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Exploring South African Pacific oyster mariculture potential through combined Earth observation and bioenergetics modelling

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ABSTRACT

The combined use of satellite-derived environmental data and a dynamic energy budget (DEB) model to determine Pacific oyster growth potential was adapted for the South African marine environment. Study areas consisted of the West Coast (high-chlorophyll, low temperature) and the South Coast (variable chlorophyll, higher temperature) ecoregions. Chlorophyll-a and sea surface temperature products from the Moderate Resolution Imaging Spectroradiometer (MODIS) were used to simulate yearly growth for 18 years. Average growth performance at the end of the culture period was mapped and compared for prominent sectors. Industry-relevant growth indicators, "days to reach commercial weight" and "optimal culture period length" were also established.

High growth potential was found in eastern nearshore sectors of the South Coast, particularly Plettenberg Bay, where oysters reached a median total weight (TW) of 271 g within 9 months. Other sectors in the region yielded Large commercial size within 150 days. However, South Coast growth hotspots were found to be highly variable, with transient unfavourable growth conditions leading to low flesh mass relative to TW. Growth potential was favourable in northern sectors of the West Coast, where oysters reached a median TW of up to 148 g in 9 months, Large commercial size within 200 days, and contained high flesh mass relative to TW.

Current oyster production sites were not found to be optimal for growth. Higher-growth sites coincide with areas in economic decline or with high levels of poverty. However, due to constraints of applying DEB models over large spatial scales, these results are considered preliminary and await *in situ* verification, as well as a spatial multi-criteria analysis, before investment and development.

1. Introduction

While aquaculture has overtaken capture fisheries as a global seafood supply (Brugère et al., 2019; Naylor et al., 2021; Pernet and Browman, 2021), in South Africa aquaculture still contributes less than 1% to the country's seafood supply despite declining fish stocks (DAFF, 2014). Considering the high primary productivity of South African coastal waters, particularly in the Benguela upwelling area (Pitcher and Jacinto, 2019), such aquaculture production is paradoxically extremely low.

Pacific oyster was introduced to South African shores in the late 1970 s for aquaculture purposes (Haupt et al., 2010; Keightley et al., 2015; Robinson et al., 2005). Although it is considered a highly invasive species elsewhere (Troost, 2010), wild populations of *C. gigas* have only been established on the South Coast, where temperatures and food sources are sufficient for survival, and high enough for spawning to occur (Keightley et al., 2015; Robinson et al., 2005). The high temperature on the East Coast, due to the warm Agulhas Current, does not allow for survival. On the West Coast, the Benguela upwelling system provides cool waters and abundant phytoplankton - an environment optimal for oysters and where studies have reported the highest recorded Pacific oyster growth rates in the world to date (Nel et al., 2014; Pieterse et al., 2012). Interestingly, along the West Coast, seawater temperature is too low for reproduction to occur and wild populations to establish (Bernard et al., 2011; Castaños et al., 2009; Dutertre et al., 2009; Haupt et al., 2010). The South African coastal environment thus provides an

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interesting location for the cultivation of this alien species, specifically on the West Coast where there is less overlap of range with native oyster species (*Pinctada capensis*, *Striostrea margaritacea, Ostrea algoensis* and *Ostrea atherstonei*) and where it can be cultivated with a lower risk of becoming invasive.

Despite unprecedented growth rates in multiple locations, there has been little success in expanding the oyster aquaculture sector, evident when comparing South African and global production estimates. Although in 2016 it was reported that there were eight farms in South Africa collectively producing 277 tons of Pacific Oyster (DAFF, 2017a), in 2019 only five farms remained. There is thus a need to find suitable sites for marine shellfish cultivation in South Africa. To ensure the viability and longevity of any oyster cultivation venture, a scientifically informed determination of potential grow-out sites and subsequent marine spatial planning is required.

Traditional site selection for aquaculture has been broadly based on either selecting for areas known to be environmentally suitable for the species, or areas where the species' cultivation has been historically documented (Krause and Stead, 2017). While this explicates where aquaculture is possible, it may not give insight into where aquaculture is optimal, nor does it uncover new sites. For the discovery of new and optimal cultivation areas, including those offshore, a combined approach of Earth Observation (EO) and ecophysiological growth models is advantageous. Observation of the spatio-temporal variability in the growth of many aquaculture species using this approach informs the optimal locations and periods for cultivation (Barillé et al., 2020; Bertolini et al., 2021; Palmer et al., 2020). The use of EO makes it possible to measure environmental variables relevant for aquaculture site selection such as sea surface temperature (SST), suspended particulate matter (SPM), and chlorophyll-a (chl-a) concentration across a variety of temporal and spatial scales (Gernez et al., 2017; Snyder et al., 2017). Gernez et al. (2021) outlined the latest use of EO to inform aquaculture planning, development, and management, noting its utility in site-selection, harmful algal bloom (HAB) monitoring and growth monitoring. This approach has been applied to South Africa for the purpose of HAB detection using Envisat/MERIS and Sentinel3/OLCI satellite missions (Pitcher et al., 2019; Smith et al., 2018; Smith and Bernard, 2020; Smith and Pitcher, 2015), but has not yet been used as a site-selection tool. By applying EO data to ecophysiological models such as the Dynamic Energy Budget (DEB) model (Palmer et al., 2020, 2021), the spatio-temporal extent of Pacific oyster potential growth can be more precisely established.

The objective of this study is to determine optimal sites for mariculture of *C. gigas* in the South African coastal waters using a combined EO-DEB model approach. The DEB model was calibrated and validated using *in situ* oyster growth data. Then, nearly two decades of satellite SST and chl-a observations (2002–2020) for South African coastal waters were used as inputs of DEB simulations to investigate the spatio-temporal variability in oyster growth, identify the most performing sites, and determine the optimal culture period duration through different model scenarios.

2. Materials and methods

2.1. Study areas

The South African Exclusive Economic Zone (EEZ) encompasses a range of climatic conditions, from tropical in the Indian Ocean to temperate in the Atlantic (Griffiths et al., 2010; Sink et al., 2018). For the purposes of Pacific oyster cultivation, the West and South Coasts were chosen due to their environmental suitability for this temperate species - low enough temperatures and sufficient phytoplankton concentration (Fig. 1). These are also areas where oyster aquaculture currently occurs or has historically been practised. As each coast is composed of distinct ecoregions, and thus have vastly different environmental characteristics, the model was calibrated and applied separately to the South and West coasts. This resulted in two study areas: the West Coast (28.60°S, 14.50°E; 35.75°S, 20.00°E), broadly encompassing the Southern Benguela Shelf Ecoregion (Fig. 1b), and the South Coast (33.30°S, 20.00°E; 36.50°S, 27.00°E), broadly encompassing the Agulhas Shelf Ecoregion (Fig. 1c). Despite falling within the Agulhas Shelf Ecoregion, False Bay was included in the West Coast study area due to its similarity in temperature and chlorophyll-a levels with Southern Benguela bays.

The Southern Benguela Shelf Ecoregion is a highly productive area characterised by large-scale upwelling from the equatorward Benguela current (Fig. 1), giving rise to high levels of phytoplankton and reduced water temperatures. Average annual chlorophyll-a (chl-a) concentration in the area ranges from 1 to 10 μg. L^{-1}, although levels can reach well over 40 μg. L^{-1} depending on the region and prevailing oceanographic conditions (Brown, 1992; Demarcq et al., 2007; Weeks et al., 2006). The

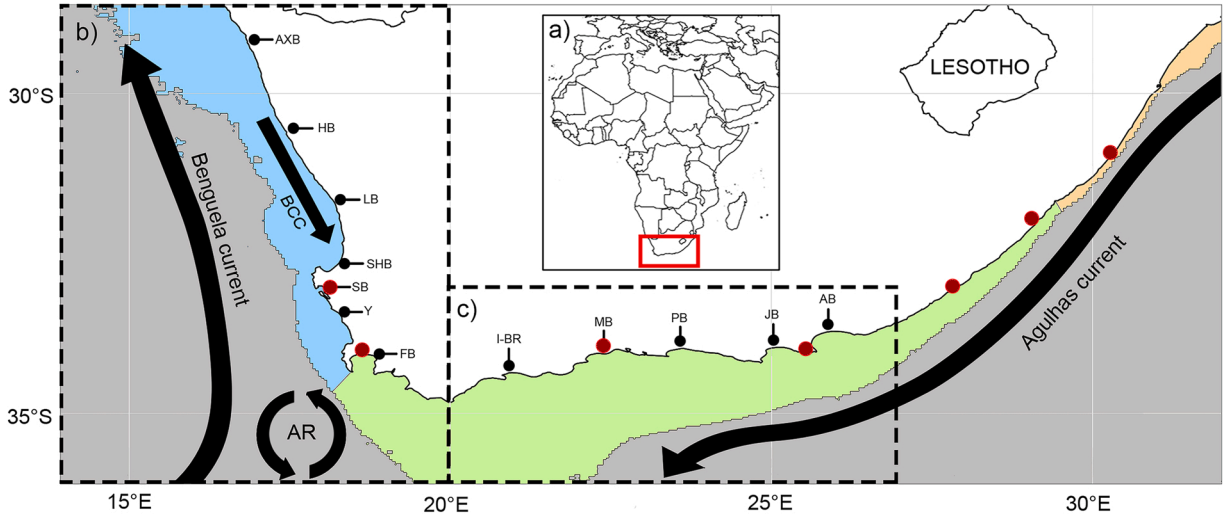

Fig. 1. Study areas with major surface currents (AR: Agulhas rings. BCC: Benguela Counter Current) and ecoregions (blue: Southern Benguela Shelf Ecoregion, green: Agulhas Shelf Ecoregion, orange: Natal Shelf Ecoregion)). Waters deeper than 200 m are masked due to infeasibility beyond this depth (Gentry et al., 2017). Sectors of interest indicated by black points (Table A3). Sectors of current *C. gigas* culture: AB (Algoa Bay) and SB (Saldanha Bay). Red points indicate main ports. A) Location of study area within the African continent, b) West Coast study site, c) South Coast study site.
Adapted from Kämpf and Chapman (2016), Picther and Jacinto (2020) and Gordon (2003).

mean annual SST in the Southern Benguela Ecoregion ranges from 9 to 18 °C, with the occurrence of cold-water (9–13 °C) upwelling cells particularly increasing in nearshore areas in the spring and summer (Griffiths et al., 2010; Weeks et al., 2006).

The South Coast is located between the Benguela current and the warm poleward Agulhas current on the East coast (Fig. 1). The environmental characteristics in the area are thus moderate, with mean annual chl-a concentration ranging from 0.1 to 6 μg. L^{-1} (Demarcq et al., 2003) and mean annual temperatures ranging from 14 to 22 °C (Demarcq et al., 2003; Schumann et al., 2005). The occurrence of salty warm-water eddies (Agulhas rings) from the Agulhas Retroflection lead to small-scale variations in surface temperature and salinity (Schumann et al., 2005). The South Coast is relatively oligotrophic compared to the West Coast, but contains several seasonal upwelling cells, most apparent when South-Westerly winds blow (Goschen et al., 2012; Mbambo, 2014). The region is also home to the native oyster and pearl oyster species, *Striostrea margaritacea*, *Pinctada capensis*, and *Ostrea atherstonei*, and has a limited number of wild Pacific oyster populations (Haupt et al., 2010; Keightley et al., 2015; Robinson et al., 2005).

Within each of the study areas, sectors of interest (Fig. 1) were chosen based on the presence of prominent coastal bays and indentations (particularly for the South Coast), the presence of relevant infrastructure (*e.g.*, road access), and regular spacing to ensure a greater extent of the coastline was sampled. For a full list of coordinates for each sector refer to Appendix A (Table A3).

2.2. Earth Observation data

All forcing data were obtained from satellite observations. Chl-a concentration, a proxy for food availability, and SST were used as inputs of the ecophysiological model (see 2.4.1). SPM or particulate inorganic matter (PIM) was not used as a forcing variable, as PIM concentration was less than 50 mg L^{-1} for both Saldanha and Algoa Bay, with a negligible impact on oyster ecophysiology and growth (Barillé et al., 1997; Luger et al., 1998; Luger and van Ballegooyen, 2000; Mbambo, 2014).

In order to reduce the number of observation gaps, 8-day composites at a spatial resolution of 4 km^2 were selected. Both chl-a concentration and SST were measured by the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Aqua satellite mission. The near-surface chl-a concentration (https://oceancolor.gsfc.nasa.gov/atbd/chlor_a/) was computed using a merged algorithm which switches between the standard ocean colour band ratio (OC4, O'Reilly et al., 1998) and the colour index (CI, Hu et al., 2012) to improve the accuracy of chl-a retrievals in clear waters. SST was computed using a long-wave infrared algorithm based on MODIS's 11 μm spectral band (https://oceancolor.gsfc.nasa.gov/atbd/sst/). For compatibility with the DEB model, which runs on daily input data, the 8-day chl-a and SST data were converted to daily data *via* linear interpolation. Missing values due to cloud cover were also estimated using linear interpolation. The proportion of missing values due to cloud cover was 13% across all 18 years and showed no seasonal effect.

2.3. In situ data

For the DEB model validation, *in situ* oyster growth measurements, Chl-a concentration, and SST were acquired from Saldanha Bay (33.00°S, 18.00°E) and Algoa Bay (33.95°S, 25.60°E), using data from Pieterse et al. (2012) and Nel et al. (2014). Saldanha Bay and Algoa Bay both contain Aquaculture Development Zones (ADZs) deemed suitable for Pacific oyster production (CSIR et al., 2019), with four farms occurring in Saldanha Bay and one in Algoa Bay as of 2019. The studies were performed for grow-out periods from May 2010 to March 2011 and June 2011 to July 2012 respectively. Growth measurements consisted of bi-monthly dry flesh mass (DFM) and total weight (TW) readings from 40 oysters per cohort in each area. Data were from 4-month-old (initial TW: 4 g) and 6-month-old (initial TW: 19 g) cohorts in Pieterse et al. (2012), and a 2-month-old cohort (initial TW: 0.5 g) in Nel et al. (2014). Since both *in situ* studies produced oysters at different depths, only measurements from those grown at a depth of 1.5 m were used, ensuring that environmental conditions better correspond to surface satellite measurements. For each of the three cohorts per area, average and standard deviation of the bi-monthly DFM and TW were calculated. As raw growth data was only provided from Nel et al. (2014), growth measurements from Pieterse et al. (2012) were obtained through a plot digitiser. *In situ* Chl-a and water temperature readings were also obtained from these studies. Although raw data were not available, daily average chl-a and water temperature measurements were likewise obtained by digitising plots from both papers.

2.4. Pacific oyster DEB model

2.4.1. Model description

The model follows the basic structure of the generic DEB model first described by Kooijman (2000) (Fig. A1; For more detail see Appendix A). Spawning is controlled by two parameters: a gonado-somatic index (GSI) threshold of 0.4 and a temperature threshold of 20 °C, below which spawning will not occur. Oysters were assumed to be under 100% immersion as culture techniques in South Africa comprises long-line and raft culture and do not make use of intertidal areas.

The final outputs of DFM and Shell Length (L) are determined by equations that relate structural volume to weight and length. An industry-relevant output of TW was then determined using the empirically derived equation $TW = 0.081\ L^3$. As *in situ* length data was not available, this equation was formulated by nonlinear regression analysis, using *C. gigas* growth data across French localities from the RESCO REMORA database for 2010–2013 (Fleury et al., 2021) (Fig. A3).

Model parameters were all taken from Palmer et al. (2020) and Thomas et al. (2016), unless otherwise specified. These model parameters were previously based on works from van der Veer et al. (2006), Pouvreau et al. (2006), Bacher and Gangnery (2006), Bourlès et al. (2009) and Bernard et al. (2011). For a full list of model parameters refer to Appendix A (Table A1).

2.4.2. Individual-based model simulations

To better account for differences in performance between individual oysters in a population, initial DFM, initial L, and half-saturation coefficient (X_k) values were randomised before applying the model. Each of the three input variables were randomised around the mean value 10 times, with a standard deviation for each variable (Table A2), thus giving 10 model iterations for each scenario, *i.e.,* acting as 10 simulations of individual oysters for each year and study area. To determine the final model outputs for a given year, averages were taken across the 10 individuals along with standard deviation.

2.4.3. Model calibration & validation

Model calibration was performed using *in situ* DFM and TW data for the 6-month-old cohort (Pieterse et al., 2012) and the 2-month-old cohort (Nel et al., 2014). Satellite data points for calibration were 33.9226°S, 25.8005°E for Algoa Bay and 33.1113°S, 17.8376°E for Saldanha Bay, thus slightly offshore compared to the *in situ* measurements. This was due to interference within the coastal zone generating numerous undefined chl-a values. Satellite coordinates were thus selected to be as close as possible to *in situ* coordinates. Daily mean water temperature and chl-a measurements were compared to their satellite-derived equivalents *via* a Spearman's correlation and a linear regression against a 1-to-1 relationship to ensure agreement.

Calibration was carried out separately for the two study sites: the South Coast, of which Algoa Bay is assumed to be representative, and the West Coast, of which Saldanha Bay is assumed to be representative (Fig. 1). This was done by calibrating the following model parameters: the half-saturation coefficient related to the feeding processes (X_k), the

shape parameter (δ), and the minimum spawning temperature threshold. Calibration involved fitting the modelled growth outputs to the *in situ* growth measurements by manipulating X_k, δ, and the spawning temperature threshold. Initial parameters used were those from Thomas et al. (2016), with modifications to the shape parameter and spawning temperature guided by Bourlès et al. (2009).

The shape parameter, describing the relationship between the Volume (*i.e.,* DFM) and Length of oysters, was modified as *in situ* data showed that the previous relationship was not consistent for *C. gigas* in South African environments. The spawning threshold was modified as the 18–20 °C value used for European waters (Thomas et al., 2016) was triggering spawning events in the simulations in contradiction with the *in situ* observations, suggesting the need for a higher value. It was modified to 25 °C for oysters in the Agulhas Ecoregion, as *in situ* data indicated that spawning did not occur, despite adequate GSI values and temperature values over 20 °C. This spawning thermic threshold initially determined for the West European Atlantic coast can indeed be higher in warmer waters such as Mediterranean lagoons (Ubertini et al., 2017).

The fit was initially considered to be suitable when the overlap between the *in situ* means ± SD and the range of the model outputs (DFM and TW) were maximised throughout the entire growth period. To confirm that the *in situ* and simulated values matched, Spearman's correlation and linear regression against a 1-to-1 line were performed. The root mean squared error (RMSE) and normalised mean bias (NMB) values for both Algoa and Saldanha Bay were calculated for each calibration result.

Model validation was performed using *in situ* DFM and TW data for the 4-month-old cohort (Pieterse et al., 2012), using the model parameters shown in Table 1. The simulations were first considered to be accurate when overlap between the *in situ* means ± SD and the range of the model outputs occurred throughout the entire growth period. The model results were then compared to their *in situ* equivalents by correlation and linear regression, weighed against a 1-to-1 relationship, to further evaluate the model's performance. The RMSE and NMB were also calculated for each validation result.

2.4.4. Model application and industry-relevant growth indicators

The individual-based model application involved applying the validated Algoa Bay parameters for the Agulhas Ecoregion and Saldanha Bay parameters for the Southern Benguela Ecoregion to 18 years of forcing data (2002–2020).

To provide insight into which areas have the highest growth potential, the model was applied to 4-month-old oyster juveniles (4 g TW) annually, from July, for a total grow-out period of 9 months (shown to be the period of best overlap with *in situ* measurements after validation).

Table 1
Input parameters for the Pacific oyster DEB model, parameterised for Algoa Bay and Saldanha Bay, South Africa, as a result of model calibration with 16 *in situ* TW and DFM data points for each region. Calibration statistics are from tests of model *vs. in situ* data for the 2-month old and 6-month-old cohorts combined. 95% significance level is indicated by ***.

Site	Algoa Bay	Saldanha Bay
Shape parameter (δ)	0.175 (van der Veer et al., 2006)	0.22
Half saturation coefficient (Xk)	2.9 ± 0. 1 μg. L^{-1} chl-a	5.5 ± 0. 1 μg. L^{-1}chl-a
Spawning temperature	25 °C	20 °C (Pouvreau, 2006)
Calibration statistics (model *vs. in situ*) for 2mo + 6mo cohorts		
R^2 (DFM)	0.86***	0.86***
RMSE (DFM)	1.18 g	1.22 g
NMB (DFM)	1.37 g	0.47 g
R^2 (TW)	0.88***	0.81***
RMSE (TW)	25.55 g	17.46 g
NMB (TW)	-12.07 g	5.23 g

Outputs included maps portraying the spatial variation of DFM, *L* and TW across the study areas at the end of the grow-out period. Average final DFM, *L* and TW (± standard deviation) were calculated for the 18-year period and mapped.

Industry-relevant indicators of TW commercial size classes and average "time to commercial weight", as described by Palmer et al. (2020) (Fig. A2), were then calculated for the 18-year period and mapped across the study areas along with the standard deviations. The time to reach a substantial commercial size of 100 g (Haupt et al., 2010; Knysna Oyster Company; Viking Aquaculture; Table 2) was specifically computed to determine if grow-out periods could be shortened to avoid HAB peak-seasons occurring in the late summer and early autumn (Pitcher and Jacinto, 2019).

To determine to what extent a shorter and earlier grow-out period would cause differences in final average DFM and TW, three different culture period lengths were assessed (150 days, 200 days, and 250 days), starting in July of each of the 18 years. The mean and standard deviation of all growth metrics were mapped across the study areas.

For each sector, DFM, *L* and TW were extracted from 1 pixel for each of the 10 individual simulations, for each of the 18 years, giving a total of 180 data points per sector for each growth metric. After testing for normality and homoscedasticity, a Welch's One-Way Analysis of Means was performed, which accounted for unequal variances, in addition to a post-hoc Games-Howell Multiple Comparisons Test to determine if final measurements differ statistically among sectors. This statistical analysis was also applied to DFM and TW outputs of the three culture periods to determine if final measurements differ statistically among sectors.

3. Results

3.1. Forcing data

3.1.1. 18-year average Chl-a and SST

MODIS data for the period 2002–2020 reflected results expected from the Agulhas and Benguela Ecoregions. The mean 18-year chl-a concentration was shown to be highest within 25 km of the shore along the West Coast, particularly between St. Helena Bay and Lambert's Bay, as well as Alexander Bay (Fig. 2a). On the South Coast, localised chl-a hotspots were observed within bays east of Mossel Bay (Fig. 2a). Chl-a hotspots near Plettenberg Bay, Lambert's Bay and St. Helena Bay, show high standard deviation, indicating that although chl-a concentration is high, it is also more variable in these areas (Fig. 2b). Average SST values confirmed a strong temperature delineation between the West, South, and East coasts of South Africa, with the mean temperature ranging from 13 to 18 °C on the West coast, 15–20 °C on the South Coast, and 20–25 °C on the East Coast (Fig. 2c). While the South Coast is slightly warmer than the West Coast, it also shows greater variability (Fig. 2d).

Table 2
Shortest culture period length (150 days, 200 days, or 250 days) required for oysters to reach each of the seven commercial size classes (measured according to total weights), indicated by sector and/or study area. For a full list of sectors refer to Table A3.

Size class	Total weight (g)	Sector/Study area (days to reach weight)
Cocktail/ Champagne	40–49 g	All sectors (150 days)
Medium	50–69 g	All sectors (200 days), South Coast (150 days), LB (150 days), SHB (150 days)
Large	**70–90 g**	**All sectors (250 days), South Coast (150 days), LB (200 days), SHB (200 days)**
X-Large	**91–110 g**	**All sectors ex. Y (150 days), MB (200 days), JB (200 days), PB (200 days)**
XX-Large/ Giant	111–130 g	PB (200 days), JB (200 days), MB (200 days), LB (250 days), SHB (250 days), AB (250 days)
Super Giant	200–380 g	JB (250 days), PB (250 days)

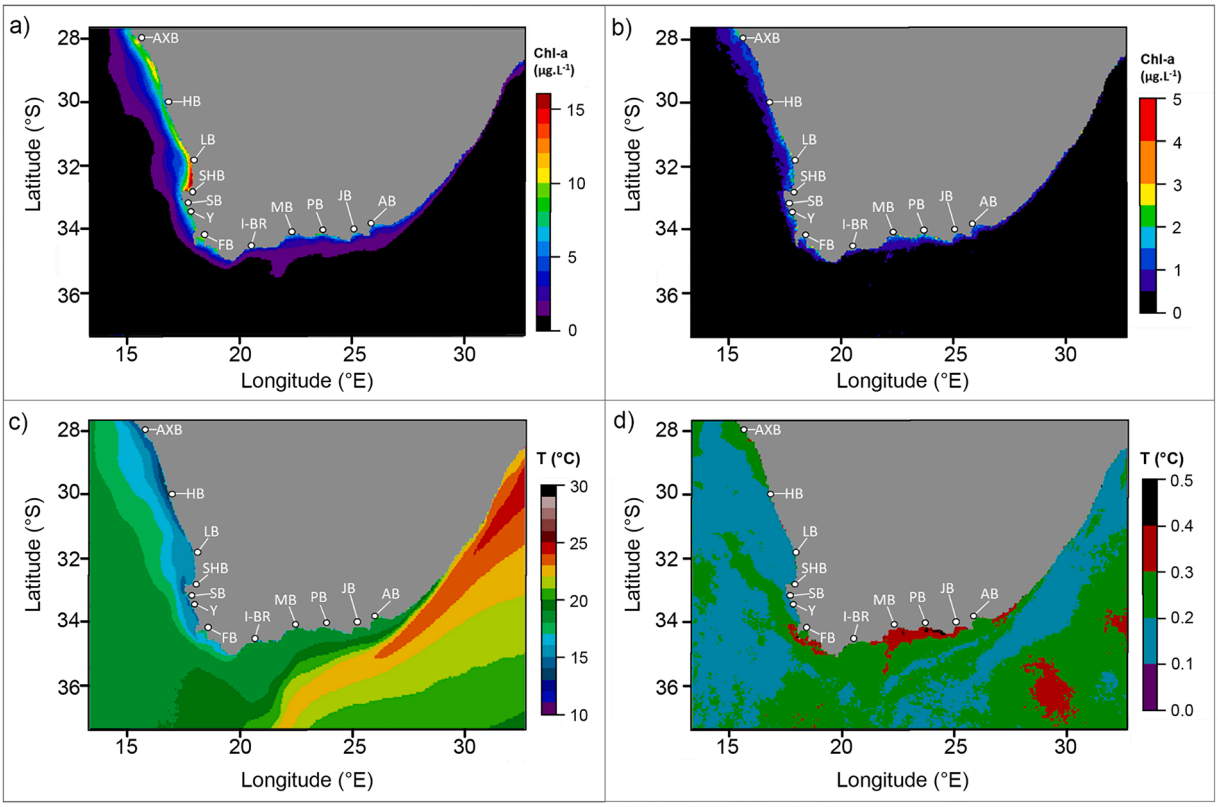

Fig. 2. 18-year a) mean and b) standard deviation of MODIS 8-day chl-a product, and 18-year c) mean and d) standard deviation of MODIS 8-day SST product within the South African marine environment for the period July 2002 – June 2020. Sector labels are indicated in white.

3.1.2. *Comparison of satellite and in situ Chl-a and Temperature*

Comparison of *in situ* and satellite-derived chlorophyll concentration across the calibration and validation periods showed a comparable range in both Algoa and Saldanha Bay. However, many mismatches of chlorophyll peak and trough timing were observed (Fig. B1a). Linear regression and correlation between satellite and *in situ* chl-a showed a weak non-significant relationship in Saldanha Bay (Spearman's $R = 0.06$, $p > 0.05$), and a weak significant relationship in Algoa Bay (Spearman's $R = 0.29$, $p < 0.05$). *In situ* and satellite data were better matched for temperature measurements and within a comparable range (Fig. B1b). Correlation showed moderate and significant relationships: $R = 0.54$, $p < 0.05$ and $R = 0.59$, $p < 0.05$ for Saldanha Bay and Algoa Bay respectively.

3.2. *Model calibration and validation*

3.2.1. *Calibration: model parameters & model output versus in situ measurements*

Model parameters resulting from calibration can be found in Table 1. To optimally match both *in situ* DFM and TW values, different shape parameters, half-saturation coefficients, and spawning temperatures were needed for Algoa and Saldanha Bay. The higher shape parameter utilised in Saldanha Bay allowed greater DFM growth with lower shell/TW growth, and the inverse for oysters grown in Algoa Bay. Half-saturation coefficients between Algoa and Saldanha Bay differed quite markedly, with a higher value required for Saldanha Bay, due to the higher food availability.

Model calibration showed a good agreement between model simulations and *in situ* DFM and TW measurements for the 2-month-old *C. gigas* cohort throughout the growth trajectory (2011–2012) (Fig. B2). However, in Saldanha Bay, modelled DFM and TW at the end of the culture period appear to underperform compared to *in situ* measurements. A good agreement was also obtained for the 6-month-old cohort (2010–2011). Linear regressions between observed and modelled DFM and TW revealed reasonably strong one-to-one relationships when considering both the 6-month-old and 2-month-old cohorts (Table 1). The RMSE values for both Algoa and Saldanha Bay DFM were less than 1.22 g. However, NMB suggested that, overall, modelled TW for Algoa Bay may be underestimated, whereas slight overestimations were observed for Saldanha Bay (Table 1).

3.2.2. *Validation: model output versus in situ measurements*

The DEB model DFM outputs were validated using the 4-month-old cohort, and significant relationships close to the 1-to-1 line were obtained between observed *in situ* and simulated DFM data (Fig. 3). The same was observed for TW. Some discrepancies were observed, with model outputs toward the end of the culture period higher than their *in-situ* equivalents (Fig. 3b). The NMB was also shown to be negative when assessing the fit of DFM, and positive when assessing TW, suggesting a trade-off between good DFM and good TW fit (Fig. 3). RMSE values for DFM were less than 1.5 g for both Saldanha and Algoa Bay. These values were expectedly higher for TW. However, the RMSE for Algoa Bay TW (45.5 g) was three times higher than that of Saldanha Bay TW (14.8 g). Due to this overestimation of TW and DFM towards the end of the culture period, a shorter 9-month culture period was applied during model application.

3.3. *Model application*

3.3.1. *Growth potential in the South Coast (Agulhas Ecoregion)*

At the end of the 9-month culture period South Coast median oyster TW ranged from 117.65 g to 271.10 g in for Infanta-Bree River Estuary and Plettenberg Bay respectively (Fig. 4a, b). Statistically significant differences were found between mean TW of all South Coast sectors (Fig. 4a; Welch's One-Way Analysis of Means, $F = 21.46$, $p < 0.01$). The current *C. gigas* production sector, Algoa Bay, was found to have a lower

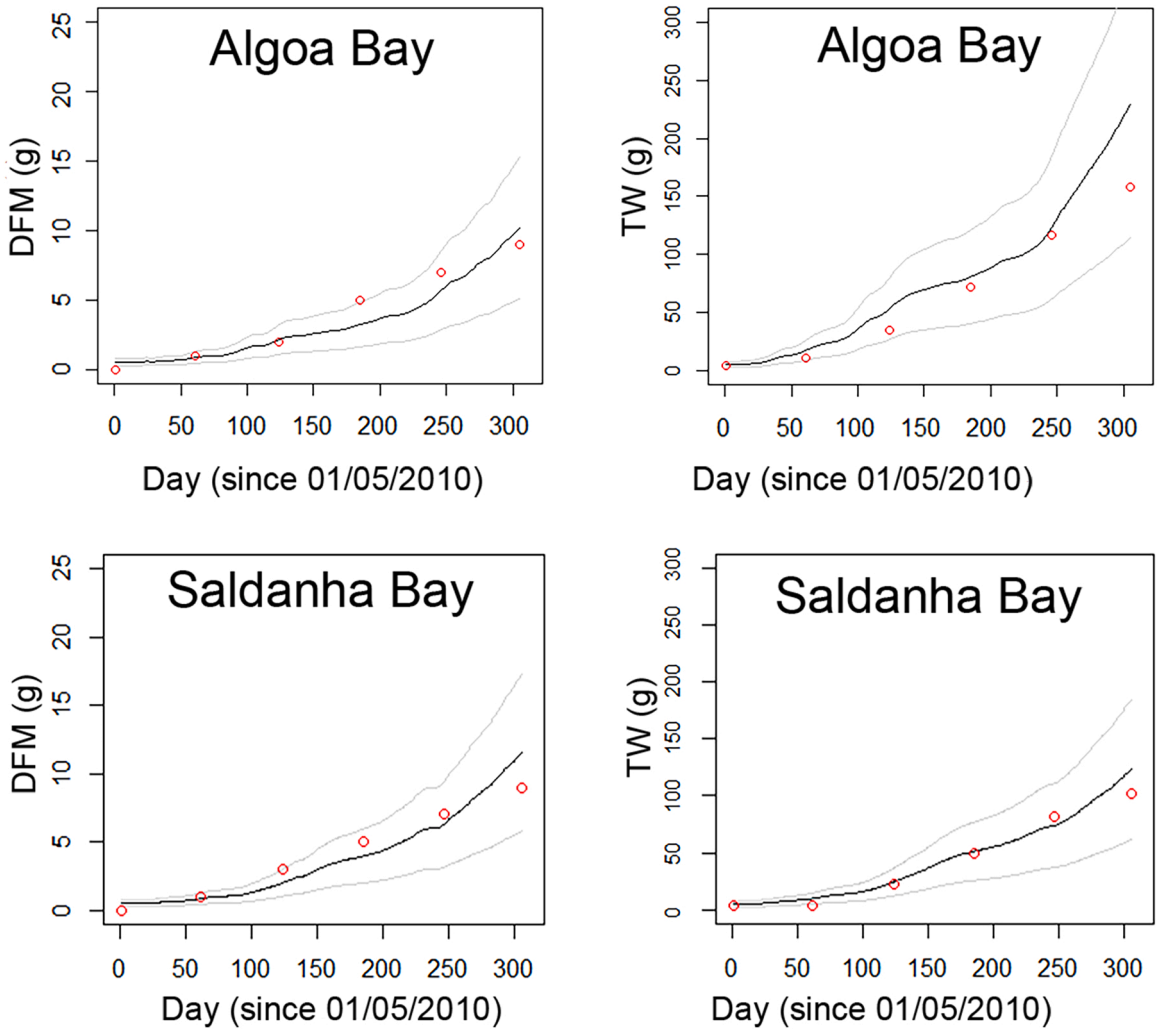

Fig. 3. Validation of the DEB parametrization for Algoa and Saldanha bays. Model outputs of oyster DFM (a,c) and TW (b,d) for Saldanha Bay and Algoa Bay, compared to *in-situ* measurements for a 4-month-old *C. gigas* cohort (initial DFM: 0.5 g, initial TW: 4 g). Grow-out period commenced in May 2010 and measurements were recorded bi-monthly from August 2010 to March 2011. *In-situ* measurements are shown in red. Normalised Mean Bias (NMB), Root Mean Square Error (RMSE) & coefficient of determination (R^2) are indicated. Statistical significance is indicated at a 99% level (***).

median TW of 162.5 g relative to high-growth sectors Plettenberg Bay & Jeffrey's Bay (216.59 g), yet higher than Infanta-Bree River Estuary & Mossel Bay (135.76 g) (Games-Howell Multiple Comparisons Test; $p < 0.01$). Generally, the closer to the shore, the greater the final weights, with elevated-growth areas located within bays on the east. Specific TW growth hotspots were observed in Plettenberg Bay, Jeffrey's Bay, Mossel Bay, and Algoa Bay. Elevated standard deviation around the mean in these growth hotspots indicated that variation in final weight is substantial, with standard deviation of TW values being comparable to mean TW values in extreme coastal areas of Plettenberg Bay and Jeffrey's Bay (Fig. B3).

Similar patterns were found for mean DFM (Fig. B3a, B3b), with higher values concentrated in the extreme nearshore areas east of Mossel Bay. High variation in coastal areas of Plettenberg Bay was also observed (Fig. B3c). Median final DFM ranged from 5.16 g (Infanta-Bree River Estuary) to 12.40 g (Plettenberg Bay).

3.3.2. Growth potential in the West Coast (Benguela Ecoregion)

At the end of the 9-month culture period median TW values ranged from 80.67 g (Alexander Bay & Hondeklip Bay) to 148.27 g (St. Helena Bay & Lambert's Bay) (Figs. B4a, 5a). Overall, significant differences in TW between West Coast sectors was found (Fig. 5a; Welch's One-Way Analysis of Means, $F = 178.98$, $p < 0.01$). The median TW values were significantly higher for Lambert's Bay and St. Helena Bay compared to all other sites (Games-Howell Multiple Comparisons Test; $p < 0.01$). Alexander Bay, Hondeklip Bay, Yzerfontein, and Saldanha Bay were lower-growth areas and not statistically different from one another.

The trend of nearshore-areas yielding higher final weights held for the West Coast, however, a large growth hotspot was observed directly north of the Cape Columbine peninsula (32.8°S, 17.85°E). Contrary to the South Coast, in the West Coast higher growth tends to occur slightly offshore, seen along the coastal areas south of Hondeklip Bay and north of Cape Columbine (Fig. 5b). The tendency of high-growth areas to have a high standard deviation is not observed here, with West Coast TW showing consistently low standard deviation (Fig. 5c).

Mean final DFM growth patterns corresponded to those of TW (Fig. B4a, B4b), however the standard deviation was less homogenous, with higher values found in high-growth hotspots (Fig. B4c). Median final DFM ranged from 6.25 g (Alexander Bay & Hondeklip Bay) to 12.39 g (Lambert's Bay & St Helena Bay).

3.3.3. Assessment of industry-relevant growth indicators

In both the Agulhas Ecoregion and Benguela Ecoregion a commercial weight of 100 g was achieved within 9 months for the majority of sites within 50 km of the shore (Figs. 4a, 5a). Exceptions to this are areas adjacent to the southernmost point of Africa, Cape Agulhas (34.83°S,

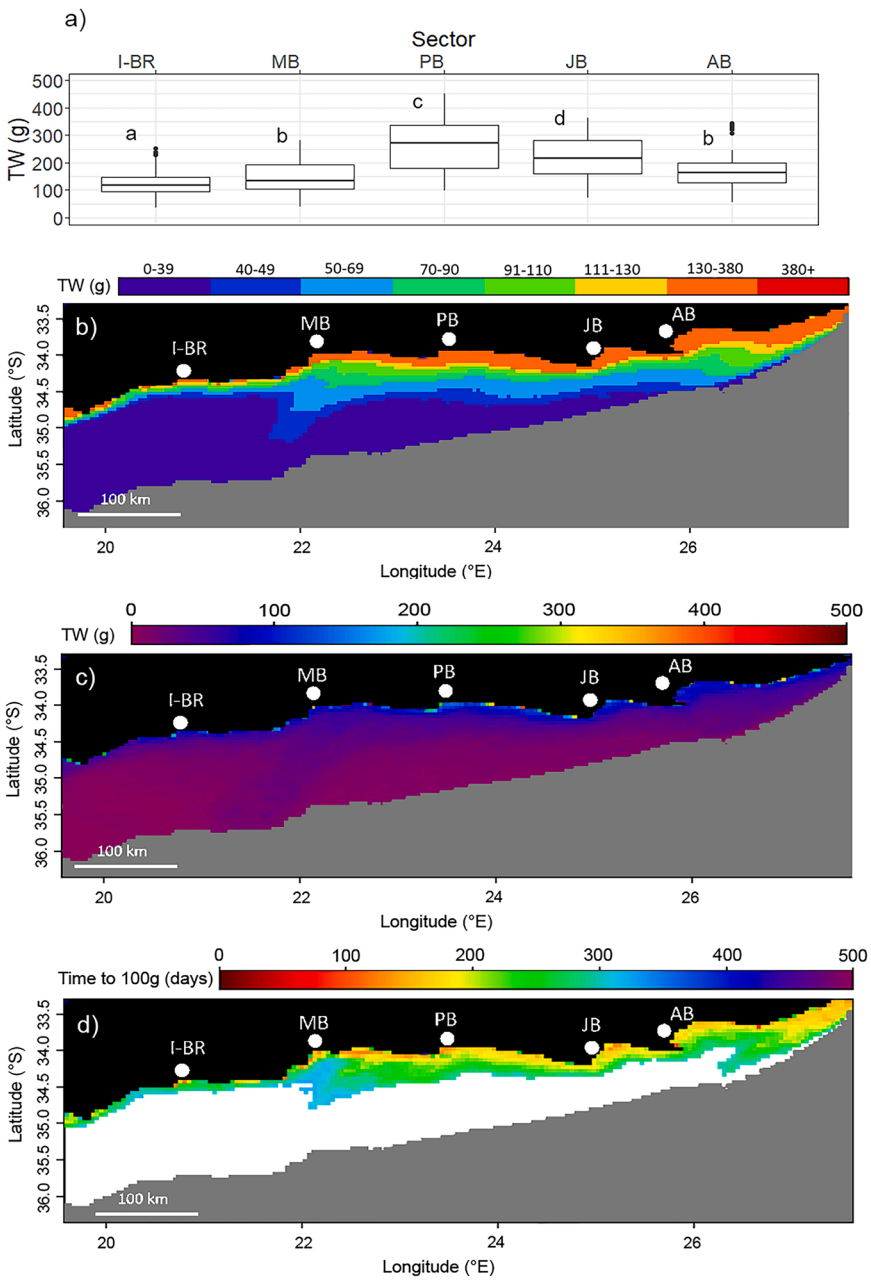

Fig. 4. a) South Coast intra- and inter-sector variability of simulated *C. gigas* Total Weight (TW) at the end of the yearly culture period (1 July–1 April) from 2002 to 2020, starting with a 4-month-old cohort (initial TW: 4 g). Letters indicate significant differences at a 99% level after a Welch's One-Way ANOVA ($p < 0.01$). Spatial variability of b) mean according to size class and c) standard deviation of TW at the end of yearly culture period, d) mean time to reach 100 g TW. Areas further than 100 km from the shore and deeper than 200 m are masked in grey. For full sector names refer to Table A3.

20.01°E), in both the South Coast and West Coast study areas. The number of days required to reach commercial weight generally increased with distance offshore (Figs. 4d, 5d). The standard deviation for the mean number of days to reach 100 g commercial weight was 5–10 days for both study areas. Coastal sections from Mossel Bay to Plettenberg Bay on the South Coast allow commercial weight to be attained within 150 days. This was also observed in the centre of Jeffree's Bay, and particular areas east of Algoa Bay. The West Coast showed consistent growth rates within the first 50 km from the shore, where oysters were able to reach commercial weight within 150 days. Areas further offshore showed slower growth rates. However, commercial weight was still achieved within 300 days, except for areas south of False Bay which were unable to reach 100 g at all.

A summary of the results of the final simulated TW achieved at each culture period (150 days, 200 days and 250 days) for each sector can be found in Table 2. These simulations showed that on average all sectors are able to reach Cocktail and Medium sizes in 150 and 200 days respectively. The more popular Large size can be reached in all sectors within a 250-day culture period, with shorter culture periods possible in South Coast sites, as well as Lambert's Bay and St Helena Bay in the West Coast. The Yzerfontein site in the West Coast showed the slowest growth rates.

In the South Coast, most areas East of Mossel Bay and within 50 km of the coast can reach the popular Large and X-Large sizes within 250 days. The same trend is observed in the West Coast; however, a greater proportion of the offshore region can meet these popular size-class targets within 250 days. High-growth areas are again highlighted as St Helena Bay and Lambert's Bay, plus False Bay and offshore Alexander Bay to a lesser extent.

4. Discussion

4.1. Oyster growth potential in South Africa

Following the 2018 Aquaculture Development Bill, the Department of Agriculture Forestry and Fisheries (DAFF; now, the Department of

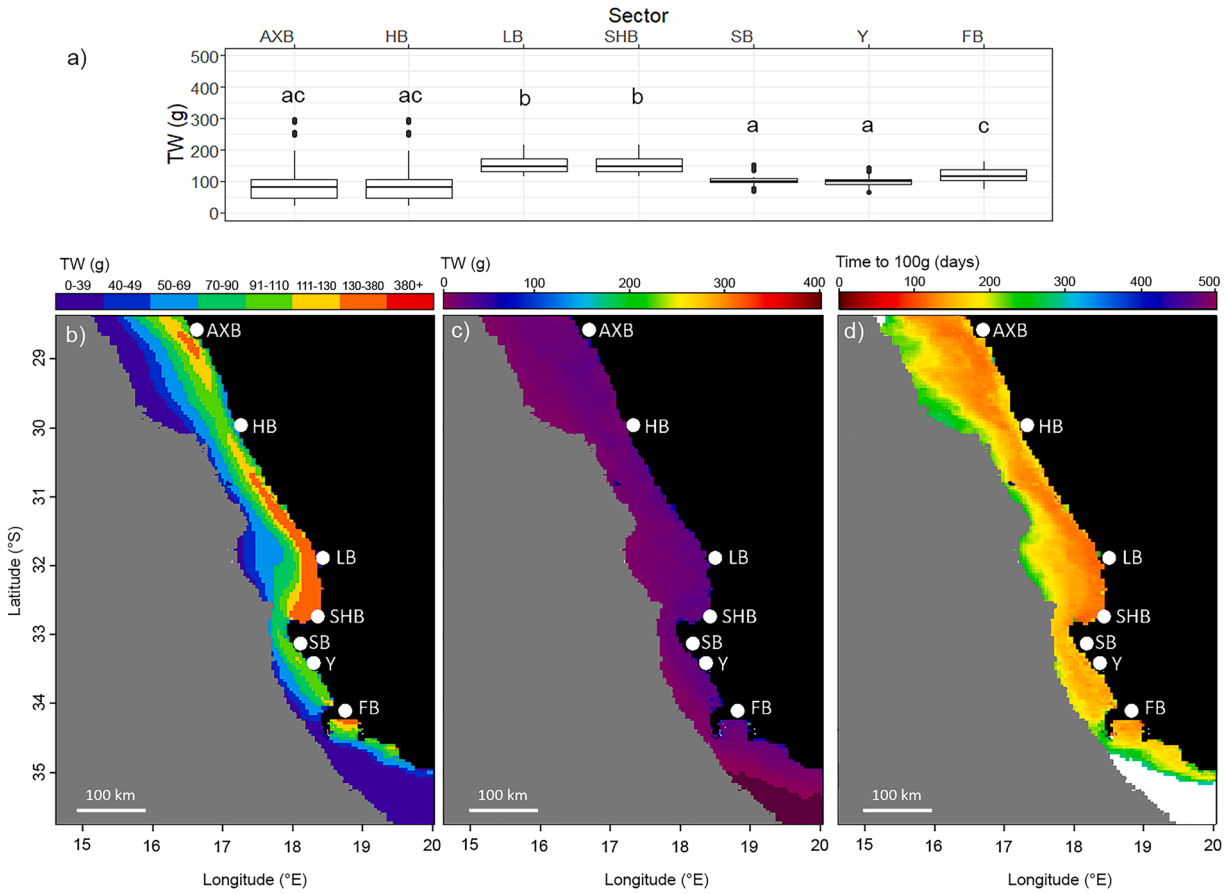

Fig. 5. a) West Coast intra- and inter-sector variability of simulated *C. gigas* Total Weight (TW) at the end of the yearly culture period (1 July–1 April) from 2002 to 2020, starting with a 4-month-old cohort (initial TW: 4 g). Letters indicate significant differences at a 99% level, after a Welch's One-Way ANOVA ($p < 0.01$). Spatial variability of b) mean according to size class and c) standard deviation of TW at the end of yearly culture period, d) mean time to reach 100 g TW. Areas further than 100 km from the shore and deeper than 200 m are masked in grey. For full sector names refer to Table A3.

Environment, Forestry and Fisheries) proposed eight marine Aquaculture Development Zones (ADZs), six of which were noted to be suitable for Pacific oyster cultivation (CSIR et al., 2019). This selection was largely based on previous oyster culture sites and temperature suitability. ADZs are in development in Saldanha Bay (an already established mussel and oyster aquaculture area) and Algoa Bay (a less productive, but historically prominent site of shellfish cultivation) (CSIR et al., 2019; DAFF, 2017b). Pacific oysters grown in these areas have reported 10-month growth of 0.4–8.9 g and 0.2–9.2 g DFM in Algoa Bay and Saldanha Bay respectively (Pieterse et al., 2012). In terms of TW, this corresponded to 3.0–150 g and 3.4–105 g. This high growth was confirmed with modelling here, where 18-year averages centred around the higher end of this range in Algoa and Saldanha Bay, and even higher for other sectors. The present study elucidates the additional influence of chlorophyll and mechanistically demonstrates how chlorophyll, together with temperature, predicts *C. gigas* growth.

Chlorophyll-a concentration was confirmed to be the greatest predictor of oyster growth potential (Bourlès et al., 2009; Monaco et al., 2019; Sarà et al., 2012), where high-chlorophyll areas showed the greatest increases in TW, *L* and particularly DFM. As expected, high-chlorophyll areas indicated in forcing data coincide with areas of upwelling. Results here also maintained that any offshore development of oyster mariculture should ideally be within 30 km from the shore and not further than 50 km, after which growth begins to decline.

Due to reasons outlined in Section 4.2., caution should be taken when interpreting the absolute growth values presented in the Results. We can, however, make spatial comparisons of growth within each ecoregion, and by doing so can deduce that current oyster cultivation sites (Algoa Bay and Saldanha Bay) have a relatively low growth potential within their respective ecoregions. Instead, our study shows that, when only considering the DEB outputs of final TW and DFM values, *C. gigas* mariculture would be better suited to Lambert's Bay (West Coast), St. Helena Bay (West Coast), and Plettenberg Bay (South Coast).

The higher variability in DFM and TW in South Coast hotspots match prevailing oceanographic conditions in the Agulhas Ecoregion. The combination of coastal, wind-driven upwelling near Jeffrey's Bay and Plettenberg Bay, divergent upwelling east of Algoa Bay, and the influence of warm-water eddies from the Agulhas current leads to highly variable environmental conditions (Demarcq et al., 2003; Goschen et al., 2012; Goschen and Schumann, 2010; Roberts, 2005; Schumann et al., 2005). Conversely, when observing the West Coast (specifically the northern Benguela Ecoregion) the large-scale and nearly constant upwelling leads to considerably less variability (Demarcq et al., 2003; Lockerbie and Shannon, 2019; Probyn et al., 2000; Roberts, 2005). Upon examining the inter-annual variability of growth potential during the study period, outliers of high DFM and TW appear for each study area, influenced by two years of anomalously high chlorophyll concentration (2008 for South Coast; 2012 for West Coast). Consistency in growth is an important factor for aquaculture ventures, as aquaculture is already considered a high-risk investment. Therefore, mariculture sites on the West Coast are preferred. Although South Coast oysters can reach greater TW values, preference for the West Coast is reinforced by higher DFM values. The discrepancy between TW and DFM (see *4.2.4*) growth is important to note since as a food source the actual flesh of the oyster is principal.

This study also shows that by moving oyster mariculture to high-

growth areas, the culture period length can be drastically reduced from 300 days to 150 days, while still producing Large size oysters. Since both the West and South coasts of South Africa experience regular HAB outbreaks (Mbambo, 2014; Olivier et al., 2013; Pitcher et al., 2011; Pitcher and Jacinto, 2019; Pitcher and Probyn, 2016), this reduction in growing period could be used to shift culture periods within the year to avoid HAB season in late summer/autumn and may also make temporary farm closures less of a hindrance.

4.2. Improvements to model performance

4.2.1. Need for a South African TW-L ratio

While the high TW values and short time to commercial size are among the most remarkable results of this study, there is some uncertainty associated with the TW-L relationship, which was obtained using oysters grown in France because such relationship is not available for the study area. Although these results can show the spatial variation of oyster growth reasonably well, the lack of a region-specific TW-*L* ratio means that actual values may differ and *in situ* verification is necessary.

The exceptionally high TW growth rate (in excess of 150 g in 9 months) can be partly attributed to the French TW-*L* relationship showing a strong exponential curve which relates moderate length with elevated TW (Fig. A3). This notion is supported by observing the *L* results for both study areas (Fig. B5, B6), where it is shown that oysters do not reach simulated lengths above 20 cm despite having such increased TW. Consequently, there is likely an overestimation of TW for oysters from 12 to 20 cm L. This is captured by the RMSE and NMB during model validation, showing that TW overestimations are more pronounced in the South Coast and explaining some of the presumably excessive TW values in South Coast sites.

Other factors that may explain differences in growth rate and TW-*L* ratio between French and South African *C. gigas* include husbandry practices. Oysters from the South African dataset were grown in open-sea suspended culture within lantern cages, whereas the French oysters were grown in the intertidal zone in off-bottom culture within mesh bags. Suspended culture has been reported to lead to shell deformities, including flattening and elongation (Marshall and Dunham, 2013), which may explain the discrepancy in TW between French and South African oysters. Differences in stocking densities were also present, with French stocking densities being approximately 3 times higher than those of the South African dataset (Fleury et al., 2001a; Pieterse et al., 2012). South African oysters were also graded every 2 months to ensure that each layer of the lantern cage did not exceed 650 g TW (Nel et al., 2014; Pieterse et al., 2012). High stocking densities have been shown to have both a positive and negative effect on oyster condition (Honkoop et al., 2002; Evans and Langdon, 2006; Marshall and Dunham, 2013; Capelle et al., 2020; Tan et al., 2021), thus should be investigated further for the South African context.

4.2.2. Calibration and validation: in situ data

The foremost issue that appeared when applying the DEB oyster model to South Africa was the lack of *in-situ*, aquaculture-centred growth studies. The two papers utilised in this study for their *in-situ* data (Nel et al., 2014; Pieterse et al., 2012) are at present the only growth data available for non-feral populations of Pacific oyster in South Africa. While these studies provide a good assessment of potential influences on oyster growth by examining the effect of location, age class, and hatchery origin in current mariculture sites (Algoa Bay and Saldanha Bay), their scalability to larger ecoregions remain to be further validated. For the DEB model to be more accurately calibrated and more successfully validated to account for both spatial and temporal variability (on a seasonal and inter-annual scale), additional studies in newly identified potential sites are necessary. Moreover, the bi-monthly growth measurements from the *in-situ* data used in this study were too infrequent to provide insight into spawning events. In situ growth studies to be used for calibration and validation of DEB models should therefore employ monthly measurements or at least more frequent measurements during the spawning season. The error observed during the validation for TW results in the South Coast (Fig. 3) again indicate that the model likely overestimates these measurements, emphasising a need for comprehensive *in situ* validation in this area.

4.2.3. Forcing data

Some discrepancies between *in situ* and satellite-derived forcing data were expected due to the offset of satellite coordinates, differences in spatial scale (4 km^2 pixel *vs.* discrete seawater sample), and the 1.5 m depth difference between field sampling and surface remote sensing. Although chl-a satellite data did show some mismatches with *in-situ* data, the overall similarity in range of chl-a concentration as well as the consistent spatial distribution and overall temporal dynamics confirmed that satellite values were acceptable for the purposes of this exploratory study.

MODIS 8-day chl-a and SST products were utilised as forcing data as they provide a standard product for a long enough time-series, have been validated globally, and have the same accuracy in both ecoregions (thus showing no regional bias). Significant improvements in the precision of satellite-derived chl-a data can only be made through region-specific chl-a retrieval algorithms (Smith et al., 2018; Pitcher et al., 2019), which could defeat the purpose of having a standardised forcing dataset that is applicable to a large region. It may be the case that until such a dataset is available, DEB models should be applied regionally, or when applied over larger scales, to act as a general guide rather than a source of exact values.

There is also the importance of incorporating food quality as well as quantity. Previous applications of DEB models have utilised phytoplankton cell number instead of chlorophyll concentration as a better gauge of food concentration (Alunno-Bruscia et al., 2011; Bernard et al., 2011; Bourlès et al., 2009; Pouvreau et al., 2006). This is especially important for South Africa, as many bloom-forming phytoplankton species in these areas are known HAB species – occurring even during the calibration period (Mbambo, 2014; Pitcher and Louw, 2021). Thus, although growth is promising, these oysters may be commercially inviable. Recently developed EO algorithms to detect HABs may thus be applicable to DEB modelling regarding the detection of chlorophyll signals from specific phytoplankton species (Caballero et al., 2020; Smith and Bernard, 2020; Wolny et al., 2020).

4.2.4. Spatial stationarity in DEB modelling and issues of uncertainty

Spatial stationarity refers to the assumption that the initial parameter estimates of the model are applicable when applying the model to other locations and populations (Monaco et al., 2019) and should be a consideration when interpreting results of species-specific mechanistic models. While stationarity has proven justifiable when applying the model regionally (*i.e.*, within the same national borders or water body; Alunno-Bruscia et al., 2011), the model could yield a higher degree of uncertainty when applied over larger spatial scales (Monaco et al., 2019). Besides environmental differences, the non-fulfilment of spatial stationarity can be due to unaccounted energy costs (*e.g.*, parasitism, wave exposure, anaerobic metabolism (Monaco et al., 2019), freshwater flooding, suboptimal food sources (Keightley et al., 2015; Robinson et al., 2005)) or genetic variability which can lead to differences in growth.

The model was able to reconstruct *in situ* growth curves reasonably well. However, incorporating different mean X_k, spawning temperatures and shape parameters (δ) for each ecoregion suggests full spatial stationarity cannot be assumed for South Africa's *C. gigas* distribution and denotes further work required on determining site-specific parameters for each region (again, limited by the availability of corresponding *in situ* data). Given that X_k values are inherently dependent on the phytoplankton concentration of the region (Alunno-Bruscia et al., 2011; Thomas and Bacher, 2018), the use of satellite forcing data may be beneficial to incorporate spatialised X_k values based on each pixel's

chl-a and PIM concentrations.

The high number of unique marine ecosystem types in South Africa's EEZ (Harris et al., 2018; Sink et al., 2018) anticipate that the spawning temperature and shape parameter will be regionally specific due to phenotypic and behavioural plasticity in reproductive and growth strategies. The mismatch between TW and DFM for the Algoa Bay calibration-validation could be attributed to the combination of high-temperature and low-food periods where a higher proportion of energy is allocated to shell growth, disproportionately increasing TW (Brown and Hartwick, 1988; Pieterse et al., 2012). Likewise, despite previous studies setting oyster DEB model spawning temperature thresholds at 18–20 °C, field-based studies have reported *C. gigas* populations with spawning temperatures of up to 26 °C in environments similar to Algoa Bay (Castaños et al., 2009; Dridi et al., 2007; Shpigel, 1989; Ubertini et al., 2017), as well as spawning temperatures as low as 14 °C (Shelmerdine et al., 2017).

While being cautious of the risk of over-parameterization, it may be beneficial to include additional unaccounted factors within future DEB models. DEB models have been adapted to incorporate the effect of too high SPM concentration on oyster gill saturation (Dutertre et al., 2007; Palmer et al., 2020; Thomas et al., 2016), the influence of biotoxins (Pousse et al., 2019) and other energy-expensive external forcing, and the effect of oysters on nutrient dynamics (Dabrowski et al., 2013). Not yet integrated into the oyster DEB model is selection efficiency. Although the mechanisms of oyster particle selection are not fully understood *in vivo*, EO techniques used in HAB detection (Melet et al., 2020; Pitcher et al., 2019; Smith and Bernard, 2020) could be developed to inform models whether preferred food species are present in forcing data, further explicating food quality in terms of X_k. Including more parameters could thus overcome the concern of spatial stationarity that occurs with the use of more generalised models, instead focusing on localised models that would have to be calibrated regionally.

4.3. Spatial multi-criteria analyses

To fully determine the best sites for oyster culture, a spatial multi-criteria analysis is needed which considers other environmental, social, and economic characteristics of the area (Graham et al., 2020). Current sites of shellfish cultivation tend to overlap with touristic and conservation areas. For example, Saldanha Bay is saturated with other users of the marine environment such as the extensive West Coast National Park MPA network, tourist resorts, sailing and kitesurfing routes, as well as an oil and gas terminal. The carrying capacity of Saldanha Bay to sustain intensified shellfish production has also been in question (Santa Marta et al., 2020). The results presented further urge the aquaculture industry to reconsider current sites, as although Algoa Bay and Saldanha Bay have reported above-average growth globally, they fall on the lower end of the growth potential scale when the entire West and South Coasts are considered. If feasible, mariculture sites should be established in the northwest and southeast nearshore regions. Feasibility needs to be efficiently assessed and the need for DEB-integrated marine spatial planning (MSP) for aquaculture is critical - especially in South Africa where environmental conditions already constrain the number of relevant sites (Haupt et al., 2010; Santa Marta et al., 2020).

There are many factors not considered by the model that should be investigated before further aquaculture development: disease risk (Thomas et al., 2018; Pernet and Browman, 2021), HAB risk (a significant problem in South Africa), wave height (important for offshore development and able to reach 7 m in South African waters; Rothman et al., 2017; Velimirov et al., 1977), current speed and the threat of invasiveness of *C. gigas* (Miossec et al., 2009). While Benguela waters are currently too cold for spawning, and feral populations are in decline in the Agulhas ecoregion, climate change and reproductive plasticity make this a relevant consideration.

High levels of inequality in South Africa necessitate attention to socio-economic factors. These may range from primary logistical considerations (the availability of harbours, road connectivity and a nearby workforce), to the presence of other marine users, to national development goals like poverty alleviation and job creation in priority economic development areas (Falconer et al., 2016; Vianna et al., 2018).

The sparsely populated Northern Cape Province (northern West Coast) suffers from a low workforce. However, oyster growth potential is high and the area is currently in economic decline (Statistics South Africa, 2021), making it a priority economic development area. And, although the variable oyster growth in the Eastern Cape (southern East Coast) makes it less favourable production-wise, this area is logistically suitable and currently shows the highest levels of inequality in the country (Statistics South Africa et al., 2019). If sites and culture techniques could be developed to minimise the effect of this variation, this becomes a priority region for aquaculture development. While these are only broad considerations, further MSP should incorporate these factors in addition to baseline growth data from the DEB model to prioritise oyster mariculture sites.

5. Conclusions and Recommendations

The Pacific oyster DEB model was successfully applied in South Africa to provide a preliminary site selection assessment. While the approach implemented here could be refined, it highlighted the potential for faster oyster growth in South African waters than previously reported, particularly for sites along the northwest and southeast coasts. West coast sites, such as Lambert's Bay and St Helena Bay, should be prioritised due to less variability in food supply than in southeast sites. Compared to these latter sites, current mariculture sites in Saldanha Bay and Algoa Bay were found to be suboptimal. When considering offshore aquaculture, future ventures should focus on development within 30 km from the coast for optimal growth.

Suggested areas coincide with priority economic development areas and should be flagged for further research. However, other factors must be considered, necessitating a Spatial Multi-Criteria Analysis and Marine Spatial Planning before any development and investment.

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CRediT authorship contribution statement

Amalia Grace Krupandan: Conceptualization, Software, Validation, Investigation, Formal analysis, Visualization, Writing – original draft. **Pierre Gernez:** Conceptualization, Writing – review & editing, Supervision. **Stephanie Palmer:** Methodology, Writing – review & editing. **Yoann Thomas:** Methodology, Writing – review & editing. **Laurent Barrilé:** Conceptualization, Writing – review & editing, Supervision.

Declaration of Competing Interest

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2022.101155.

References

Alunno-Bruscia, M., Bourlès, Y., Maurer, D., Robert, S., Mazurié, J., Gangnery, A., Goulletquer, P., Pouvreau, S., 2011. A single bio-energetics growth and reproduction model for the oyster Crassostrea gigas in six Atlantic ecosystems. J. Sea Res. 66, 340–348. https://doi.org/10.1016/j.seares.2011.07.008.

Bacher, C., Gangnery, A., 2006. Use of dynamic energy budget and individual based models to simulate the dynamics of cultivated oyster populations. J. Sea Res. 56 (2), 140–155. https://doi.org/10.1016/j.seares.2006.03.004.

Barillé, L., Le Bris, A., Goulletquer, P., Thomas, Y., Glize, P., Kane, F., Falconer, L., Guillotreau, P., Trouillet, B., Palmer, S., Gernez, P., 2020. Biological, socio-economic, and administrative opportunities and challenges to moving aquaculture offshore for small French oyster-farming companies. Aquaculture 521. https://doi.org/10.1016/j.aquaculture.2020.735045.

Barillé, L., Prou, J., Héral, M., Razet, D., 1997. Effects of high natural seston concentrations on the feeding, selection, and absorption of the oyster Crassostrea gigas (Thunberg). J. Exp. Mar. Biol. Ecol. 212, 149–172. https://doi.org/10.1016/S0022-0981(96)02756-6.

Bernard, I., de Kermoysan, G., Pouvreau, S., 2011. Effect of phytoplankton and temperature on the reproduction of the Pacific oyster Crassostrea gigas: Investigation through DEB theory. J. Sea Res. 66, 349–360. https://doi.org/10.1016/j.seares.2011.07.009.

Bertolini, C., Brigolin, D., Porporato, E.M.D., Hattab, J., Pastres, R., Tiscar, P.G., 2021. Testing a Model of Pacific Oysters' (Crassostrea gigas) Growth in the Adriatic Sea: Implications for Aquaculture Spatial Planning. Sustainability 13 (6), 3309. https://doi.org/10.3390/su13063309.

Bourlès, Y., Alunno-Bruscia, M., Pouvreau, S., Tollu, G., Leguay, D., Arnaud, C., Goulletquer, P., Kooijman, S.A.L.M., 2009. Modelling growth and reproduction of the Pacific oyster Crassostrea gigas: advances in the oyster-DEB model through application to a coastal pond. J. Sea Res. 62, 62–71. https://doi.org/10.1016/j.seares.2009.03.002.

Brown, J.R., Hartwick, E.B., 1988. A habitat suitability index model for suspended tray culture of the Pacific oyster, Crassostrea gigas Thunberg. Aquac. Res. 19, 109–126. https://doi.org/10.1111/j.1365-2109.1988.tb00414.x.

Brown, P.C., 1992. Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the southern Benguela/Agulhas ecosystem. South Afr. J. Mar. Sci. 12, 515–525. https://doi.org/10.2989/02577619209504722.

Brugère, C., Aguilar-Manjarrez, J., Beveridge, M.C.M., Soto, D., 2019. The ecosystem approach to aquaculture 10 years on – a critical review and consideration of its future role in blue growth. Rev. Aquac. 11, 493–514. https://doi.org/10.1111/raq.12242.

Caballero, I., Fernández, R., Escalante, O.M., Mamán, L., Navarro, G., 2020. New capabilities of Sentinel-2A/B satellites combined with in situ data for monitoring small harmful algal blooms in complex coastal waters. Sci. Rep. 10, 1–14. https://doi.org/10.1038/s41598-020-65600-1.

Capelle, J.J., Hartog, E., Creemers, J., Heringa, J., Kamermans, P., 2020. Effects of stocking density and immersion time on the performance of oysters in intertidal off-bottom culture. Aquacult. Int. 28, 249–264. https://doi.org/10.1007/s10499-019-00460-9.

Castaños, C., Pascual, M., Camacho, A.P., 2009. Reproductive biology of the non-native oyster, Crassostrea gigas (Thunberg, 1793), as a key factor for its successful spread along the rocky shores of Northern Patagonia, Argentina. J. Shellfish Res. 28, 837–847. https://doi.org/10.2983/035.028.0413.

CSIR D.E.A., D.A.F.F., 2019. SEA for marine and freshwater aquaculture development in South Africa. Part 2: Identification of aquaculture focus areas. Cape Town, South Afr.

Dabrowski, T., Lyons, K., Curé, M., Berry, A., Nolan, G., 2013. Numerical modelling of spatio-temporal variability of growth of Mytilus edulis (L.) and influence of its cultivation on ecosystem functioning. J. Sea Res. 76, 5–21. https://doi.org/10.1016/j.seares.2012.10.012.

DAFF, 2017a. Aquaculture Yearbook 2016 South Africa.

DAFF, 2017b. Aquaculture & Mussels: Feasibility study of oyster and mussels aquaculture in South Africa. Cape Town.

DAFF, 2014. Operation Phakisa: Unlocking the Economic Potential of South Africa's Oceans: Aquaculture. Cape Town.

Demarcq, H., Barlow, R., Hutchings, L., 2007. Application of a chlorophyll index derived from satellite data to investigate the variability of phytoplankton in the Benguela ecosystem. Afr. J. Mar. Sci. 29, 271–282. https://doi.org/10.2989/AJMS.2007.29.2.11.194.

Demarcq, H., Barlow, R.G., Shillington, F.A., 2003. Climatology and variability of sea surface temperature and surface chlorophyll in the Benguela and Agulhas ecosystems as observed by satellite imagery. Afr. J. Mar. Sci. 25, 363–372. https://doi.org/10.2989/18142320309504022.

Dridi, S., Romdhane, M.S., Elcafsi, M., 2007. Seasonal variation in weight and biochemical composition of the Pacific oyster, Crassostrea gigas in relation to the gametogenic cycle and environmental conditions of the Bizert lagoon, Tunisia. Aquaculture 263, 238–248. https://doi.org/10.1016/j.aquaculture.2006.10.028.

Dutertre, M., Barillé, L., Haure, J., Cognie, B., 2007. Functional responses associated with pallial organ variations in the Pacific oyster Crassostrea gigas (Thunberg, 1793). J. Exp. Mar. Biol. Ecol. 352, 139–151. https://doi.org/10.1016/j.jembe.2007.07.016.

Dutertre, M., Beninger, P.G., Barillé, L., Papin, M., Rosa, P., Barillé, A.L., Haure, J., 2009. Temperature and seston quantity and quality effects on field reproduction of farmed oysters, Crassostrea gigas, in Bourgneuf Bay, France. Aquat. Living Resour. 22, 319–329. https://doi.org/10.1051/alr/2009042.

Evans, S., Langdon, C., 2006. 'Direct and Indirect Responses to Selection on Individual Body Weight in the Pacific Oyster (Crassostrea gigas)'. Aquaculture 261, 546–555. https://doi.org/10.1016/j.aquaculture.2006.07.037.

Falconer, L., Telfer, T.C., Ross, L.G., 2016. Investigation of a novel approach for aquaculture site selection. J. Environ. Manag. 181, 791–804. https://doi.org/10.1016/j.jenvman.2016.07.018.

Fleury, P.G., Goyard, E., Mazurié, J., Claude, S., Bouget, J.F., Langlade, A., Le Coguic, Y., 2001. The assessing of Pacific oyster (Crassostrea gigas) rearing performances by the IFREMER/REMORA network: method and first results (1993–98) in Brittany (France). In: Burnell, G. (Ed.), Coastal Shellfish — A Sustainable Resource. Springer Netherlands, Dordrecht, pp. 195–208. https://doi.org/10.1007/978-94-010-0434-3_20.

Fleury, E., Normand, J., Lamoureux, A., Bouget, J.F., Lupo, C., Cochennec-Laureau, N., Petton, S., Petton, B., Pouvreau, S., 2021. RESCO REMORA Database : National monitoring network of mortality and growth rates of the sentinel oyster Crassostrea gigas. SEANOE. https://doi.org/10.17882/53007.

Gentry, R.R., Froehlich, H.E., Grimm, D., Kareiva, P., Parke, M., Rust, M., Gaines, S.D., Halpern, B.S., 2017. Mapping the global potential for marine aquaculture. Nat. Ecol. Evol. 1, 1317–1324. https://doi.org/10.1038/s41559-017-0257-9.

Gernez, P., Doxaran, D., Barillé, L., 2017. Shellfish aquaculture from Space: Potential of Sentinel2 to monitor tide-driven changes in turbidity, chlorophyll concentration and oyster physiological response at the scale of an oyster farm. Front. Mar. Sci. 4, 1–15. https://doi.org/10.3389/fmars.2017.00137.

Gernez, P., Palmer, S.C.J., Thomas, Y., Forster, R., 2021. Editorial: remote sensing for aquaculture. Front. Mar. Sci. 7, 638156 https://doi.org/10.3389/fmars.2020.638156.

Gordon, A.L., 2003. Oceanography: the brawniest retroflection. Nature 421, 904–905. https://doi.org/10.1038/421904a.

Goschen, W., Schumann, E., Bernard, K., Bailey, S., Deyzel, S., 2012. Upwelling and ocean structures off Algoa Bay and the south-east coast of South Africa. Afr. J. Mar. Sci. 34, 525–536. https://doi.org/10.2989/1814232X.2012.749810.

Goschen, W.S., Schumann, E.H., 2010. Ocean current and temperature structures in Algoa Bay and beyond in November 1986 7615. ⟨https://doi.org/10.2989/025776188784379198⟩.

Graham, P., Falconer, L., Telfer, T., Mossone, P., Viale, I., Carboni, S., 2020. A modelling approach to classify the suitability of shallow Mediterranean lagoons for pacific oyster, Crassostrea gigas (Thunberg, 1793) farming. Ocean Coast. Manag. 192, 105234 https://doi.org/10.1016/j.ocecoaman.2020.105234.

Griffiths, C.L., Robinson, T.B., Lange, L., Mead, A., 2010. Marine biodiversity in South Africa: an evaluation of current states of knowledge. PLoS One. https://doi.org/10.1371/journal.pone.0012008.

Harris, L.R., Sink, K., Skowno, A., Van Niekerk, L., 2018. National Biodiversity Assessment 2018: Technical Report Volume 5: Coast.

Haupt, T.M., Griffiths, C.L., Robinson, T.B., Tonin, A.F.G., Bruyn, P.A.De, 2010. The history and status of oyster exploitation and culture in South Africa. J. Shellfish Res. 29, 151–159. https://doi.org/10.2983/035.029.0109.

Honkoop, P.J.C., Bayne, B.L., 2002. Stocking density and growth of the Pacific Oyster (Crassostrea gigas) and the Sydney Rock Oyster (Saccostrea Glomerata) in Port Stephens, Australia. Aquaculture 213, 171–186. https://doi.org/10.1016/S0044-8486(02)00030-3.

Hu, Y.C., Chiang, C.Y., Chen, W.L., Chou, W.K., 2012. Lossless index coding for indexed colour images. Imaging Sci. J. 60, 54–63. https://doi.org/10.1179/1743131×11Y.0000000007.

Kämpf, J., Chapman, P., 2016. The benguela current upwelling system. In: Upwelling Systems of the World. Springer International Publishing, pp. 251–314. https://doi.org/10.1007/978-3-319-42524-5_7.

Keightley, J., von der Heyden, S., Jackson, S., 2015. Introduced Pacific oysters Crassostrea gigas in South Africa: demographic change, genetic diversity and body condition. Afr. J. Mar. Sci. 37, 89–98. https://doi.org/10.2989/1814232X.2015.1020874.

Kooijman, S.A.L.M., 2000. Dynamic Energy and Mass Budgets in Biological Systems, 2nd ed. Cambridge University Press.

Krause, G., Stead, S.M., 2017. Governance and offshore aquaculture in multi-resource use settings, Aquaculture Perspective of Multi-Use Sites in the Open Ocean: The Untapped Potential for Marine Resources in the Anthropocene. ⟨https://doi.org/10.1007/978-3-319-51159-7_7⟩.

Lockerbie, E.M., Shannon, L., 2019. Toward exploring possible future states of the Southern Benguela. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00380.

Luger, S.A., Schoones, J.S., Mocke, G.P., Smit, F., 1998. Predicting and evaluating turbidity caused by dredging in the environmentally sensitive Saldanha Bay. Coast. Eng. 3561–3574.
Luger, S.A., van Ballegooyen, R.C., 2000. In: Brebbia, C.A., Rodriguez, G.R. (Eds.), Environmental and Coastal Regions III. WIT Press, Stellenbosch, South Africa.
Marshall, R.D., Dunham, A., 2013. 'Effects of Culture Media and Stocking Density on Biofouling, Shell Shape, Growth, and Survival of the Pacific Oyster (Crassostrea gigas) and the Manila Clam (Venerupis philippinarum) in Suspended Culture'. Aquaculture 406, 68–78. https://doi.org/10.1016/j.aquaculture.2013.05.003.
Mbambo, S.W., 2014. Scales of Variability of Phytoplankton Composition and Biomass in Algoa Bay, South Africa. University of Cape Town.
Melet, A., Teatini, P., Le Cozannet, G., Jamet, C., Conversi, A., Benveniste, J., Almar, R., 2020. Earth Observations for Monitoring Marine Coastal Hazards and Their Drivers, Surveys in Geophysics. Springer, Netherlands. https://doi.org/10.1007/s10712-020-09594-5.
Miossec, L., Le Deuff, R.M., Goulletquer, P., 2009. Alien species alert: Crassostrea gigas (Pacific oyster). ICES Coop. Res. Rep. 299, 1–42.
Monaco, C.J., Porporato, E.M.D., Lathlean, J.A., Tagliarolo, M., Sarà, G., McQuaid, C.D., 2019. Predicting the performance of cosmopolitan species: dynamic energy budget model skill drops across large spatial scales. Mar. Biol. https://doi.org/10.1007/s00227-018-3462-4.
Naylor, R.L., Hardy, R.W., Buschmann, A.H., Bush, S.R., Cao, L., Klinger, D.H., Little, D. C., Lubchenco, J., Shumway, S.E., Troell, M., 2021. A 20-year retrospective review of global aquaculture. Nat | 591, 551.
Nel, A., Pitcher, G.C., Richoux, N.B., Jackson, S., 2014. Culture environment and hatchery of origin influence growth, condition and feeding organ morphology in the Pacific oyster Crassostrea gigas in South Africa. Afr. J. Mar. Sci. 36, 481–491. https://doi.org/10.2989/1814232X.2014.982187.
O'Reilly, J.E., Maritorena, S., Mitchell, B.G., Siegel, D.A., Carder, K.L., Garver, S.A., Kahru, M., McClain, C., 1998. Ocean color chlorophyll algorithms for SeaWiFS. J. Geophys. Res. Ocean. 103, 24937–24953. https://doi.org/10.1029/98JC02160.
Olivier, D., Heinecken, L., Jackson, S., 2013. Mussel and oyster culture in Saldanha Bay, South Africa: potential for sustainable growth, development and employment creation. Food Secur. 5, 251–267. https://doi.org/10.1007/s12571-013-0244-1.
Palmer, S.C.J., Barillé, L., Kay, S., Ciavatta, S., Buck, B., Gernez, P., 2021. Pacific oyster (Crassostrea gigas) growth modelling and indicators for offshore. Aquac. Eur. Clim. Change Uncertain. Aquac. 532. https://doi.org/10.1016/j.aquaculture.2020.736116.
Palmer, S.C.J., Gernez, P.M., Thomas, Y., Simis, S., Miller, P.I., Glize, P., Barillé, L., 2020. Remote Sensing-Driven Pacific Oyster (Crassostrea gigas) growth modeling to inform offshore aquaculture site selection. Front. Mar. Sci. 6, 1–19. https://doi.org/10.3389/fmars.2019.00802.
Pernet, F., Browman, H.I., 2021. The future is now: marine aquaculture in the Anthropocene. ICES J. Mar. Sci. 78, 315–322. https://doi.org/10.1093/icesjms/fsaa248.
Pieterse, A., Pitcher, G., Naidoo, P., Jackson, S., 2012. Growth and condition of the Pacific oyster Crassostrea gigas at three environmentally distinct South African oyster farms. J. Shellfish Res. 31, 1061–1076. https://doi.org/10.2983/035.031.0418.
Pitcher, G.C., Krock, B., Cembella, A.D., 2011. Accumulation of diarrhetic shellfish poisoning toxins in the oyster Crassostrea gigas and the mussel Choromytilus meridionalis in the southern Benguela ecosystem. Afr. J. Mar. Sci. 33, 273–281. https://doi.org/10.2989/1814232X.2011.600372.
Pitcher, G.C., Probyn, T.A., 2016. Suffocating phytoplankton, suffocating waters—Red Tides and Anoxia. Front. Mar. Sci. 3. https://doi.org/10.3389/fmars.2016.00186.
Pitcher, G.C., Foord, C.J., Macey, B.M., Mansfield, L., Mouton, A., Smith, M.E., Osmond, S.J., van der Molen, L., 2019. Devastating farmed abalone mortalities attributed to yessotoxin-producing dinoflagellates. Harmful Algae 81, 30–41. https://doi.org/10.1016/j.hal.2018.11.006.
Pitcher, G.C., Jacinto, G.S., 2019. 3.3. Ocean deoxygenation links to harmful algal blooms. Ocean Deoxygenation: Everyone's problem - causes, impacts, consequences and solutions, 1st. Gland Switzerland: IUCN, pp. 153–170.
Pitcher, G.C., Louw, D.C., 2021. Harmful algal blooms of the Benguela Eastern Boundary upwelling system. Harmful Algae 102, 101898.
Pousse, É., Flye-sainte-marie, J., Alunno-bruscia, M., Hégaret, H., Rannou, É., Pecquerie, L., Marques, G.M., Thomas, Y., Castrec, J., Fabioux, C., Long, M., Lassudrie, M., Hermabessiere, L., Amzil, Z., Soudant, P., Jean, F., 2019. Modelling paralytic shellfish toxins (PST) accumulation in Crassostrea gigas by using Dynamic Energy Budgets (DEB). J. Sea Res. 143, 152–164. https://doi.org/10.1016/j.seares.2018.09.002.
Pouvreau, S., Bourlès, Y., Lefebvre, S., Gangnery, A., Alunno-Bruscia, M., 2006. Application of a dynamic energy budget model to the Pacific oyster, Crassostrea gigas, reared under various environmental conditions. J. Sea Res. 56, 156–167. https://doi.org/10.1016/j.seares.2006.03.007.
Probyn, T.A., Pitcher, G.C., Monteiro, P.M.S., Boyd, A.J., Nelson, G., Pitcher, G.C., Monteiro, P.M.S., Boyd, A.J., Nelson, G., Bay, I.N.S., Africa, S., 2000. Physical processes contributing to harmful algal blooms in Saldanha Bay, South Africa. South Afr. J. Mar. Sci. 22, 285–297. https://doi.org/10.2989/025776100784125807.
Roberts, M.J., 2005. Chokka squid (Loligo vulgaris reynaudii) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. ICES J. Mar. Sci. 62, 33–55. https://doi.org/10.1016/j.icesjms.2004.10.002.
Robinson, T.B., Griffiths, C.L., Tonin, A., Bloomer, P., Hare, M.P., 2005. Naturalized populations of oysters, Crassostrea gigas along the South African coast: Distribution, abundance and population structure. J. Shellfish Res. 24, 443–450. https://doi.org/10.2983/0730-8000(2005)24[443:NPOOCG]2.0.CO;2.
Rothman, M.D., Bolton, J.J., Stekoll, M.S., Boothroyd, C.J.T., Kemp, F.A., Anderson, R.J., 2017. Geographical variation in morphology of the two dominant kelp species, Ecklonia maxima and Laminaria pallida (Phaeophyceae, Laminariales), on the west coast of Southern Africa. In: Journal of Applied Phycology. Springer Netherlands, pp. 2627–2639. https://doi.org/10.1007/s10811-017-1255-7.
Santa Marta, A., Ferreira, J.G., Pitcher, G.C., Lencart e Silva, J., 2020. Sustainable shellfish aquaculture in Saldanha Bay, South Africa. Afr. J. Mar. Sci. 42, 151–166. https://doi.org/10.2989/1814232X.2020.1760935.
Sarà, G., Reid, G.K., Rinaldi, A., Palmeri, V., Troell, M., Kooijman, S.A.L.M., 2012. Growth and reproductive simulation of candidate shellfish species at fish cages in the Southern Mediterranean: dynamic Energy Budget (DEB) modelling for integrated multi-trophic aquaculture. Aquaculture 324–325, 259–266. https://doi.org/10.1016/j.aquaculture.2011.10.042.
Shelmerdine, R., Mouat, B., Shucksmith, R., 2017. The most northerly record of feral Pacific oyster Crassostrea gigas (Thunberg, 1793) in the British Isles. BIR 6, 57–60. https://doi.org/10.3391/bir.2017.6.1.09.
Schumann, E.H., Churchill, J.R.S., Zaayman, H.J., 2005. Oceanic variability in the western sector of Algoa Bay, South Africa. Afr. J. Mar. Sci. 27, 65–80.
Shpigel, M., 1989. Gametogenesis of the European flat oyster (Ostrea edulis) and Pacific oyster (Crassostrea gigas) in warm water in Israel. Aquaculture 80, 343–349. https://doi.org/10.1016/0044-8486(89)90181-6.
Sink, K.J., Van Der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P., Karenyi, N.F., 2018. South African National Biodiversity Assessment 2018 Technical Report Volume 4: Marine Realm, South African National Biodiversity Institute.
Smith, M.E., Bernard, S., 2020. Satellite ocean color based harmful algal bloom indicators for aquaculture decision support in the Southern Benguela. Front. Mar. Sci. 7, 1–13. https://doi.org/10.3389/fmars.2020.00061.
Smith, M.E., Pitcher, G.C., 2015. Saldanha Bay, South Africa I: the use of ocean colour remote sensing to assess phytoplankton biomass. Afr. J. Mar. Sci. 37, 503–512. https://doi.org/10.2989/1814232X.2015.1093023.
Smith, M.E., Lain, L.R., Bernard, S., 2018. An optimized Chlorophyll a switching algorithm for MERIS and OLCI in phytoplankton-dominated waters. Remote Sens. Environ. 215, 217–227. https://doi.org/10.1016/j.rse.2018.06.002.
Statistics South Africa, 2021. Gross domestic product 4th quarter 2020..
Snyder, J., Boss, E., Weatherbee, R., Thomas, A.C., Brady, D., Newell, C., 2017. Oyster Aquaculture Site Selection Using Landsat 8-Derived Sea Surface Temperature, Turbidity, and Chlorophyll a. Front. Mar. Sci. 4, 190. https://doi.org/10.3389/fmars.2017.00190.
Statistics South Africa, 2019. Southern Africa labour and development research unit, Agence Francaise de Development, African centre of excellence for inequality research. Inequal. Trends South Afr. Stat. South Afr.
Tan, K., Deng, L., Zheng, H., 2021. Effects of stocking density on the aquaculture performance of diploid and triploid, Pacific oyster Crassostrea gigas and Portuguese oyster C. angulata in warm water aquaculture. Aquac. Res. 52, 6268–6279. https://doi.org/10.1111/are.15489.
Thomas, Y., Bacher, C., 2018. Assessing the sensitivity of bivalve populations to global warming using an individual-based modelling approach. Glob. Chang. Biol. 24, 4581–4597. https://doi.org/10.1111/gcb.14402.
Thomas, Y., Cassou, C., Gernez, P., Pouvreau, S., 2018. Oysters as sentinels of climate variability and climate change in coastal ecosystems. Environ. Res. Lett. 13, 104009 https://doi.org/10.1088/1748-9326/aae254.
Thomas, Y., Pouvreau, S., Alunno-Bruscia, M., Barillé, L., Gohin, F., Bryère, P., Gernez, P., 2016. Global change and climate-driven invasion of the Pacific oyster (Crassostrea gigas) along European coasts: A bioenergetics modelling approach. J. Biogeogr. 43, 568–579. https://doi.org/10.1111/jbi.12665.
Troost, K., 2010. Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster Crassostrea gigas in continental NW European estuaries. J. Sea Res. 64, 145–165. https://doi.org/10.1016/j.seares.2010.02.004.
Ubertini, M., Lagarde, F., Mortreux, S., Le Gall, P., Chiantella, C., Fiandrino, A., Bernard, I., Pouvreau, S., Roque d'Orbcastel, E., 2017. Gametogenesis, spawning behavior and larval abundance of the Pacific oyster Crassostrea gigas in the Thau lagoon: evidence of an environment-dependent strategy. Aquaculture 473, 51–61. https://doi.org/10.1016/j.aquaculture.2017.01.025.
van der Veer, H.W., Cardoso, J.F.M.F., van der Meer, J., 2006. The estimation of DEB parameters for various Northeast Atlantic bivalve species. J. Sea Res. 56 (2), 107–124. https://doi.org/10.1016/j.seares.2006.03.005.
Velimirov, B., Field, J.G., Griffiths, C.L., Zoutendyk, P., 1977. The ecology of kelp bed communities in the Benguela upwelling system. Helgoländer Wiss. Meeresunters. 30, 495–518.
Vianna, L.F., de, N., Filho, J.B., 2018. Spatial analysis for site selection in marine aquaculture: an ecosystem approach applied to Baía Sul, Santa Catarina, Brazil. Aquaculture 489, 162–174. https://doi.org/10.1016/j.aquaculture.2017.12.039.
Weeks, S.J., Barlow, R., Roy, C., Shillington, F.A., 2006. Remotely sensed variability of temperature and chlorophyll in the southern Benguela: upwelling frequency and phytoplankton response. Afr. J. Mar. Sci. 28, 493–509. https://doi.org/10.2989/18142320609504201.
Wolny, J.L., Tomlinson, M.C., Schollaert Uz, S., Egerton, T.A., McKay, J.R., Meredith, A., Reece, K.S., Scott, G.P., Stumpf, R.P., 2020. Current and future remote sensing of harmful algal blooms in the chesapeake bay to support the shellfish industry. Front. Mar. Sci. 7, 337. https://doi.org/10.3389/fmars.2020.00337.