Influence of environmental variables on the larval stages of anchovy, *Engraulis encrasicolus*, and sardine, *Sardinops sagax*, in Algoa Bay, South Africa

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Abstract We investigated the environmental drivers of larval abundance of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in Algoa Bay, Eastern Cape (South Africa). This study comprised a pre-drought post-drought time period, comparing the responses of the fish larvae to different factors before and after the drought. The current study presents, for the first time, which environmental variables are affecting the anchovy and sardine larvae populations in the region. Easterly wind speed and zooplankton density were the only environmental variables that presented a significant change between the pre- and post-drought periods, increasing after the drought. Generalized additive models (GAMs) were used in order to explore the effects that environmental factors might have in the abundance of anchovy and sardine larvae in Algoa Bay. Specifically, the GAM that best explained the deviance of the anchovy larvae dynamics included the

covariates rainfall, easterly wind speed, Chl *a* concentration, sardine larvae abundance and the interactions *SST*Chla* and *sard*SST*. The GAM best explaining sardine larvae abundance included only the easterly wind speed as a covariate. This model showed that there was a positive relationship between the higher values of wind speed and sardine larvae abundance.

Keywords Climate shifts · GAMs · Ichthyoplankton · Recruitment · Small pelagic fish

Introduction

Fluctuations in the small pelagic fish populations have a major impact on the ecosystem and on fisheries (Cury et al. 2000). Therefore, an understanding of their dynamics is essential. The response of small pelagic fish species to the environmental variability is manifested as inter-annual oscillations in recruitment success (Cury and Roy 1989; Cushing 1996; Bakun 2006); thus, environmental regime shifts have resulted in abundance and distributional changes between sardine and anchovy in most upwelling areas worldwide (Roy et al. 2007; Coetzee et al. 2008). Recruitment variability stands as one of the major issues in fisheries research (Houde 2008). Because the larval fish stages have the highest vulnerability to mortality, these life-stages are the principal determinant of recruitment (Caley et al. 1996; Bergenius et al. 2002).

The combination of physical factors and food availability has become widely accepted as the main

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environmental determinant of larval fish survival (Leggett and Deblois 1994; Cushing 1996; Costalago et al. 2011), and thereby fish population dynamics (Beaugrand and Reid 2003). Nevertheless, new insights have demonstrated that recruitment variability can result from numerous abiotic and biotic processes, including fishing, maternal condition and other anthropogenic factors, operating on many different spatio-temporal scales, and represents an integrated process acting throughout early life stages of fishes (Houde 2008). With the increasing threat of global climate change, there is an urge to understand which environmental factors influence the early stages of key species like sardine and anchovy and thereby further comprehend how these factors alter population growth.

Algoa Bay in the Eastern Cape, South Africa, is an area in which both sardine and anchovy adults are found and where their larvae are known to complete their pelagic phase in the bay (Patrick and Strydom 2008). The influence of environmental variables on the fluctuations between sardine and anchovy have largely been studied in the Benguela Current system (Shannon et al. 1984; van der Lingen et al. 2006), in the western coast of South Africa. However, there is a particular lack of knowledge regarding the dynamics of their larval stages in the Agulhas Current system (Hutchings et al. 2002; Patrick and Strydom 2008), which flows southwards and then southwestwards along the eastern and southern coasts of South Africa.

Thus, it is urgent to provide information about the state of the pelagic ecosystem in Algoa Bay, and in particular for anchovy and sardine, as these species are extremely relevant economically and ecologically. Algoa Bay also hosts important populations of marine top predators, such as South African fur seals, bottlenose and common dolphins, cape gannets and the world's largest African penguin colony (Pichegru et al. 2010), which feed predominantly on small pelagic fish (Batchelor and Ross 1984; David 1987; Young and Cockcroft 1994). Moreover, there is an ongoing discussion about the potential impacts that the prospective finfish farming activity planned in Algoa Bay (Bloom 2012; Hutchings et al. 2013). Potential impacts of tourism (shark cage diving, whale watching, recreation fishing), on pollution levels, fishing activities, boat traffic and existing and planned Marine Protected Area in the bay, are currently being assessed (Bloom 2012, 2013).

With this work, we thus intend to elucidate what environmental (among wind, rainfall, water temperature

and chlorophyll *a* as an indicator of productivity) and other factors (food availability, i.e. zooplankton density, and larval fish abundance) are the major regulators of the abundance of the larvae of anchovy and sardine in Algoa Bay.

Material and methods

Study site

Algoa Bay is characterized by important seasonal environmental fluctuations (Patrick and Strydom 2008; Goschen et al. 2012), combined with complex circulation as the Agulhas Current leaves the coast following the shelf break (Goschen and Schumann 1988; Boyd et al. 1992).

Algoa Bay (Fig. 1) is situated on the southeast coast of South Africa, on the eastern limit of the Agulhas Bank. The Agulhas Current flows south-westward, around 80 km offshore of Algoa Bay, bringing nutrient poor, tropical waters (Lutjeharms 1981). The bay is encompassed by Cape Recife in the west and Woody Cape in the east, and has a wide mouth (~ 90 km) which allows free exchange of water between the bay and the Agulhas Bank waters (Goschen and Schumann 1994, 2011). The shelf width extends for ~ 55 km, reaching a maximum depth of ~ 73 m (Bremner 1991).

Algoa Bay has a warm temperate climate with sea surface temperature ranging 10–24 °C throughout the year (Smit et al. 2013). The area experiences an annual rainfall of 400 to 800 mm per annum (Dent et al. 1987), with peaks of rainfall in autumn and spring (Whitfield 1998). However, between 2008–2010 Algoa Bay received <250–300 mm per annum of rainfall, which classified those years as a drought period. During summer, the water column is stratified but the winds during winter largely contribute to the mixing of water such that little or no stratification is evident (Goschen 1991). Wind seasonality is highly variable between the winter and summer months. Strong easterly winds dominate in summer and these winds induce local upwelling events (Schumann et al. 1991). The Sundays and Swartkops Rivers play an important role in the runoff and input of nutrients and energy into the nearshore coastal ecosystem of the bay (Lukey et al. 2006; Patrick and Strydom 2008).

Fig. 1 Geographic location and map of Algoa Bay, South Africa. The stations where the zooplankton and larval fish were caught are marked by the stars

Larval fish and mesozooplankton collection

From March 2005 to January 2007 (i.e. before the drought period), samples of larval fishes were collected once a month during two successive months per season (March and April as autumn months, June and July as winter months, September and October as spring months, and December and January as summer months), in order to determine seasonal trends in ichthyoplankton (Pattrick and Strydom 2008). At each station (Fig. 1), larvae were collected by means of ski-boat based plankton tows using a set of bongo nets. Plankton nets were 3.5–4 m long with a mouth diameter of 750 mm, and a mesh size of 500 μm . A calibrated flowmeter was fitted to the 12 mm thick stainless steel frame of each net to calculate the volume of water sampled. The nets were pulled parallel to shore using a stepped oblique tow at a speed of 2 knots. Bottom, mid and subsurface waters were sampled for 2 min

each, and including hauling, each tow lasted approximately 8 min.

After the 2008–2010 drought period, larval fish were collected monthly from August 2010 to May 2013 within the bay as part of an ongoing plankton monitoring programme initiated by the South African Environmental Observation Network (SAEON). Larvae were sampled monthly at the six stations (Fig. 1), also by means of ski-boat based plankton ring net tows as described above for the pre-drought period.

Alongside with the fish larvae, zooplankton samples were collected. Zooplankton was sampled using a WP2 style net (420 mm diameter, 90 μm mesh size and 2 m long). The samples were fixed on site in 10% formalin. The zooplankton was measured as dry weight (mg/m^3).

In the laboratory larval fish were sorted and identified to the lowest possible taxonomical level (Olivar and Shelton 1993) and standard length (SL) measured to the closest 0.1 mm using an eye piece micrometer. The

abundance of sardine and anchovy larvae for each sample was estimated as density using the following formula:

$$\text{Density} = 100 * \frac{\text{No. of larvae}}{(\text{flow meter revolutions} \div \text{calibration value in m}^3)}$$

Environmental factors

Rainfall, wind speed and wind direction were obtained from the South African Weather Service (SAWS) for Coega (33°48'18"S, 25°41'11"E; Fig. 1) during the study period. The mean wind speed of all days with wind directions from 56.24° to 123.74° (taken as easterly components, which induce upwelling in the bay) was calculated and squared, thereby producing a pseudo-stress index (m^2/s^2) that represented the average speed of all easterly winds in that month (Daskalov et al. 2003). Average monthly rainfall (mm) was used.

Satellite data from the NASA Earth Observations satellite platform (MODIS-Aqua Mission; www.neoscience.gsfc.nasa.gov) provided information on Sea surface temperature (SST) and chlorophyll *a* concentration. Chlorophyll *a* concentrations were recorded as monthly averages (mg/m^3) at a 1×1 km scale. Chlorophyll *a* is taken as a representation of phytoplankton biomass (Shannon et al. 1984). Both chlorophyll *a* and SST data were retrieved on March 2015. Mesozooplankton concentrations in the bay, collected at the same six sites where the larval fish densities were sampled, were obtained from the SAEON (see detailed methodology in Dali 2011).

Data analyses

Statistical analyses were performed with the R software v. 3.2.0. Significance levels of $p < 0.05$ were used. All data were tested for normality using the Shapiro-Wilk test. Wilcoxon tests were used to determine differences in densities in anchovy and sardine larvae, in zooplankton density and in the environmental variables between 2005–2007 (before the drought) and 2010–2013 (after the drought ended).

To assess which environmental factors were affecting larval anchovy and sardine dynamics, Generalised Additive Models (GAMs), as implemented in the *mgcv* library of R (Wood 2001). Easterly wind speed, rainfall, mesozooplankton density, sea surface temperature (SST), chlorophyll *a* concentration and the other larval fish species abundance (i.e., sardine as a covariate in the

anchovy model and vice-versa) were used as covariates. In a previous analysis, no correlation among covariates was detected (Suppl. Fig. 1) All the interactions between variables that resulted significant at $p < 0.01$ in an ANCOVA test were included in the initial GAMs of the larval abundance. Then, the covariates (and interactions) whose partial effect had the lowest significance level (i.e. the covariate with the highest p -value) were removed one by one. The family link used was quasi-Poisson to accommodate for the dispersion and zero-values. No lag time was used between the larval density and the environmental factors as during sampling the larval fish were only a few days old. Effective covariates were selected following Wood (2001). Covariates were deleted from the models if the following three criteria were met: (i) the estimated degrees of freedom was close to 1; (ii) the confidence interval was zero everywhere; and (iii) the generalized cross validation (GCV) score decreased when the term was dropped. The GCV method was used to select a best fit model, with lower GCV score being better.

Results

Larval and mesozooplankton abundance

Larval anchovy abundance was much higher than larval sardine (Fig. 2). Larval anchovy had similar abundance throughout the year, but showed the highest abundance in spring while larval sardine had the highest densities per month in winter. Larval anchovy increased significantly between the two sampling periods ($F = 0.05$, $p < 0.0001$; $t = -4.44$, $p < 0.0001$), while larval sardine densities did not change significantly between 2005–2007 and 2010–2013 ($F = 0.69$, $p = 0.237$; $t = -0.1$, $p = 0.445$). Anchovy larvae were present during 88.0% of the sampling trips and averaged 1.7 ± 3.3 larvae/ 100m^3 during 2005–2007 and 14.2 ± 14.1 larvae/ 100m^3 during 2010–2013. The combined average for all the samples for anchovy larvae was 9.7 ± 12.9 larvae/ 100m^3 per sample (range 0 – 45 larvae/ 100m^3 per month). Sardine larvae were present during 70.9% of the sampling trips and averaged 1.4 ± 2.2 larvae/ 100m^3 per sample when present (range 0 – 9.4 larvae/ 100m^3 per month). Total length of anchovy and sardine larvae ranged from 1.6 – 10.5 mm and 3 – 8.5 mm, respectively. Mesozooplankton density was highest in summer

Fig. 2 Larval density for sardine and anchovy per month for March 2005–January 2007 and August 2010–July 2013 in Algoa Bay, Eastern Cape. Larval fish were not sampled in the bay

between these two periods. The vertical dotted line separates both periods (pre-drought and post-drought)

with $54.0 \pm 31.9 \text{ mg/m}^3$ on average, and lowest in winter with a mean of $25.0 \pm 12.7 \text{ mg/m}^3$.

The differences between the pre-drought and post-drought periods were significant in anchovy and zooplankton density (Fig. 3).

Environmental variability

Before the drought (2005–2006), the mean monthly rainfall in the region was $39.05 \pm 24.16 \text{ mm/month}$. During the drought, monthly rainfall was between 20.5–24.36 mm/month. The years 2011 and 2012, which saw the beginning of the post-drought period, had more than double the rainfall than during the drought, with 55.21 mm/month in 2010–2011 and 73.21 mm/month in 2012–2013. Annual easterly wind index ranged from 7.94–22.8 m^2/s^2 between 2005–2013 (Suppl. Fig. 2). Monthly easterly winds were highest in spring and summer, with much weaker winds dominating autumn and winter. These strong winds were closely followed by peaks in chlorophyll *a* in autumn, spring and summer. Chlorophyll *a* ranged from $3.3 \pm 0.1 \text{ mg/m}^3$ in winter to $6.9 \pm 1.03 \text{ mg/m}^3$ in autumn (Suppl. Fig. 2). Across all years, monthly

concentrations ranged between 0.65–22.4 mg/m^3 (Suppl. Fig. 2). Sea surface temperature ranged 17.24–23.15 °C in the pre-drought period, and 16.69–23.45 °C in the post-drought period (Suppl. Fig. 2).

Regarding the differences between the pre-drought and post-drought periods, significance ($p < 0.05$) was found only in the easterly wind speed (Fig. 3).

Relationships between environmental factors and larval abundances

The interactions that presented a significant effect ($p < 0.01$) on anchovy larvae abundance were SST and chlorophyll *a* and sardine larvae abundance and SST. These interactions were included in the initial GAM model for anchovy (Table 1). A smoother was added to the covariates (or interactions) that presented a non-linear effect (Table 1).

To explain anchovy larvae abundance, there were two GAMs with very similar GCV values: A2 and A3 (GCV = 142.12 and 142.07, respectively). A2 included the terms *rain*, *wind*, *Chla*, *sard*, *SST*, *SST*Chla* and *sard*SST* and explained 46.3% of the variance (Table 1), whereas A3 included the terms *rain*, *wind*, *Chla*, *sard*,

Fig. 3 Boxplots showing median (bold line), first and third quartiles (box) and 95% confidence intervals (whiskers) for the variables that were significantly different between the pre-drought and post-drought periods: easterly wind speed ($p < 0.05$), zooplankton density ($p < 0.01$) and larval anchovy density ($p < 0.001$)

$SST \times Chla$ and $sard \times SST$ and explained 43% of the variance (Table 1). An ANOVA test did not show significant differences between these two models. We chose the A3, which had the lowest GCV value and a lower number of terms than A2, as the best fit. The *sard* term (sardine larvae abundance) was the most significant explanatory variable of the best-fit model, followed by wind speed.

Looking at the best-fit model, larval anchovy abundance was higher at intermediate rainfall levels (approx. 100 mm/month). Concurrently, higher values of wind speed and *Chl a* concentration had a positive effect on anchovy larvae abundance (Fig. 4A). Anchovy larvae abundance was higher at the lowest levels of sardine larvae abundance (Fig. 4A). When higher than 80, interaction $SST \times Chla$ had a negative effect on the anchovy larvae population; contrarily, the interaction $sard \times SST$ had a positive effect on the anchovy larvae abundance (Fig. 4A).

The ANCOVA indicated that none of the possible covariate interactions presented a significant effect on sardine abundance. Rainfall and wind were the only variables that presented a non-linear effect on sardine abundance and thus a smoother was added to each variable in the initial model. The GAM for sardine larvae abundance with the lowest GCV score (8.31) was S6, which explained 41.9% of the deviance and included only the term *wind* (Table 1). This GAM best explaining sardine larvae abundance (Fig. 4B) showed that there was a positive relationship between the higher values of easterly wind speed ($> 15 \text{ m}^2/\text{s}^2$) and sardine larvae abundance.

The residuals of the best models (with the lowest GCV) for both anchovy and sardine abundance response variables were visually explored for violations from the model assumptions. There was no significant linear trend in residuals plotted against the predicted response, and residuals appeared to be normally distributed in the case of the best fit models for anchovy and sardine larvae abundance (Suppl. Fig. 3). No autocorrelation is evident for the data.

Discussion

The results of this study show that, following a drought period of about two years in Algoa Bay, anchovy larvae become significantly more abundant than before the drought happened, whereas the sardine larvae population in the region did not show any significant change in size after the drought period. These two species of small pelagic fish play a particularly important role in the pelagic food web (Cury et al. 2000; Pikitch et al. 2014), as well as they are commercially relevant (Pikitch et al. 2014). Thus, it is important to identify which factors might be affecting the dynamics of the early life stages of their populations in the region. The

Table 1 Forward stepwise General Additive Models of fish larvae abundance and selected environmental variables in Algoa Bay during the entire period of study

Models	Deviance explained	n	Estimate	Std. Error	t-value	p(z)	r ²	GCV
Response: Anchovy larvae abundance								
A1.- (rain) + wind + (zooplk) + Chla* + sard + SST + SST:Chla* + sard:SST	50.7%	40	9.301	1.638	5.678	<0.0001	0.35	144.64
A2.- (rain) + wind* + Chla* + sard* + SST + SST:Chla* + sard:SST*	46.3%	42	9.772	1.635	5.976	<0.0001	0.34	142.12
A3.- (rain) + wind* + Chla* + sard** + SST:Chla* + sard:SST**	43%	42	9.772	1.660	5.887	<0.0001	0.32	142.07
A4.- wind* + Chla* + sard* + SST:Chla* + sard:SST**	38.3%	42	9.772	1.695	5.766	<0.0001	0.29	142.59
A5.- Chla* + sard* + SST:Chla* + sard:SST**	29.9%	42	9.772	1.775	5.506	<0.0001	0.22	151.19
A6.- sard + SST:Chla + sard:SST*	23.1	42	9.772	1.844	5.300	<0.0001	0.16	160.32
Response: Sardine larvae abundance								
S1.- (rain) + (wind) + zooplk + Chla + anch + (SST)	43.3%	40	1.690	0.398	4.247	0.0002	0.22	8.89
S2.- (rain) + (wind)* + zooplk + Chla + (SST)	41.9%	41	1.649	0.387	4.256	0.0001	0.23	8.31
S3.- (wind) + zooplk + Chla + (SST)	35.5%	41	1.649	0.394	4.187	0.0002	0.21	7.99
S4.- (wind)* + zooplk + Chla	24.6%	41	1.649	0.404	4.079	0.0002	0.16	7.59
S5.- (wind)* + zooplk	23.5%	42	1.611	0.393	4.099	0.0002	0.12	7.14
S6.- (wind)*	28.4	44	1.573	0.368	4.268	0.0001	0.21	6.73

The best model for each species is highlighted in **bold**. Covariates with smoother are presented in brackets. The significance of each term in each model is marked with * ($p < 0.05$) and ** ($p < 0.01$)

anch, anchovy larvae density; *Chla*, chlorophyll *a* concentration; *rain*, monthly rainfall; *sard*, sardine larvae density; *SST*, sea surface temperature; *wind*, easterly wind speed; *zooplk*, mesozooplankton density; *GCV*, Generalized Cross Validation

current study presents, for the first time, which environmental variables are affecting the anchovy and sardine larvae populations in the region. Easterly wind speed and zooplankton density were the only environmental variables that presented a significant change between the pre- and post-drought periods, increasing after the drought. We show here that, together with wind, it was rainfall, chlorophyll *a* and sardine larvae abundance, and the interactions between temperature and chlorophyll *a* and between temperature and sardine larvae abundance, the variables that better explained the changes in the anchovy larvae population. Regarding the sardine larvae population, its variability was better explained by wind speed than by any other environmental variable.

In South African waters, adult anchovy may be found inshore but are more often found over 100 km from the coastline, whereas adult sardines tend to live within 50 km of the coast, and are commonly found inshore (Barange et al. 1999; van der Lingen et al. 2001; Fairweather et al. 2006). While anchovies are indeed spawning in Algoa Bay (Hutchings et al. 2002; Van der Lingen and Huggett 2003), sardines spawn only sporadically along the East coast of South Africa (Hutchings

et al. 2002; Connell 2010) because adult sardine congregate mostly around the inshore regions of the western Agulhas Bank (Beckley and van der Lingen 1999). The relatively low abundance of sardine larvae found within Algoa Bay reinforces the fact that this is not a primary spawning area for sardine (van der Lingen et al. 2001). The warm waters of the east and south coast of South Africa, including Algoa Bay, promote the increase of anchovy larvae abundance (van der Lingen et al. 2001). While both sardine and anchovy use this bay to spawn and complete their pelagic phase, anchovy larvae are far more abundant as they are less tolerant of the cold waters along the west coast and therefore thrive in the warmer waters of Algoa Bay.

Larvae of anchovy and sardine collected for this study ranged 1.7–8.9 mm and 2.9–9.5 mm SL, respectively, and thus are unlikely to be able to consume mesozooplankton (Muck et al. 1989; Costalago et al. 2012). Therefore, an increase in larval abundance following a proliferation in this food source should not be expected. This helps to explain why a significant effect of mesozooplankton on the abundances of anchovy and sardine larvae was not detected, as fish at this size are

feeding mainly on microplankton. Microplankton usually represents 70–90% of total zooplankton in coastal

areas, but when the total zooplankton abundance increases, there is generally a decrease in the

Fig. 4 Best fit multivariate generalized additive model (GAM) terms showing the estimated partial effects (solid line) that each predictor variable has on the abundance of (a) anchovy (model A3 as in Table 1) and (b) sardine (model S6 as in Table 1) larvae during the entire period of study. The grey-shaded areas are the 95% confidence intervals, and the small lines along the x axis indicate the location of the sample plots. anch: anchovy larvae abundance; chl a : chlorophyll a concentration; rain: monthly rainfall; sard: sardine larvae abundance; SST: sea surface temperature; wind: easterly wind speed; zooplk: mesozooplankton density

microplankton/mesozooplankton ratio, probably due to the higher predation of mesozooplankton on microplankton (Calbet et al. 2001). Thus, a moderate abundance of mesozooplankton in Algoa Bay might benefit the populations of small clupeid larvae through an increase in microplankton.

Both larval anchovy abundance and mesozooplankton density were significantly higher during the post-drought period than during the pre-drought period, suggesting that mesozooplankton might influence anchovy larvae positively. The explanation for that is likely to be related to the adults spawning in Algoa Bay. Anchovy adults feed mostly on mesozooplankton (van der Lingen et al. 2006; Costalago et al. 2012), and thus a higher prey availability ultimately translates into a greater adult presence and thereby egg production (Kjesbu et al. 1996).

Chlorophyll a is a measure of phytoplankton in surface waters (Shannon et al. 1984). Higher chlorophyll a concentrations have been associated with feeding grounds of both sardine and anchovy (van der Lingen et al. 2006; Bellido et al. 2008). Higher easterly wind speeds, which are related to upwelling events and higher chlorophyll a concentration (Goschen and Schumann 1995), alter the dynamics of the surface waters creating currents and turbulence. That turbulence may harm small fish larvae and the currents may result in offshore transport (Boyd et al. 1992; Hutchings et al. 2002) away from the sampling sites. However, the important input of nutrients brought up by the upwelling events following intense periods of easterly winds have an overall positive effect on the abundance of anchovy larvae, as shown by the GAM.

Low levels of chlorophyll a during summer in Algoa Bay are related to strong southwesterly winds, which favor mixing of the water column and suppress upwelling activity. On the other hand, strong northeasterly winds in the region promote upwellings (Schumann et al. 1991). The upwelling events associated with easterly winds occurred mainly in the post-drought years

(McInnes et al. 2017). This supports the results of our GAMs, which show a significant influence of high levels of easterly wind speed and Chl a concentration on anchovy larvae. Although both anchovy and sardine in Algoa Bay seem to spawn throughout the year, a higher abundance of anchovy larvae is generally observed during the summer. Furthermore, moderate levels of turbulence are important for larval fish, since this developmental stage is far more dependent than adult fish on winds and tides as a means of prey encounter (MacKenzie and Leggett 1991).

The GAMs showed that moderate levels of levels in Algoa Bay benefit the size of the anchovy larvae population. This is likely due to the nutrient inflow from the rivers into the Bay (Patrick and Strydom 2008). On the contrary, low, but also very high amounts of rain seemed to have a negative effect on the fish larvae. The drought period might have limited the survival of the larvae and the recruitment of anchovy and sardine in the Bay, thus keeping the larval abundance registered after the drought from increasing any further. Possibly, this effect has been counterbalanced by the moderate rains in the post-drought period, but especially by the relatively strong easterly winds. Moreover, McInnes et al. (2017) described an unusual spike in Chl a in Algoa Bay during April–May 2012 and again in May 2013, and they linked it to water pulses offshore in the Agulhas Current and the associated influxes of cool, upwelled waters into the Bay. McInnes et al. (2017) claimed that, through an enhancement in the regional primary production, these pulses led to the increase in pelagic fish abundance, especially around Bird Island.

Another environmental variable which can potentially influence the abundance of anchovy and sardine larvae in the Bay is the sea surface temperature (SST). The mean SST in the southern Benguela Current system ranges from 14.0 – 17.8 °C during calm conditions but decreases to 9.3 – 10.2 °C during upwelling events (Pitcher et al. 1996), which is far lower than the mean SST for Algoa Bay. This temperature variability in the southern Benguela Current system affects the spawning success of sardine and anchovy (van der Lingen and Huggett 2003), where anchovy prefer to spawn in warmer waters while sardine can spawn at a wider range of temperatures (van der Lingen et al. 2001), but prefer cooler temperatures. The temperature of the water not only affects spawning success but also the survival of larval stages (Clemmesen et al. 2003; Green and Fisher 2004). The larval phase of pelagic fish is susceptible to

changes in metabolism associated with variation in temperature (Rombough 1997). This, in turn, affects physiological processes, growth, development and behavioural responses (Green and Fisher 2004).

In the Benguela Current, sardine (*Sardinops sagax*) spawn successfully between 15.2–20.5 °C and anchovy (*Engraulis encrasicolus*) spawn between 17.4–21.1 °C (Van der Lingen and Huggett 2003). Sardine spawn along the South African coast throughout most of the year (Coetzee et al. 2008), peaking in the spring and summer months (Crawford 1981), and are relatively non-specific in their choice of spawning areas and may successfully spawn on the west and south coast (van der Lingen et al. 2001; Coetzee et al. 2008). In contrast, anchovy spawning peaks in summer and eggs are rarely found in the autumn and winter months (Crawford 1981). Once sexual maturity is reached, the temperature preference of each species changes, with sardine more likely to be found in warmer waters closer to the shore line, and anchovy more likely to be found farther offshore in cooler, oceanic waters (van der Lingen et al. 2001).

In other areas of the world where anchovy and sardine species co-exist, the larvae of both species are usually not found together [e.g., in the Mediterranean Sea *E. encrasicolus* and *Sardina pilchardus* spawn at different times of the year so that their larvae do not occur simultaneously (Palomera et al. 2007)]. When the early life stages of both anchovy and sardine in non-upwelling regions occur together, competition for food is more likely to take place (Costalago et al. 2012; Costalago et al. 2014) compared to upwelling areas where plankton would be more abundant [e.g., Benguela Current system (van der Lingen et al. 2006)]. This competition for relatively scarce resources is further exacerbated in clupeid larvae, since anchovy and sardine start having different diets only after they have developed their gill rakers at an advanced juvenile stage (Costalago et al. 2012; Costalago et al. 2014). Therefore, competition for food might also be an important factor limiting the abundance of anchovy and/or sardine larvae in Algoa Bay. Given the difficulty to measure inter-species competition, which, in addition, is rarely independent of other factors (Hollowed et al. 2000), the estimation of this parameter requires indirect ways of quantification. Food limitation, predation risk, foraging behavior and carrying capacity of the system are just some examples of the ecological parameters commonly

connected to competition for food (Hollowed et al. 2000; Fulton et al. 2005; Johnson 2007).

The present analysis shows that larval abundance of sardine and anchovy in Algoa Bay can be at least partially modelled using a limited number of environmental predictors, and provides an important update in the state-of-the-art of the marine ecosystem. Moreover, the high relevance of small pelagic fish in the marine ecosystem and in the economy of the region and the urgent requirement of scientific information to help assess the risks and/or benefits of Marine Protected Areas (Pichegru et al. 2012; Sherley et al. 2013) or of fish farming activities (Bloom 2012, 2013; Hutchings et al. 2013) in Algoa Bay make the present study particularly necessary.

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