankhurst & Munday 2011; recruitment: Brosset et al. 2017; condition: Saraux et al. 2019), as well as climate change and variability on their catches and biomass (Alheit et al. 2014; Tsikliras et al. 2019). The

geographic variability of sardine growth across the Atlantic and Mediterranean Sea populations has been previously reported especially for comparing western Mediterranean and Atlantic growth patterns (Silva et al. 2008), as well as historical variability in growth in the eastern Mediterranean (Tsikliras & Koutrakis 2013). The growth clusters that were identified here and correspond to asymptotic length and lifespan patterns appear to capture quite well what has been previously reported on the growth of sardine. Indeed, previous research has identified variable growth patterns among the populations of sardine with a declining growth performance in the Atlantic Ocean from north to south and in the Mediterranean Sea from west to east (Silva et al. 2008). These differences have been attributed to the different trophic status among these areas and the general oligotrophy of the eastern Mediterranean Sea, but also to genetic distance among the populations (Silva et al. 2008; Tsikliras & Koutrakis 2013).

However, the strong positive relationship of asymptotic length with oxygen concentration and the moderately strong negative relationship with sea temperature clearly indicates that the populations living in the cooler and fresher waters of the NE Atlantic attain larger body sizes and longer lifespans, whereas those of the warmer and less oxygenated eastern Mediterranean remain smaller and attain shorter lifespan. An intermediate group, that of the western and central Mediterranean, does exist because intermediate oxygen and temperature conditions also occur between the two extremes. The growth curves (Fig. 2), growth clusters (Fig. 3), and their correlation with oxygen and temperature (Fig. 4) may support the gill-oxygen limitation theory (GOLT), which proposes that oxygen limitation in warming waters is the mechanism that best explains intraspecific variation in growth of water breathing ectotherms (Pauly 2021). The results of the present work also support the James' Rule (James 1970), according to which, within a species, populations with smaller body size are generally found in warmer environments (Audzijoynte et al. 2019). Similar intraspecific growth variability linked to sea temperature has been reported for the Atlantic cod (*Gadus morhua*) in the North Atlantic (see Fig. 5 in Pauly 2021 and references therein) and eelpout (*Zoarces viviparous*) in the North Sea compared to colder areas (Pörtner & Knust 2007). Besides sea temperature and oxygen limitation,

growth variability may be the result of fisheries over-exploitation, local trophodynamics and environmental parameters or a combination of these factors (Tsikliras & Koutrakis 2013).

According to the GOLT, sea warming as a result of climate change and the associated oxygen limitation will result in fishes of smaller sizes; this, in turn, should reduce many biological characteristics that are linked to growth, such as size at sexual maturity (Meyer & Schill 2021) and fecundity (Pauly 2021), while natural mortality should increase (Levangie et al. 2021). Apart from its obvious link to specific biological characteristics at the individual or population level, body size scales with a number of ecological properties including population growth rate, trophic level, and competitive interactions (Arendt 2007). Therefore, the reduced potential for somatic growth is one of the severe and universal effects of climate change, which together with distribution shifts, the migration of alien species, and seasonal shifts in life cycle events (Daufresne et al. 2009) will have to be dealt with in the next decades (or years if climate change is not halted). A reduction in the average individual body size may also have economic implications for local fisheries given the positive relationship of fish market price with body size (Tsikliras & Polymeros 2014).

Besides resolving the long-standing ichthyology issue of what limits fish growth (Pauly 2010), the GOLT has numerous practical implications in aquaculture and fisheries (Pauly 2019) that are particularly important for the fast warming eastern Mediterranean Sea (Tsikliras et al. 2015). The two main areas of the eastern Mediterranean, the Aegean and Levantine Seas, host the majority of marine aquaculture operations in the Mediterranean Sea (Stergiou et al. 2009) and are hot spots of non-indigenous species (Galil et al. 2018). The incoming non-indigenous species are usually species able to tolerate higher temperatures and lower oxygen levels compared to the indigenous species that will be oxygen limited and grow to smaller sizes if sea warming continues. This will create a competitive advantage in favour of non-indigenous species and is expected to affect local ecosystems and fisheries catch composition (Tsikliras et al. 2015) as well as yield-per-recruit (Baudron et al. 2014). Near future scientific efforts are suggested to focus on determining thermal performance curves for many marine populations, especially in the eastern

Mediterranean Sea, aiming to assess the effects of climate-induced changes and habitat loss on marine populations and potential risk for fisheries (Butzin & Pörtner 2016).

**Acknowledgements** We would like to thank Daniel Pauly for the useful suggestions he provided on the draft of this manuscript and two anonymous reviewers for their helpful comments and suggestions that improved our work.

**Data availability** The datasets generated and/or analysed during the current study are available by the authors upon reasonable request.

**Declarations**

**Ethics approval** No approval of research ethics committees was required to accomplish the goals of this study because no experimental work was conducted.

**Conflict of interest** The authors declare no competing interests.

**References**

Akyol O, Tokac A, Unsal S (1996) An investigation on the growth and reproduction characteristics of the sardine (*Sardina pilchardus* Walbaum, 1792) in the Bay of Izmir (Aegean Sea). *Su Urunleri Dergisi* 13(3–4):383–394

Alemaný F, Álvarez F (1993) Growth differences among sardine (*Sardina pilchardus* Walb.) populations in Western Mediterranean. *Sci Mar* 57(2–3): 229–234.

Alheit J, Licandro P, Coombs S, Garcia A, Giraldez A, Santamaria MTG, Slotte A, Tsikliras AC (2014) Atlantic Multi-decadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic. *J Mar Syst* 131:21–35

Andreu B, Rodriguea-Roda J, Larrañeta MG (1950) Contribución al estudio de la talla, edad y crecimiento de la sardina (*Sardina pilchardus* Walb.) de las costas españolas de Lovante (Noviembre 1949-Mayo 1950). *Publ Inst Biol Apl Barc* 7:159–189

Antonakakis K, Giannoulaki M, Machias A, Somarakis S, Sanchez S, Ibaibarriaga L, Uriarte A (2011) Assessment of the sardine (*Sardina pilchardus* Walbaum, 1792) fishery in the eastern Mediterranean basin (North Aegean Sea). *Medit Mar Sci* 12:333–357

Apostolidis C, Stergiou KI (2014) Estimation of growth parameters from published data for several Mediterranean fishes. *J Appl Ichthyol* 30:189–194

Arendt J (2007) Ecological correlates of body size in relation to cell size and cell number: patterns in flies, fish, fruits and foliage. *Biol Rev Camb Philos Soc* 82:241–256

Assis J, Tyberghein L, Bosh S, Verbruggen H, Serrão EA, De Clerck O (2017) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Glob Ecol Biogeogr* 27(3): 277–284.

Audzijonyte A, Barneche DR, Baudron AR, Belmaker J, Clark TD, Marshall CT, Morrongiello JR, van Rijn I (2019) Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Glob Ecol Biogeogr* 28:64–77

Barraca I, Pestana G (1985) Growth studies, using scales of *Sardina pilchardus* (Walb.) in Portuguese waters (1979–1984). *ICES C.M. /H:22*.

Baudron AR, Needle CL, Rijndorp AD, Marshall CT (2014) Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Glob Change Biol* 20:1023–1031

Bianchi CN, Morri C (2003) Global sea warming and “tropicalization” of the Mediterranean Sea: biogeographic and ecological aspects. *Biogeographia* 24:319–328

Bouchereau JL, Djabali F, Do Chi T, Mouhoub R, Pastor X, Tomasini JA (1985) Essais d’évaluation de l’état d’exploitation des stocks de sardines dans les divisions statistiques Baléares et golfe du Lion, par quelques méthodes analytiques simples. *FAO Fish Rep* 347:163–185

Bougis P (1952) La croissance des poissons méditerranéens. *Vie Milieu Suppl* 2:118–146

Brahmi B, Bennoui A, Oualiken A (1998) Estimation de la croissance de la sardine (*Sardina pilchardus*, Walbaum, 1792) dans la région centre de la côte algérienne. *Cah Opt Méd* 35:57–64

Brosset P, Fromentin JM, Van Beveren E, Lloret J, Marques V, Basilone G, Bonanno A, Carpi P, Donato F, Čikeš Keč V, De Felice A, Ferreri R, Gašparević D, Giráldez A, Gücü A, Iglesias M, Leonori I, Palomera I, Somarakis S, Tičina V, Torres P, Ventero A, Zorica B, Ménard F, Saroux C (2017) Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Prog Oceanogr* 151:149–162

Butzin M, Pörtner H-O (2016) Thermal growth potential of Atlantic cod by the end of the 21st century. *Glob Change Biol* 22:4162–4168

Campillo A (1992) Les pêcheries françaises de Méditerranée: synthèse des connaissances. Institut Français de Recherche pour l’Exploitation de la Mer, France. 206

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish* 10:235–251

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Zeller D, Pauly D (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob Change Biol* 16:24–35

Cheung WWL, Sarmiento JL, Dunne J, Fröhlicher TL, Lam VWY, Palomares MLD, Watson R, Pauly D (2013a) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat Clim Chang* 3:254–258

Cheung WWL, Watson R, Pauly D (2013b) Signature of ocean warming in global fisheries catch. *Nature* 497:365–368

Colloca F, Cardinale M, Maynou F, Giannoulaki M, Scarcella G, Jenko K, Bellido JM, Fiorentino F (2013) Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. *Fish Fish* 14:89–109

- Coro G, Gonzalez Vilas L, Magliozzi C, Ellenbroek A, Scarpioni P, Pagano P (2018) Forecasting the ongoing invasion of *Lagocephalus scleratus* in the Mediterranean Sea. *Ecol Model* 371:37–49
- Cury P, Pauly D (2000) Patterns and propensities in reproduction and growth of marine fishes. *Ecol Res* 15:101–106
- D'Ancona U (1937) La croissance chez les animaux méditerranéens. *Rapp P-V Réun CIEM* 10:162–224
- Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. *Proc Natl Acad Sci* 106:12788–12793
- Delgado A, Fernandez MAR, Goni R (1981) Contribución al estudio de la sardina (*Sardina pilchardus* Walb.) en aguas de Africa Occidental. III. Estudio del crecimiento por lectura directa de otolitos y por retrocálculo mediante escalimetría de escamas. *Bol Inst Esp Oceanogr* 6:139–164
- Dimarchopoulou D, Makino M, Prayoga MR, Zeller D, Vianna GM, Humphries AT (2021) Responses in fisheries catch data to a warming ocean along a latitudinal gradient in the western Pacific Ocean. *Environ Biol Fishes*. <https://doi.org/10.1007/s10641-021-01162-z>
- Djabali F, Boudraa S, Bouhdid A, Bousbia H, Bouchelaghem EH, Brahmī B, Dob M, Derdiche O, Djekrir F, Kadri L, Mammasse M, Stambouli A, Tehami B (1990) Travaux réalisés sur les stocks pélagiques et démersaux de la région de Béni-saf. *FAO Fish Rep* 447:160–165
- Fage L (1920) Engraulidae, Clupeidae. Report on the Danish Oceanographical Expeditions 1908–1919 to the Mediterranean and adjacent seas, vol. 2, no. 6. 140
- Froese R, Pauly D (2021) FishBase. In: R. Froese & D. Pauly (Editors). World Wide Web electronic publication. [www.fishbase.org](http://www.fishbase.org), 15 July, 2021
- Galil BS, Marchini A, Occhipinti-Ambrogi A (2018) East is east and West is west? Management of marine bioinvasions in the Mediterranean Sea. *Estuar Coast Shelf Sci* 201:7–16
- Gattuso J-P, Magnan A, Billee R, Cheung WWL, Howes EL, Joos F, Allemand D, Bopp L, Cooley SR, Eakin CM, Hoegh-Guldberg O, Kelly RP, Pörtner H-O, Rogers AD, Baxter JM, Laffoley D, Osborn D, Rankovic A, Rochette J, Sumaila UR, Treyer S, Turley C (2015) Contrasting futures for ocean and society from different anthropogenic CO<sub>2</sub> emissions scenarios. *Science* 349:6243
- GFCM (1981) Working party on resource appraisal and fishery statistics report of technical consultation on stock assessment in the Balearic and Gulf of Lions statistical divisions, Palma de Mallorca, Spain. *FAO Fish Rep* 227:1–151
- Golani D, Azzuro E, Dulčić J, Massuti E, Orsi-Relini L (2021) Atlas of exotic fishes in the Mediterranean Sea, 2ed edn. CIEM Publishers, Paris/Monaco, p 365
- Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. *Ecol Lett* 9(2):228–241
- Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol* 15:56–61
- Idrissi M (1987) Note sur la pêche des espèces pélagiques en Méditerranée. *FAO Fish Rep* 395:133–139
- James F (1970) Geographic size variation in birds and its relationship to climate. *Ecology* 51:365–390
- Kartas F (1981) Les clupéidés de Tunisie. Caractéristiques biométriques et biologiques. Etude comparée des populations de l'Atlantique est et de la Méditerranée. Thèse de Doctorat d'Etat, Université de Tunis, Faculté des sciences, 608
- Larrañeta G (1965) Les constantes de la croissance de la sardine de Castellón. *Proc Gen Fish Coun Médit* 8:273–276
- Larrañeta MG, Lopez J (1958) El crecimiento de la sardina (*Sardina pilchardus* Walb.) de las costas de Castellón. *Invest Pesq* 6:53–82
- Laskaridis K (1948) Study of the biology of the sardine (*Clupea pilchardus* Walb.) in Greek waters. *Prakt Hellen Hydrobiol Inst* 2:11–88
- Lee JY (1961) Le sardine du golfe du Lion (*Sardina pilchardus sardina* Regan). *Rev Trav Inst Pêches Marit* 25:417–512
- Lenoir J, Svenning J-C (2015) Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography* 38:15–28
- Levangie PEL, Blanchfield PJ, Hutchings JA (2021) The influence of ocean warming on the natural mortality of marine fishes. *Environ Biol Fishes*. <https://doi.org/10.1007/s10641-021-01161-0>
- Lopez J (1963) Age de la sardine (*Sardina pilchardus* Wald.) de Barcelone. *Proc Gen Fish Coun Médit* 7:299–308
- Meyer KA, Schill DJ (2021) The Gill-Oxygen Limitation Theory and size at maturity/ maximum size relationships for salmonid populations occupying flowing waters. *J Fish Biol* 98:44–49
- Mouhoub R (1986) Contribution à l'étude de la dynamique de la population exploitée de la sardine (*Sardina pilchardus*, Walbaum, 1792) des côtes algéroises. USTHB. Alger. 163 p. Thèse de Magister.
- Mozzi C, Duo A (1958) Croissance et âge des sardines de la Haute Adriatique débarquées à Chioggia. *Tech Pap Gen Fish Coun Médit* 5(10):1–15
- Muzinic R (1957) Sur la croissance de la jeune sardine (*Sardina pilchardus* Wald.) dans les eaux de Split. *Biljeske, Split* (12).
- Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935
- Pankhurst NW, Munday PL (2011) Effects of climate change on fish reproduction and early life history stages. *Mar Freshw Res* 62:1015–1026
- Pauly D (1994) On the Sex of the Fish and the Gender of Scientists. Chapman and Hall, London, p 250
- Pauly D (1998) Tropical fishes: patterns and propensities. *J Fish Biol* 53(Suppl A):1–17
- Pauly D (2010) *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals*. Excellence in Ecology (22), International Ecology Institute, Oldendorf/Luhe, Germany
- Pauly D (2019) A précis of Gill-Oxygen Limitation Theory (GOLT), with some Emphasis on the Eastern Mediterranean. *Medit Mar Sci* 20 Special Issue: 660–668
- Pauly D (2021) The gill-oxygen limitation theory (GOLT) and its critics. *Sci Adv* 7: eabc6050
- Penas Lado E (1978) Estudio sobre la dinámica y la estrategia de explotación del “stock” de sardina (*Sardina pilchardus*,

- Walbaum) de la costas de Castellón. Bol Inst Esp Oceanogr 4(3):143–160
- Perez N, Proteiro C, Alvarez F (1985) Contribucion al conocimiento de la biología de la sardina de Galicia. Bol Inst Esp Oceanogr 2:27–37
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate Change and Distribution Shifts in Marine Fishes. Science 308:1912–1915
- Porteiro C, Alvarez F (1985) Determinacion del crecimiento de la sardina, *Sardina pilchardus*, en aguas gallegas, mediante lectura directa de otolitos. Inst Esp Oceanogr Informes Tecnicos, No. 14
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–97
- Rodriguez-Roda J, Larrañeta MG (1955) El crecimiento de la sardina (*Sardina pilchardus* Wald.) de mento de las costas de Alicante. Invest Pesq 2:9–20
- Sabatés A, Martín P, Lloret J, Raya V (2006) Sea warming and fish distribution: the case of the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. Glob Change Biol 12:2209–2219
- Saraux C, Van Beveren E, Brosset P, Queiros Q Bourdeix J-H, Dutto G, Gasset E, Jac C, Bonhommeau S, Fromentin J-M (2019) Small pelagic fish dynamics: a review of mechanisms in the Gulf of Lions. Deep-Sea Res II 159: 52–61
- Scientific, Technical and Economic Committee for Fisheries (STECF) (2013) 2012 Assessment of Mediterranean Sea stocks part II (STECF 13–05). Publications Office of the European Union, Luxembourg, EUR 25309 EN, JRC 81592, 618
- Silva A, Carrera P, Masse J, Uriarte A, Santos MB, Oliveira PB, Soares E, Porteiro C, Stratoudakis Y (2008) Geographic variability of sardine growth across the northeastern Atlantic and the Mediterranean Sea. Fish Res 90:56–69
- Sinovic G (1983) Summary of biological parameters of sardine (*Sardina pilchardus* Walb.) from the central Adriatic. FAO Fish Rep 290:147–148
- Stergiou KI, Tsikliras AC, Pauly D (2009) Farming up the Mediterranean food webs. Conserv Biol 23:230–232
- Sumaila UR, Cheung WWL, Lam VWY, Pauly D, Herrick S (2011) Climate change impacts on the biophysics and economics of world fisheries. Nat Clim Chang 1:449–456
- Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. Nat Clim Chang 2:686–690
- Tserpes G, Tsimenides N (1991) Evaluation of growth rate differences in populations of *Sardina pilchardus* (Walbaum 1792) (Clupeidae) from the Aegean and Ionian Seas. Cybium 15:15–22
- Tsikliras AC (2008) Climate-related geographic shift and sudden population increase of a small pelagic fish (*Sardinella aurita*) in the eastern Mediterranean Sea. Mar Biol Res 4:477–481
- Tsikliras AC, Koutrakis ET (2013) Growth and reproduction of European sardine, *Sardina pilchardus* (Pisces: Clupeidae), in northeastern Mediterranean. Cah Biol Mar 54: 365–374
- Tsikliras AC, Polymeros K (2014) Fish market prices drive overfishing of the 'big ones'. Peer J 2: e638
- Tsikliras AC, Stergiou KI (2014) Mean temperature of the catch increases quickly in the Mediterranean Sea. Mar Ecol Progr Ser 515:281–284
- Tsikliras AC, Peristeraki P, Tserpes G, Stergiou KI (2015) Mean temperature of the catch (MTC) in the Greek Seas based on landings and survey data. Front Mar Sci 2:23
- Tsikliras AC, Licandro P, Pardalou A, McQuinn IH, Gröger JP, Alheit J (2019) Synchronization of Mediterranean pelagic fish populations with the North Atlantic climate variability. Deep-Sea Res II 159:143–151
- Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: A global environmental dataset for marine species distribution modelling. Glob Ecol Biogeogr 21:272–281
- Ulman A, Yildiz T, Demirel N, Canak O, Yemişkend E, Pauly D (2021) The biology and ecology of the invasive silver-cheeked toadfish (*Lagocephalus sceleratus*), with emphasis on the Eastern Mediterranean. NeoBiota 68:145–175. <https://doi.org/10.3897/neobiota.68.71767>
- Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH et al (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B: Biol Sci 281:20140846
- Voulgaridou P, Stergiou KI (2003) Trends in various biological parameters of the European sardine, *Sardina pilchardus* (Walbaum, 1792), in the Eastern Mediterranean Sea. Sci Mar 67: 269–280

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.