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Integrating mechanistic models and climate change projections to predict invasion of the mussel, *Mytilopsis sallei*, along the southern China coast

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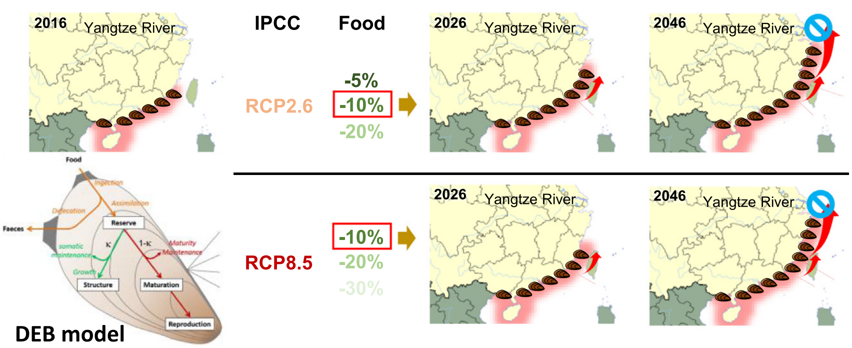
HIGHLIGHTS

- The mussel, *Mytilopisis sallei*, is invasive along the southern China coast.
- A DEB model was used to predict future mussel life history traits.
- Warming will enhance, while food limitation will limit, mussel invasion.
- The Yangtze River remains an important biogeographic barrier.
- Predictive models allow spatially explicit assessment of invasion risk.

GRAPHICAL ABSTRACT



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ABSTRACT

Species invasion is an important cause of global biodiversity decline and is often mediated by shifts in environmental conditions such as climate change. To investigate this relationship, a mechanistic Dynamic Energy Budget model (DEB) approach was used to predict how climate change may affect spread of the invasive mussel *Mytilopsis sallei*, by predicting variation in the total reproductive output of the mussel under different scenarios. To achieve this, the DEB model was forced with present-day satellite data of sea surface temperature (SST) and chlorophyll-*a* concentration (Chl-*a*), and SST under two warming RCP scenarios and decreasing current Chl-*a* levels, to predict future responses. Under both warming scenarios, the DEB model predicted the reproductive output of *M. sallei* would enhance range extension of the mussel, especially in regions south of the Yangtze River when future declines in Chl-*a* were reduced by less than 10%, whereas egg production was inhibited when Chl-*a* decreased by 20–30%. The decrease in SST in the Yangtze River may, however, be a natural barrier to the northward expansion of *M. sallei*, with colder temperatures resulting in a strong decrease in egg production. Although the invasion path of *M. sallei* may be inhibited northwards by the Yangtze River, larger geographic regions south of the Yangtze River run the risk of invasion, with subsequent negative impacts on aquaculture through competition for food with farmed bivalves and damaging aquaculture facilities. Using a DEB model approach to characterise the life history traits of *M. sallei*, therefore, revealed the importance of food availability and

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temperature on the reproductive output of this mussel and allowed evaluation of the invasion risk for specific regions. DEB is, therefore, a powerful predictive tool for risk management of already established invasive populations and to identify regions with a high potential invasion risk.

1. Introduction

Species invasion, defined as the successful establishment and spread of species outside their native range, is a common phenomenon, yet the current extent and frequency of invasions are increasing at unprecedented rates (Sax et al., 2005). Such invasions can have detrimental consequences, including loss of biodiversity and disruption of invaded ecosystem functions, human health risks and impacts on agriculture and aquaculture (Galil et al., 2014). The rate and extent of species invasions, however, are dependent on various life history traits of species such as growth rate, reproductive success and larval output and how these parameters interact with changes in environmental conditions in the areas that alien species encounter (Sarà et al., 2013a; Thomas et al., 2016). One of the key prerequisites for successfully establishing a population is being present in sufficient numbers to produce viable populations. Population density, which is supported by fecundity at a functional level, plays a crucial role in determining the success of a new species and their ability to colonise novel habitats (Kramer et al., 2009). The arrival alien species does not, for example, automatically lead to successful establishment unless invaders reproduce asexually. In this regard, climatic factors play an important role by affecting the reproductive output of any given population. Environmental change associated with climate change, such as seawater warming and coastal eutrophication, have been shown to increase the success of invasive species by promoting greater reproductive output, enhanced larval development and juvenile recruitment and thereby facilitating their geographic spread (Stachowicz et al., 2002; Valdizan et al., 2011; Galil et al., 2015). Climate change is also understood to be a major cause of changes in species' life history traits by altering environmental conditions, leading to shifts in species' performance, their competitive ability and geographic distribution (Parmesan and Yohe, 2003; Pörtner and Farrell, 2008).

At regional, continental and global scales, there are strong spatial and temporal variations in environmental conditions. The extremes of these spatio-temporal environmental conditions typically harbour very different ecological communities (Buckley and Jetz, 2008), with species in each community responding to the physical environmental prevailing at each location (Srinivasan et al., 2018). Under current climate change, environmental conditions are changing greatly and at different rates (IPCC, 2013). Seawater warming, for example, is heterogeneous across space, with some regions warming faster than others (Lima and Wethey, 2012). Climate change is, therefore, an important driver responsible for global changes in species' distribution ranges and its influence can be seen in the increasing invasion of alien species in various regions of the world (Cheung et al., 2009; Pederson et al., 2011; Sarà et al., 2018). As a result of these changes in species ranges, there is an urgent need to understand and predict the impacts of spatio-temporal changes in environmental conditions in the context of climate change on invasive species' life history traits.

Predicting these changes is challenging, but mechanistic models, such as the Dynamic Energy Budget model (DEB; Kooijman, 2010), can provide a valuable platform for predicting species' life history traits. The DEB model integrates ecophysiological parameters of a species to simulate its bioenergetics (i.e., changes in energy uptake and allocation) under varying environmental conditions, resulting in a powerful approach for predicting species' distributions under changing environments (Lavaud et al., 2017; Kooijman, 2020; Mangano et al., 2020). Recently, DEB models have been combined with environmental data such as temperature and food availability obtained from satellites and/or climate models to predict the life history traits of invasive species in response to predicted spatio-temporal fluctuations of their environment, and subsequently possible future expansion under climate change (Sarà et al., 2013a; Thomas et al., 2016; Agüera and Byrne, 2018).

Here, using a mechanistic DEB-approach, coupled with satellite data and climate models, we modelled the fitness of an invasive bivalve, the black-striped mussel, *Mytilopsis sallei*, along the southern coast of China. *M. sallei* is native to the Pacific coast of Panama and successfully spread to Hong Kong in 1980 through ship ballast waters (Morton, 1989). Ten years later, it had extended northwards to Fujian province, China (Cai et al., 2005) where it has negatively impacted the aquaculture industry (for fish, mussels and oysters) in Fujian Province through damaging aquaculture facilities and reducing water quality, resulting in local economic loss (Cai et al., 2006, 2014). In the context of climate change and biological invasions, the increase in sea surface temperature (SST) projected by the end of the century (IPCC, 2013) is likely to facilitate the northwards expansion of *M. sallei*, and cause further impact on important aquaculture areas along the southern and central coast of China. Another impact of climate change is altering coastal chlorophyll-*a* (Chl-*a*), which represents the food available for filter feeders such as mussels and oysters, and thus will directly influence the life history traits of the mussel *M. sallei*. While employing offensive strategies against invasive species (e.g., eradication) is expensive and rarely successful (Mack et al., 2000; Hilliard, 2004), early detection of invasion risk can be crucial to prevent or limit expansion and consequently minimize impacts on the ecology and economy of at-risk areas (Branch and Steffani, 2004). The aims of this study were, therefore, to analyse the spatio-temporal variations in reproductive output of *M. sallei* and its potential geographic expansion along the southern coast of China. By predicting changes in life history traits, the possible colonization paths of *M. sallei* in the near future associated with climate change can be inferred to help develop appropriate mitigation and management strategies against this invasive species.

2. Materials and methods

2.1. Model domain

The current reported northern limit for *M. sallei* in China is in Fujian Province (25°N). In order to predict the potential northern shift of this invasive mussel under climate change, we performed DEB simulations for the area from 21–32°N and 110–122°E, which includes the current distribution of *M. sallei* and extends to the major biogeographic break at the Yangtze River mouth where the ocean currents and/or decrease in SST due to freshwater discharge and precipitation are likely to act as physical barriers, limiting the dispersal of planktonic larvae (Dong et al., 2012; Guo et al., 2011, 2015; Fig. 1).

2.2. Environmental data

Level 3 satellite-observed daily SST and Chl-*a* for the period 2015–2016 from the National Aeronautics and Space Administration (NASA) Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua level 3 were downloaded from the Ocean Color Web portal (https://oceancolor.gsfc.nasa.gov/). The spatial resolution of these data is 4 km × 4 km.

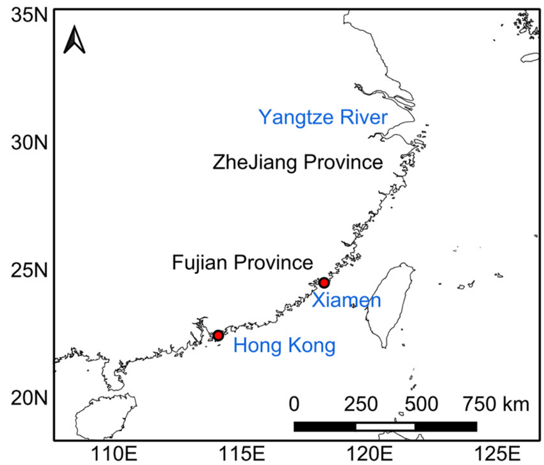

Fig. 1. Map of the southern coast of China. Xiamen is the northern limit reported for *Mytilopsis sallei* and the Yangtze River may act as a major biogeographic break for expansion of this mussel as noted for other species (Dong et al., 2012; Guo et al., 2015).

Projected monthly SST for the years 2025–2026 and 2045–2046 were obtained from World Climate Research Programme (WCRP) Coupled Model Intercomparison Project Phase 5 (CIMP5) simulation (model: Max-Planck-Institut für Meteorologie Earth-System Model running on Medium Resolution grid, MPI-ESM-MR). This MPI-ESM-MR data has a spatial resolution of 1.865° x 1.875° and was downloaded from the Earth System Grid Federation (ESGF) data portal. Two future climate change scenarios (Representative Concentration Pathways (RCP): conservative RCP2.6 and severe RCP8.5) were considered. Due to the low accuracy of projected Chl-*a* data (Roxy et al., 2016), two RCPs projections were used following a sensitivity analysis wherein present-day Chl-*a* levels were decreased by 5, 10, 20% for RCP2.6 and 10, and 20, 30% for RCP8.5 (Fig. 2) as previous modelling studies suggest global

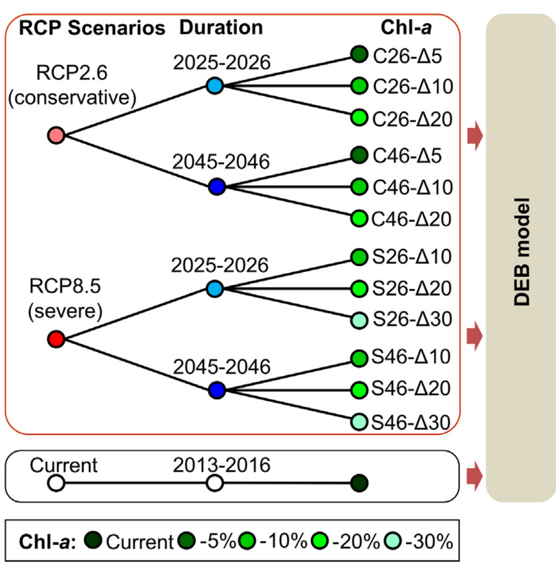

Fig. 2. Conceptual framework showing the scenarios of temperature and chlorophyll-*a* concentrations used in the Dynamic Energy Budget models for the predictions of the current and future total reproductive output of *Mytilopsis sallei* under three time periods (Duration). The abbreviations indicate Conservative (RCP2.6, C) or Severe (RCP8.5, S) scenarios; time duration (2025–2026 = 26, 2045–2046 = 46); and delta decrease in chlorophyll-*a* (5, 10, 20, 30%).

warming will result in decreases in Chl-*a* within the northeast Pacific Ocean region (Sarmiento et al., 2004; Hashioka and Yamanaka, 2007; Bopp et al., 2013; Moore et al., 2013).

These downloaded environmental data were then extracted to obtain the appropriate information within 12 km from the shore of China (maximum distance of aquaculture conducted offshore; A.L.S.T., personal communication with local aquaculture famers) which covered from 21–32°N and 110–122°E. These environmental data were regrided to the same spatial resolution of 0.036° x 0.036° (~4 km × 4 km) with a total of 3083 pixels per environmental data layer.

2.3. DEB model

The DEB model is a mechanistic model which defines the process of energy acquisition and utilization in an organism under varying environmental conditions (primarily temperature and food availability; Nisbet et al., 2000; van der Meer, 2006), as applied to species-specific parameters that describe the responses of a species to environmental conditions and allows subsequent prediction of life history traits (e.g., growth and reproduction, fully described in Kooijman, 2010). In DEB models, SST and Chl-*a* are important forcing variables which can be used to predict shellfish life history traits (Thomas et al., 2011, 2016). The DEB model for *M. sallei* (see Fig. S1 and Appendix A in supporting information for DEB theory and details) was, therefore, coupled to satellite or climate models (described above). As *M. sallei* has a maximum life span of 22 months (Morton, 1989), simulations using specific DEB parameters (Table 1; Tan, 2019) following standard parameterization methods (see Appendix B in supporting information; as used by Sarà et al., 2013b; Cheng et al., 2018) were run for two years at each pixel in the study region for three periods, 2015–2016, 2025–2026, and 2045–2046 (hereafter referred to as 2016, 2026 and 2046) representing present-day (at time of model generation), short- and long-term future scenarios respectively.

To predict the potential expansion of *M sallei*, the total reproductive output for the mussel was extracted from the simulation performed for each pixel and presented as a geographic forecast map (performed using the '*Oce package*' in R, Kelley, 2018). Total reproductive output was used as a metric to measure potential invasive success as variation in a species' reproductive output (e.g., total number of eggs produced,

Table 1
List of parameters used in Dynamic Energy Budget model simulations for *Mytilopsis sallei* adopted from Tan (2019 and see Appendix B) and available online at: - https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Mytilopsis_sallei/Mytilopsis_sallei_res.html.

Parameter	Unit	Description	*Mytilopsis sallei*
T_A	°K	Arrhenius temperature	4515
T_L	°K	Lower boundary of tolerance range	283
T_H	°K	Upper boundary of tolerance range	311
T_{AL}	°K	Lower boundary of Arrhenius temperature	6257
T_{AH}	°K	Upper boundary Arrhenius temperature	13,589
$\{\dot{J}_{Xm}\}$	$Jcm^{-2}d^{-1}$	Maximum surface area specific ingestion rate	61.72
$\{\dot{p}_{Am}\}$	$Jcm^{-2}d^{-1}$	Maximum surface area specific assimilation rate	58.05
$[\dot{p}_M]$	$Jcm^{-3}d^{-1}$	Volume specific maintenance costs	43.08
$[E_m]$	Jcm^{-3}	Maximum storage density	905
$[E_G]$	Jcm^{-3}	Volume specific costs for growth	1081
X_k	μg chl *a* L^{-1}	Half saturation coefficient	1.41
AE	–	Assimilation efficiency	0.94
δ_m	–	Shape coefficient	0.2268
κ	–	Fraction of allocated energy spent on maintenance and growth	0.8
κ_R	–	Reproduction efficiency	0.95

oocyte size and spawning date) under different environmental conditions has been demonstrated to be an important factor determining range expansion (see Cardoso et al., 2007; Thomas et al., 2016) and proliferation of an invasive species depends at least in part on its successful reproduction (Valdizan et al., 2011). To determine how total reproductive output would change spatially and temporally under the two RCP scenarios, percent change was calculated for total reproductive output in the study area, following the calculation used in Steeves et al. (2018):

$$\text{Change in total reproductive output } (\%) = [(\text{Future} - \text{Present})/\text{Present}] \times 100\%$$

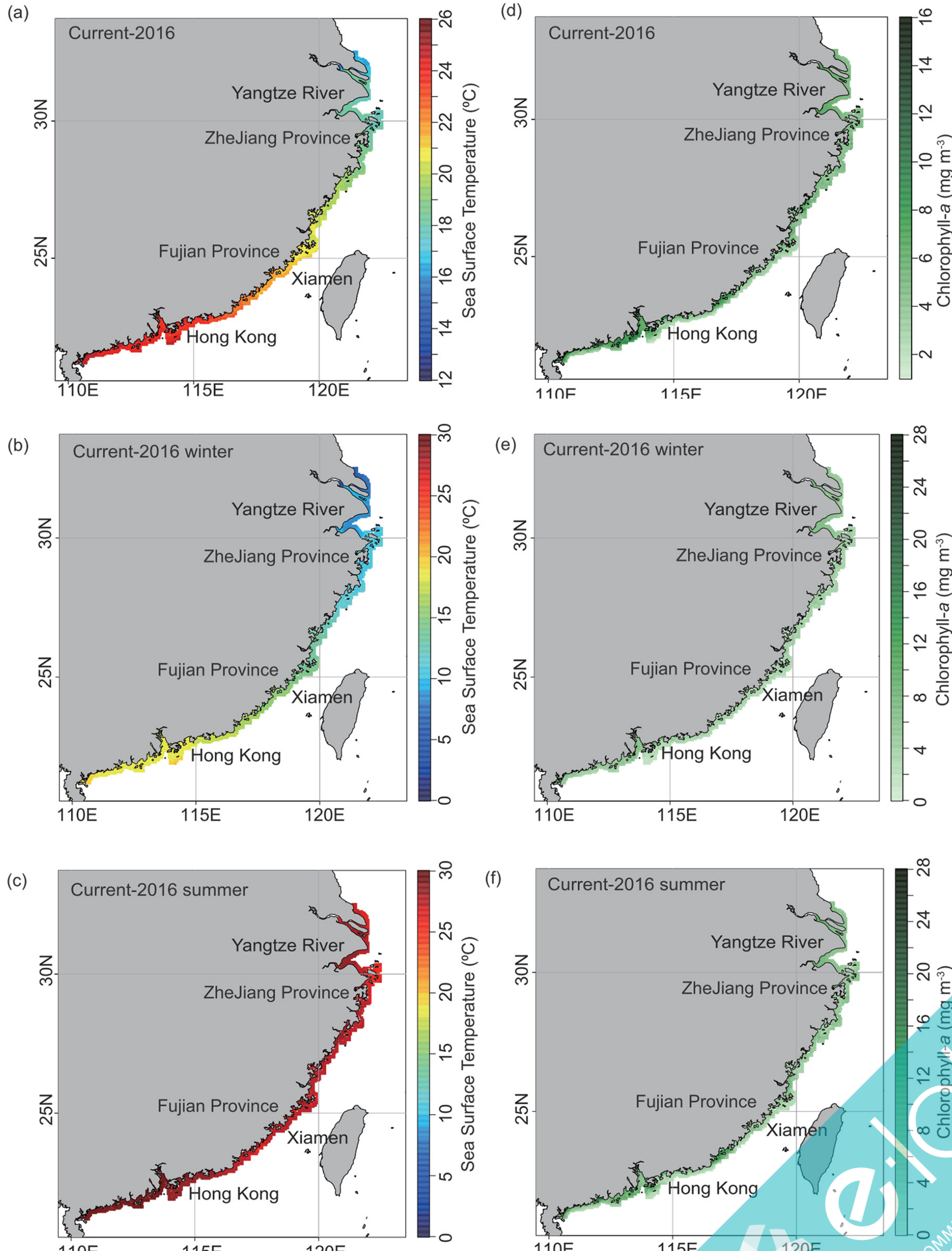

Fig. 3. (a) Yearly, (b) winter, (c) summer mean sea surface temperature (°C), and (d, e, and f) mean chlorophyll-*a* concentration (mg m^{-3}) between 2015 and 2016 along the southern coast of China derived from satellite data.

3. Results

3.1. Characterization of environmental data

The yearly mean SST for the present-day (i.e., 2016) along the southern coast of China showed that temperature increased from south to north and ranged between 12 and 26 °C (Fig. 3a). The average winter temperature along the southern China coastline ranges between 2 and 20 °C (Fig. 3b). In summer, the temperature gradient from north to south is more gradual as compared to winter with average seawater temperature between 23 and 29 °C (Fig. 3c). Unlike SST, there was a strong difference in Chl-*a* between summer and winter seasons along the southern China coastline (Fig. 3e, f), however the annual mean Chl-*a* was spatially variable and varied widely from 1.5–15.4 mg m^{-3} (Fig. 3d).

The climate model indicated that SST warming will be spatially dependent within the study region. Under both RCPs, the mean SST over two periods (2026 and 2046) was projected to increase between 1 and 6 °C along the southern China coastline, except at the Yangtze River (30–32°N), where it was projected to decrease by 1–3 °C compared to the present-day (Fig. 4). Due to the predicted different warming patterns, the study region was separated into two broad regions: southern China (i.e., below the Yangtze River) and the Yangtze River. In the southern region, differential warming rates were observed between the study periods and RCP scenarios. The mean SST, for example, was projected to warm by 2 °C (Fig. 4a) or 2.2 °C (Fig. 4c) by 2026 and 2.3 °C (Fig. 4b) or 2.7 °C (Fig. 4d) by 2046 under RCP2.6 and RCP8.5 scenarios, respectively. In contrast, SST in the Yangtze River delta was predicted to decrease by an average of 2 °C (Fig. 4a) or 2.2 °C (Fig. 4c) by 2026 and 1.7 °C (Fig. 4b) or 1.5 °C (Fig. 4d) by 2046 under RCP2.6 and RCP8.5 scenarios, respectively.

3.2. Dynamic Energy Budget predictions: total reproductive output

Under the present-day climate, the DEB model predicted the total reproductive output produced by *M. sallei* in two years would be spatially variable, with a significant decrease in total reproductive output from north to south (linear regression of eggs produced vs latitude, $y = -22{,}609x + 873{,}998$, $r^2 = 0.338$, $p < 0.0001$) with a range between 7.8–73.2 × 10^4 eggs (Fig. 5). The DEB model predicted 57–83% of pixels (i.e., mainly concentrated in the region above Hong Kong) with an increase in egg production under the two warming scenarios (RCP2.6 and RCP8.5) associated with a 10% decrease in Chl-*a* along southern China (Figs. 6 and 7). From 2016 to 2026, egg production was predicted to increase from 31 to 32 × 10^4 eggs (2.3–5.4%) under both RCP scenarios, while, under C46-Δ10 (conservative scenario of RCP2.6 at year 2046 with 10% decrease in Chl-*a*) and S46-Δ10 (severe scenario of RCP8.5 at year 2046 with 10% decrease in Chl-*a*) it was predicted to increase to 33 × 10^4 eggs (7.7%) and 34 × 10^4 eggs (8.9%), respectively (Table 2). The predicted mean total reproductive output was predicted to increase to 34 × 10^4 (10.9%) and 35 × 10^4 (13.2) under C26-Δ5 and C46-Δ5 scenarios, respectively (Table 2).

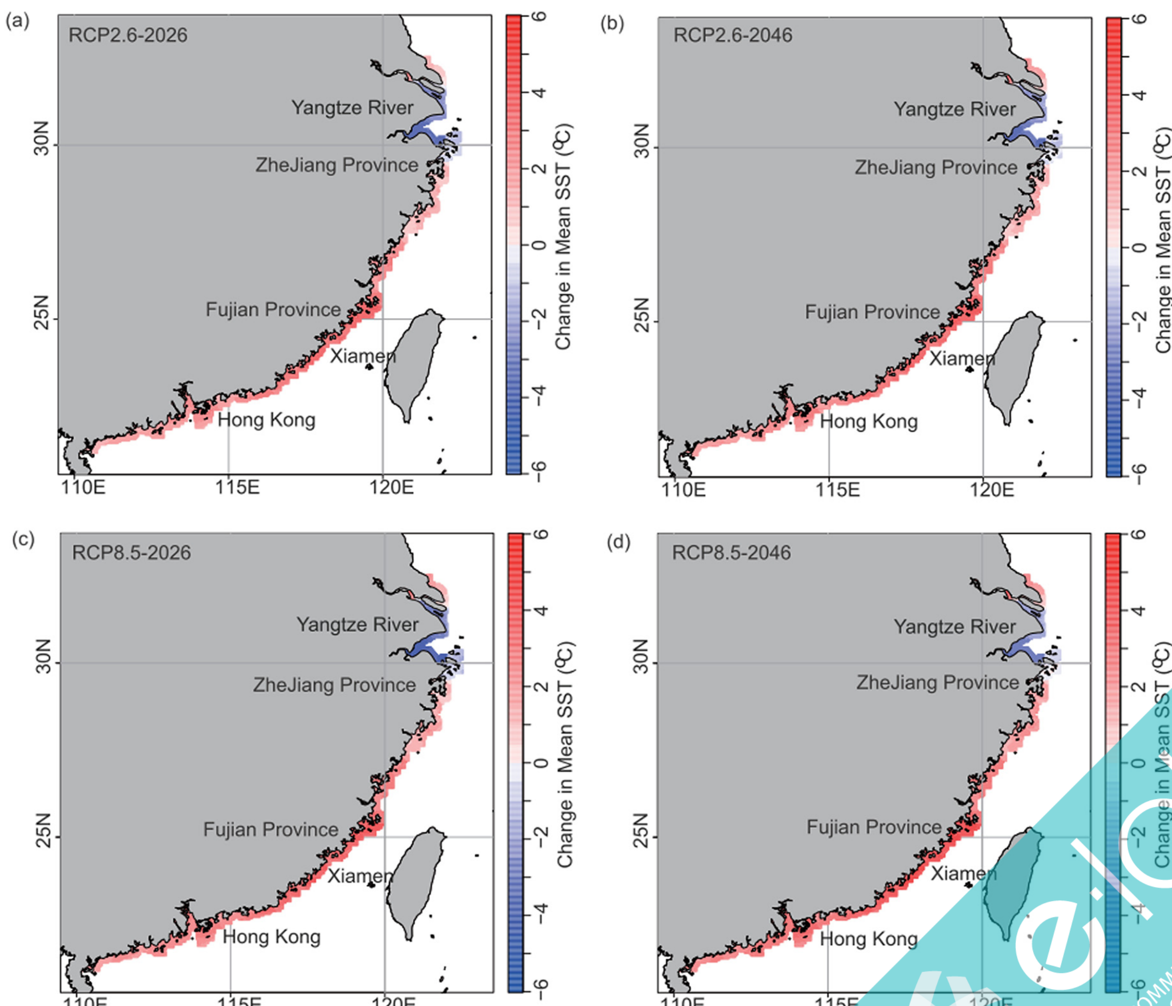

Fig. 4. Predicted change in mean sea surface temperature (°C) along the southern coast of China in (a, c) 2026 and (b, d) 2046 under scenarios of (top panel) RCP2.6 and (below panel) RCP8.5 relative to present-day (2016) conditions.

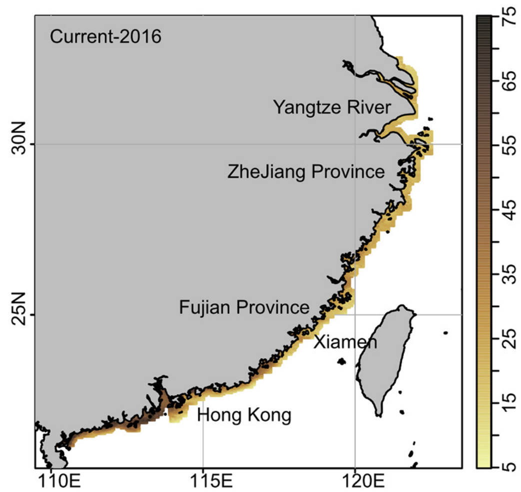

Fig. 5. DEB model predictions of total number of eggs produced by *Mytilopsis sallei* in two years along the southern coast of China under present-day (2016) conditions.

Under future decreasing Chl-*a* of 20–30% relative to present-day conditions, 3–40% of pixels showed an increase in egg production (Figs. 6 and 7), while a 3.9–20% reduction is predicted in the production of eggs along the southern China coast under both RCP scenarios (Table 2). In the Yangtze River (30–32°N), however, the model predicted that only 2–16% of pixels would show an increase in egg production and fewer total eggs would be produced (i.e., 14.2–55.6% decrease) by *M. sallei* under all future food levels and RCP scenario combinations (Table 2).

4. Discussion

As a result of climate change the biogeographic range of many species has shifted northwards (in the northern hemisphere, i.e., polewards) by as much as 50 km per decade during the last century, leading to the introduction of novel species into ecosystems (Helmuth et al., 2006), and exacerbating the success of invasion (Stachowicz et al., 2002). The reported present northern boundary of *M. sallei* along the southern coast of China is Fujian Province (25°N), however, the DEB model simulated reproductive success (i.e., greater egg production as compared to current day) for this species as far north as the Yangtze River (32°N) under present-day conditions. The DEB model predicted, for example, that *M. sallei* could produce 7.8–73.2 $\times$ 10^4 eggs in two years under present-day conditions, which is near to and/or higher than the average number of eggs (10–20 $\times$ 10^4) reported by Qi (2011) for *M. sallei* in Xiamen, its current reported northern limit. The increased predicted total reproductive output of *M. sallei*, combined with suitable environmental conditions that allow persistence, suggests the capacity for a further population expansion northwards along the coastline of China.

Life history traits are a product of a series of physiological processes which increase with body temperature until the optimal temperature of a species is reached (Huey and Stevenson, 1979; Atkinson, 1997; Reznick et al., 2000). For ectotherms, such as the mussel, *M. sallei*, body temperature is highly dependent on environmental temperature, and so an increase in environmental temperature results in enhanced species' life history traits when food supply is not limiting (Shephard et al., 2010; Valdizan et al., 2011). Consequently, the DEB model predicted the mean total reproductive output of *M. sallei* would increase by about 2–13% when the model was run with a <10% decrease in Chl-*a* under both RCP scenarios and future time points (2026 to 2046), with more eggs produced under warmer scenarios (i.e., RCP8.5 as compared to RCP2.6). The scallop, *Pecten maximus*, in the Irish Sea (Shephard et al., 2010) and the invasive slipper limpet, *Crepidula fornicata*, at Bourneuf Bay, France (Valdizan et al., 2011) also showed increases in egg production under warmer water and higher food supply. Shephard et al. (2010) and Valdizan et al. (2011) suggested that this improved egg production may not only increase the local population but also enhance invasion under future warming scenarios. A similar case was also demonstrated for the oyster, *Crassostrea gigas*, where a rise in seawater temperature and phytoplankton concentration increased the reproductive effort of the oyster and was responsible for its expansion along European Atlantic coasts from Gibraltar to Norway (Thomas et al., 2016). The predicted increase in egg production for *M. sallei* in the present study, therefore, suggests that the mussel has sufficient food supply even given a 10% decrease in Chl-*a* and will likely sustain its local populations and expand its range in southern China under the two RCPs scenarios.

The positive effect of a warming environment is, however, limited by reduced food supply. Under both RCPs scenarios, the mean production of eggs by *M. sallei* was predicted to decrease by 5–20% under 2026 scenarios when Chl-*a* decreased by 20–30% relative to present-day conditions. Similar, but less extreme, patterns were predicted under 2046 scenarios when Chl-*a* decreased by 20–30% relative to 2016, with a reduction in range between 2–14%. Energy trade-offs often occur when species have to cope with environmental changes (Sokolova et al., 2012; Cheng et al., 2018). High temperatures and variable environmental conditions, for example, can lead to greater energy investment per egg and the production of larger, but fewer, eggs (Appeldoorn, 1995). As reproductive output is predicted to be less affected under warmer scenarios (i.e., RCP8.5 and 2046) as compared to RCP2.6 and 2026, therefore, it would appear that higher temperatures may benefit reproduction of *M. sallei* even under poor food conditions. Under the same food conditions, for example, the scallop, *Pecten maximus*, showed greater reproductive effort at higher acclimated temperatures when compared to those from lower acclimated temperatures (Saout et al., 1999). The alien mussel, *Perna viridis*, was also predicted to increase its egg production by 14% (RCP2.6) and 113% (RCP8.5) when compared to present-day conditions in Hong Kong resulting in a higher chance of expanding its geographic distribution (Cheng, 2016). The predicted greater egg production under warmer scenarios may, therefore, suggest that the northwards shift (as indicated by increasing reproductive output) of *M. sallei* will be further facilitated by climate change.

As reproductive output is predicted to be higher under warmer SST, the decrease in total reproductive output in the Yangtze River under all scenarios was driven by the decrease in SST in this region. This predicted decrease in mean SST is likely due to the predicted increase in precipitation and floods at the lower reaches of the Yangtze River (Zhang et al., 2006; Guo et al., 2011). *M. sallei* is a tropical species, inhabiting warm waters (temperatures ranging from 25 to 31 °C) and requires a minimum temperature of 18 °C to induce spawning (Morton, 1981; Qi, 2011). Currently, the mean SST in the Yangtze River mouth is 16–18 °C and this is predicted to decrease by 1–3 °C under both RCP scenarios by 2046, which appears to be the main factor limiting reproduction of *M. sallei*. Accordingly, the Yangtze River region may act as a natural barrier for the expansion of *M. sallei* under future climate change scenarios. Although quantitative estimation of a species' fecundity is a crucial aspect to predict its future distribution (Araújo and Peterson, 2012), establishment success does not depend exclusively on adult reproductive output but on several other factors such as dispersal ability (i.e., current, mode of larvae dispersal; length of the larval dispersal stage), space available for larval settlement and human interventions (Branch and Steffani, 2004; Troost, 2010). A number of previous studies have suggested that ocean currents and/or Yangtze River freshwater discharge act as physical barriers that limit both the northwards (Guo et al., 2015) or southwards (Dong et al., 2012) dispersal of planktonic larvae. While species with a planktonic larval stage are more likely to become invasive than direct developers (Scheltema, 1986), the density of planktonic larvae, however, will decrease with increasing travel

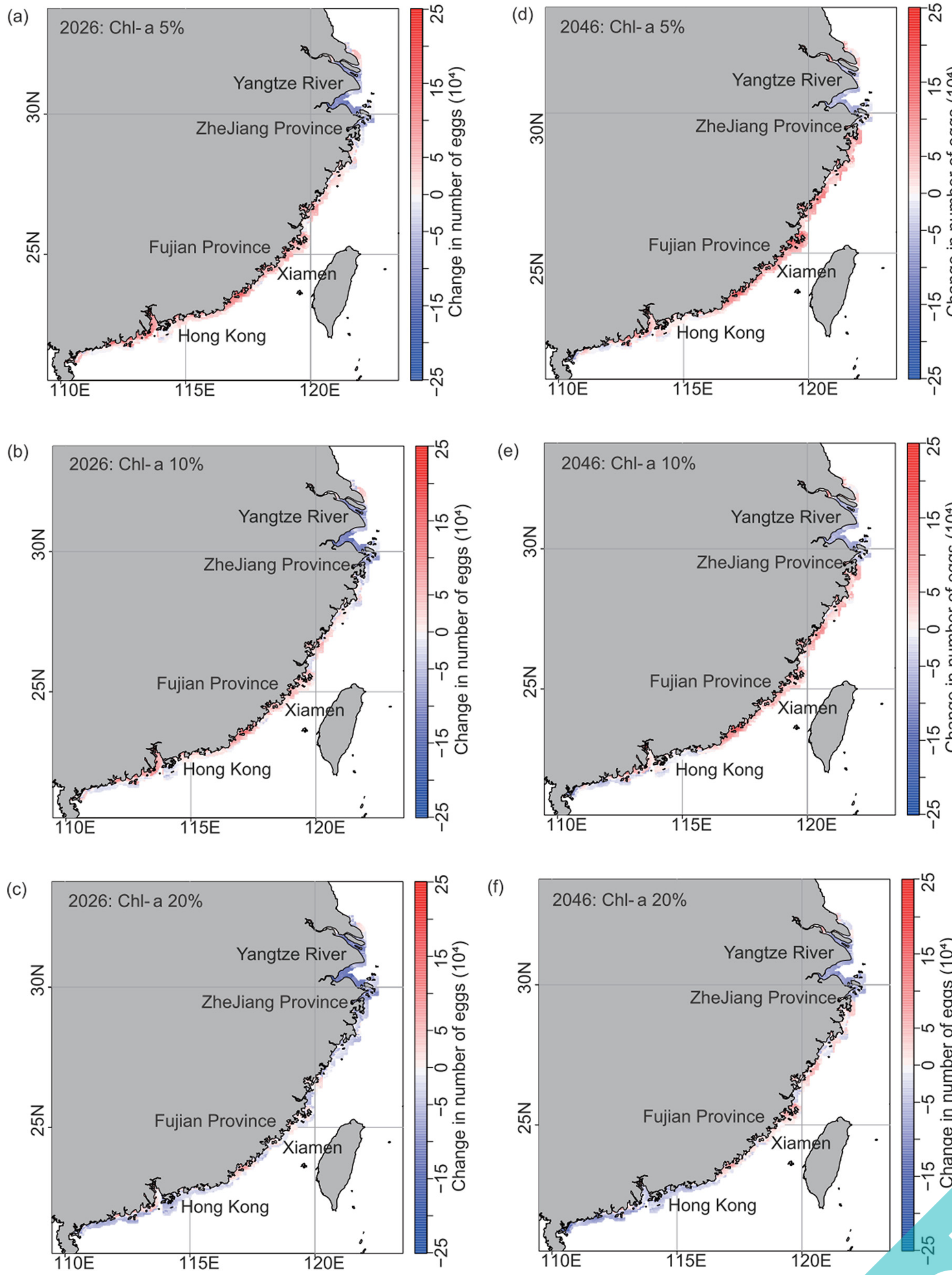

Fig. 6. Predicted change in the total number of eggs produced by *Mytilopsis sallei* along the southern coast of China, in comparison to 2016 under RCP2.6 sea surface temperature scenarios associated with three different decreasing chlorophyll-*a* concentrations (5%, 10% and 20%) for 2026 (a, b, and c) and 2046 (d, e, and f).

distance and thus fewer individuals may arrive simultaneously to form new populations (Paulay and Meyer, 2002). Rock platforms and artificial structures may act as stepping-stones and facilitate dispersal of a species over longer distances (Ruiz et al., 2009). The intermittent islands and artificial structures (e.g., dams and harbours) along the Yangtze River region may, therefore, provide suitable substrates for settlement of planktonic larvae and act as stepping-stones for dispersal and/or colonization in the future (Dong et al., 2012). Although arguments made in previous studies relate to rocky intertidal species, *M. sallei* has been recorded both intertidally and sub-tidally on a variety of natural and

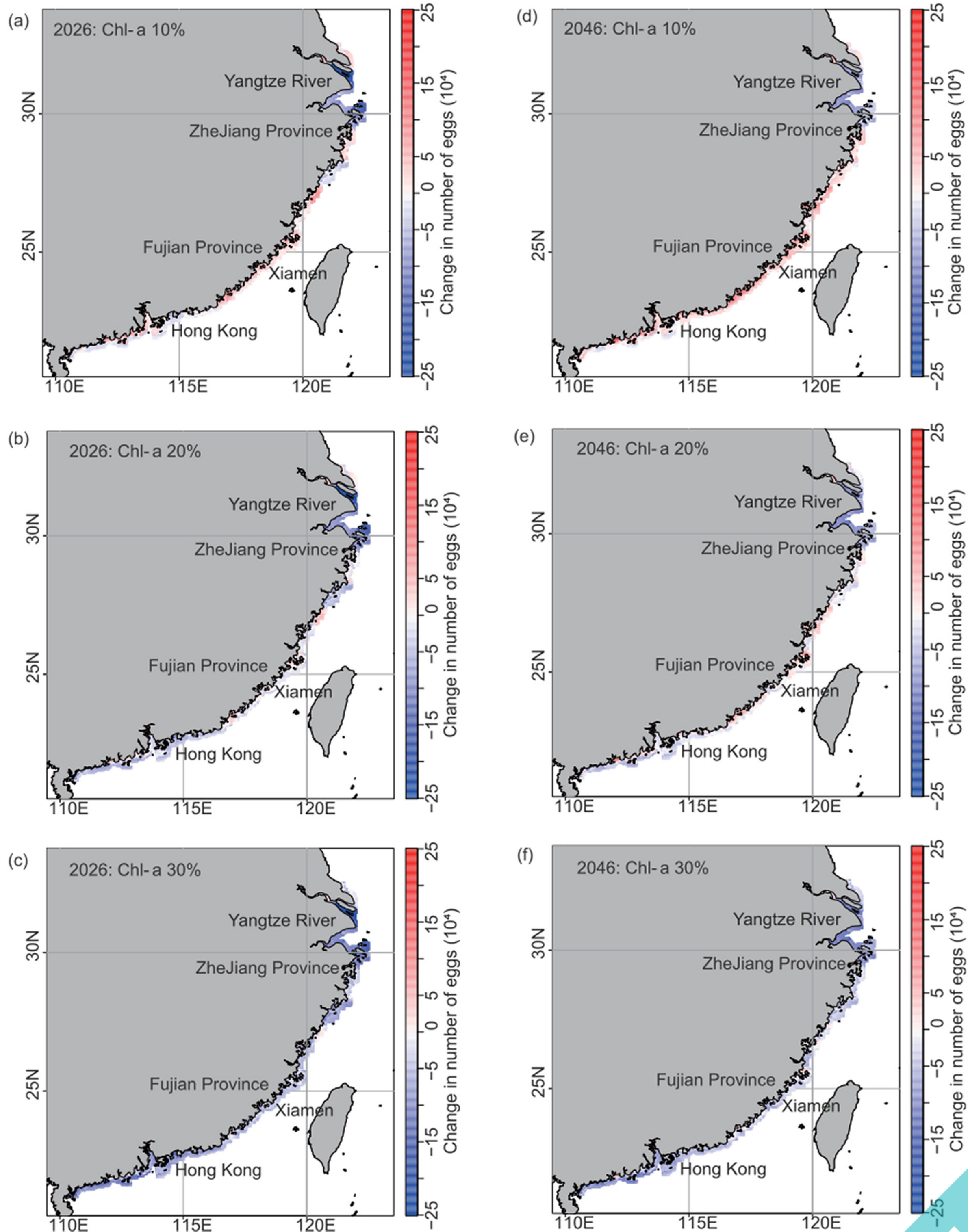

Fig. 7. Predicted change in the total number of eggs produced by *Mytilopsis sallei* along the southern coast China, in comparison to 2016 under RCP8.5 sea surface temperature scenarios associated with three different decreasing chlorophyll-*a* concentrations (10%, 20% and 30%) for 2026 (a, b, and c) and 2046 (d, e, and f).

artificial substrata (see review by Tan and Tay, 2018) indicating that the dispersal potential of *M. sallei* may also be facilitated by these structures. As the mean SST north of the Yangtze River mouth is predicted to increase by 1–2 °C under both RCP scenarios by 2046 and range between 12–17 °C (Tan, 2019), *M. sallei* is unlikely to expand its range further north of the Yangtze River in the near future.

The large increase in fecundity of *M. sallei* below the Yangtze River is likely to increase invasion risk and spread along the southern China coast under climate change, leading to a challenge for local biosecurity. Previous studies reported that *M. sallei* has successfully invaded coasts of southern China where most aquaculture facilities are located, leading to severe declines in abundance of native and/or aquaculture species (Tan and Tay, 2018). The predicted increase in the northwards invasion ability of *M. sallei* may, therefore, induce negative impacts on aquaculture industries at higher latitudes along the coast of southern China, particularly ZheJiang Province, an important fish

Table 2
Summary of predictions from DEB models for mean egg production below and within the Yangtze River for 2026 and 2046 associated with three different decreasing chlorophyll-*a* concentrations under RCP2.6 (5%, 10% and 20% chlorophyll-*a* levels) and RCP8.5 (10%, 20% and 30% chlorophyll-*a* levels) and the percentage change of egg production (in brackets) relative to present-day (2016) conditions. The colour gradient from light to dark red represents a decrease in mean total reproductive output, while light to dark blue represents an increase in total reproductive output.

			Below Yangtze	Yangtze
Current	2016		312,813	203,043
RCP26	2026	−5%	346,867 (10.9%)	148,919 (−26.6%)
		−10%	329,646 (5.4%)	142,292 (−29.9%)
		−20%	294,913 (−5.7%)	128,091 (−36.9%)
	2046	−5%	354,149 (13.2%)	174,030 (−14.2%)
		−10%	336,921 (7.7%)	166,283 (−18.1%)
		−20%	300,377 (−3.9%)	149,581 (−26.3%)
RCP85	2026	−10%	320,093 (2.3%)	113,880 (−43.9%)
		−20%	286,671 (−8.5%)	102,591 (−49.9%)
		−30%	249,764 (−20.1%)	90,092 (−55.6%)
	2046	−10%	340,765 (8.9%)	146,619 (−27.7%)
		−20%	305,846 (−2.2%)	131,926 (−35.1%)
		−30%	266,145 (−14.1%)	115,697 (−43.1%)

and shellfish aquaculture region (Guo et al., 1999; Nobre et al., 2009) As eradication of an established invasive species is expensive and often very difficult (Mack et al., 2000; Hilliard, 2004), and such species have already impacted aquaculture practices in China (costing 74 million USD in 2000, Xu et al., 2006), local aquaculture farmers in southern China (especially in ZheJiang Province) should pay careful attention to the future arrival of *M. sallei*, as such invasion is likely to contribute substantial operation costs for aquaculture businesses.

5. Conclusion

Understanding how environmental conditions influence life history traits such as reproductive success of a species and, thereby, the success of species colonization is important in order to prevent and/or inhibit the spread of invasive species (Sakai et al., 2001). The present study illustrates the importance of coupling DEB modelling and satellite and/or climate change projections to develop a mechanistic and spatially explicit picture of the life history traits of invasive species and, subsequently allow the prediction of invasion risk for specific regions. As climate facilitation of species invasions will create new and unexcepted challenges for biodiversity, these predictions will be vital for the understanding of possible strategies to be adopted in the management and mitigation of species' invasions.

CRediT authorship contribution statement

Alicia Lee Sian Tan: Data curation, Methodology, Writing - original draft. **Martin Chun Fai Cheng:** Resources, Writing - review & editing. **Antonio Giacoletti:** Software, Writing - review & editing. **Jing Xiang Chung:** Data curation, Writing - review & editing. **Juneng Liew:** Data curation, Writing - review & editing. **Gianluca Sarà:** Software, Writing - review & editing. **Gray A. Williams:** Funding acquisition, Supervision, Writing - review & editing.

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 and B. Supplementary data

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References

Agüera, A., Byrne, M., 2018. A Dynamic Energy Budget model to describe the reproduction and growth of invasive starfish *Asterias amurensis* in southeast Australia. Biol. Invasions 20 (8), 2015–2031.
Appeldoorn, R.S., 1995. Covariation in life-history parameters of soft-shell clams (*Mya arenaria*) along a latitudinal gradient. ICES marine science symposia. 199, pp. 19–25.
Araújo, M.B., Peterson, A.T., 2012. Uses and misuses of bioclimatic envelope modelling. Ecology 93 (7), 1527–1539.
Atkinson, D., 1997. Ectotherm life-history responses to developmental temperature. In: Johnston, I.A., Bennett, A.F. (Eds.), (2008). *Animals and temperature: phenotypic and evolutionary adaptation*. vol. 59. Cambridge University Press, Cambridge, UK, pp. 183–204.
Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Tjiputra, J., 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences 10, 6225–6245.
Branch, G.M., Steffani, C.N., 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). J. Exp. Mar. Biol. Ecol. 300 (1–2), 189–215.
Buckley, L.B., Jetz, W., 2008. Linking global turnover of species and environments. Proc. Natl. Acad. Sci. 105 (46), 17836–17841.
Cai, L.Z., Gao, Y., Zeng, G.S., Yang, L., Liu, W.M., Lin, X.C., 2005. Spatial and temporal distribution of exotic species, *Mytilopsis sallei*, in sea water outside of shrimp ponds in Maluan Bay, Xiamen. Journal of Xiamen University (Natural Science) 44, 54–57.
Cai, L.Z., Gao, Y., Liu, W.M., Lin, X.C., Zhou, X.P., Jin, L., ... Zeng, G.S., 2006. Effect of exotic species *Mytilopsis sallei* on macrozoobenthos in the Maluan Bay, Xiamen in China. Acta Oceanol. Sin. 28 (5), 83–89.
Cai, L.Z., Hwang, J.S., Dahms, H.U., Fu, S.J., Zhuo, Y., Guo, T., 2014. Effect of the invasive bivalve *Mytilopsis sallei* on the macrofaunal fouling community and the environment of Yundang Lagoon, Xiamen, China. Hydrobiologia 741 (1), 101–111.
Cardoso, J.F., Langlet, D., Loff, J.F., Martins, A.R., Witte, J.I., Santos, P.T., van der Veer, H.W., 2007. Spatial variability in growth and reproduction of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) along the west European coast. J. Sea Res. 57, 303–315.
Cheng, C.F., 2016. The Influence of Temperature Acclimation and Food on the Physiology and Dynamic Energy Budget of *Perna viridis*. Mphill dissertation, The University of Hong Kong.
Cheng, M.C.F., Tan, A.L.S., Rinaldi, A., Giacoletti, A., Sarà, G., Williams, G.A., 2018. Predicting effective aquaculture in subtropical waters: a Dynamic Energy Budget model for the green lipped mussel, *Perna viridis*. Aquaculture 495, 749–756.
Cheung, W.W., Lam, V.W., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D., 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish. 10 (3), 235–251.
Dong, Y.W., Wang, H.S., Han, G.D., Ke, C.H., Zhan, X., Nakano, T., Williams, G.A., 2012. The impact of Yangtze River discharge, ocean currents and historical events on the biogeographic pattern of *Cellana toreuma* along the China coast. PLoS One 7 (4), e36178.
Galil, B.S., Marchini, A., Occhipinti-Ambrogi, A., Minchin, D., Narščius, A., Ojaveer, H., Olenin, S., 2014. International arrivals: widespread bioinvasions in European seas. Ethol. Ecol. Evol. 26 (2–3), 152–171.
Galil, B.S., Boero, F., Campbell, M.L., Carlton, J.T., Cook, E., Fraschetti, S., ... Marchini, A., 2015. Double trouble': the expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. Biol. Invasions 17 (4), 973–976.
Guo, X., Ford, S.E., Zhang, F., 1999. Molluscan aquaculture in China. J. Shellfish Res. 18, 19–31.
Guo, J., Chen, H., Xu, C.Y., Guo, S., Guo, J., 2011. Prediction of variability of precipitation in the Yangtze River Basin under the climate change conditions based on automated statistical downscaling. Stoch. Env. Res. Risk A. 26 (2), 157–176.
Guo, X., Zhao, D., Jung, D., Li, Q., Kong, L.F., Ni, G., ... Lee, H.J., 2015. Phylogeography of the Rock Shell *Thais clavigera* (Mollusca): evidence for long-distance dispersal in the northwestern Pacific. PloS one 10 (7), e0129715.
Hashioka, T., Yamanaka, Y., 2007. Ecosystem change in the western North Pacific associated with global warming using 3D-NEMURO. Ecol. Model. 202, 95–104.
Helmuth, B., Mieszkowska, N., Moore, P., Hawkins, S.J., 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. Annu. Rev. Ecol. Evol. Syst. 37, 373–404.
Hilliard, R., 2004. Best practice for the management of introduced marine pests–a review. Global Invasive Species Programme. IUCN, Australia.
Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. 19 (1), 357–366.
IPCC, 2013. Climate change 20013 the physical science basis. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
Kelley, D.E., 2018. The OCE package. Oceanographic Analysis with R. Springer, New York, USA, pp. 91–101.
Kooijman, S.A.L.M., 2010. Dynamic Energy Budget Theory for Metabolic Organisation. Cambridge University Press, Cambridge, UK.

Kooijman, S.A.L.M., 2020. The standard Dynamic Energy Budget model has no plausible alternatives. Ecol. Model. 428, 109106.
Kramer, A.M., Dennis, B., Liebhold, A.M., Drake, J.M., 2009. The evidence for Allee effects. Popul. Ecol. 51 (3), 341.
Lavaud, R., La Peyre, M.K., Casas, S.M., Bacher, C., La Peyre, J.F., 2017. Integrating the effects of salinity on the physiology of the eastern oyster, *Crassostrea virginica*, in the northern Gulf of Mexico through a dynamic energy budget model. Ecol. Model. 363, 221–233.
Lima, F.P., Wethey, D.S., 2012. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat. Commun. 3 (1), 1–13.
Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10 (3), 689–710.
Mangano, M.C., Mieszkowska, N., Helmuth, B., Domingos, T., Sousa, T., Baiamonte, G., ... Johnson, M., 2020. Moving toward a strategy for addressing climate displacement of marine resources: a proof-of-concept. Front. Mar. Sci. 7, 408.
Moore, J.K., Lindsay, K., Doney, S.C., Long, M.C., Misumi, K., 2013. Marine ecosystem dynamics and biogeochemical cycling in the community earth system model [CESM1 (BGC)]: comparison of the 1990s with the 2090s under the RCP4 5 and RCP8 5 scenarios. J. Clim. 26, 9291–9312.
Morton, B., 1981. The biology and functional morphology of *Mytilopsis sallei* (Recluz) (Bivalvia: Dreissenacea) fouling Visakhapatnam Harbour, Andhra Pradesh, India. J. Molluscan Stud. 47 (1), 25–42.
Morton, B., 1989. Life-history characteristics and sexual strategy of *Mytilopsis sallei* (Bivalvia: Dreissenacea), introduced into Hong Kong. J. Zool. 219 (3), 469–485.
Nisbet, R.M., Muller, E.B., Lika, K., Kooijman, S.A.L.M., 2000. From molecules to ecosystems through dynamic energy budget models. J. Anim. Ecol. 69, 913–926.
Nobre, A.M., Musango, J.K., De Wit, M.P., Ferreira, J.G., 2009. A dynamic ecological–economic modeling approach for aquaculture management. Ecol. Econ. 68 (12), 3007–3017.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
Paulay, G., Meyer, C., 2002. Diversification in the tropical Pacific: comparisons between marine and terrestrial systems and the importance of founder speciation. Integr. Comp. Biol. 42 (5), 922–934.
Pederson, J., Mieszkowska, N., Carlton, J.T., Gollasch, S., ... Jelmert, A., 2011. ICES Position Paper on Climate Change Chapter 11: Climate Change and Non-Native Species in the North Atlantic. CES status report on climate change in the North Atlantic. P.C. Reid & L. Valdés. ICES, Copenhagen, pp. 174–190.
Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. Science 322, 690–692.
Qi, J.F., 2011. Study on the Embryonic Development, Larval Settlement and Metamorphosis of *Mytilopsis sallei*. MPhill dissertation. Xiamen University, China.
Reznick, D., Nunney, L., Tessier, A., 2000. Big houses, big cars, superfleas and the costs of reproduction. Trends Ecol. Evol. 15 (10), 421–425.
Roxy, M.K., Modi, A., Murtugudde, R., Valsala, V., Panickal, S., ... Kumar, S.P.Lévy, 2016. A reduction in marine primary productivity driven by rapid warming over the tropical Indian Ocean. Geophy Res. Lett. 43, 826–833.
Ruiz, G.M., Freestone, A.L., Fofonoff, P.W., Simkanin, C., 2009. Habitat distribution and heterogeneity in marine invasion dynamics: The importance of hard substrate and artificial structure. Marine Hard Bottom Communities. Springer, Berlin, Heidelberg, pp. 321–332.
Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., ... McCauley, D.E., 2001. The population biology of invasive species. Ann. Rev. Ecol. Syst. 32 (1), 305–332.
Saout, C., Quéré, C., Donval, A., Paulet, Y.M., Samain, J.F., 1999. An experimental study of the combined effects of temperature and photoperiod on reproductive physiology of *Pecten maximus* from the bay of Brest (France). Aquaculture 172 (3–4), 301–314.
Sarà, G., Palmeri, V., Rinaldi, A., Montalto, V., Helmuth, B., 2013a. Predicting biological invasions in marine habitats through eco-physiological mechanistic models: a case study with the bivalve *Brachidontes pharaonis*. Divers. Distrib. 19 (10), 1235–1247.
Sarà, G., Palmeri, V., Montalto, V., Rinaldi, A., Widdows, J., 2013b. Parameterisation of bivalve functional traits for mechanistic eco-physiological Dynamic Energy Budget (DEB) models. Mar. Ecol. Prog. Ser. 480, 99–117.
Sarà, G., Porporato, E.M., Mangano, M.C., Mieszkowska, N., 2018. Multiple stressors facilitate the spread of a non-indigenous bivalve in the Mediterranean Sea. J. Biogeogr. 45 (5), 1090–1103.
Sarmiento, J.L., Slater, R., Barber, R., Bopp, L., Doney, S.C., ... Hirst, A.C.Soldatov, 2004. Response of ocean ecosystems to climate warming. Global Biogeochem. Cycles 18, 1–23.
Sax, D.F., Stachowicz, J.J., Gaines, S.D., 2005. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer Associates Incorporated Publishers, Sunderland, Massachusetts, USA.
Scheltema, R.S., 1986. Long-distance dispersal by planktonic larvae of shoal-water benthic invertebrates among central Pacific islands. Bull. Mar. Sci. 39 (2), 241–256.
Shephard, S., Beukers-Stewart, B., Hiddink, J.G., Brand, A.R., Kaiser, M.J., 2010. Strengthening recruitment of exploited scallops *Pecten maximus* with ocean warming. Mar. Biol. 157 (1), 91–97.
Sokolova, I.M., Frederich, M., Bagwe, R., Lannig, G., Sukhotin, A.A., 2012. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Mar. Environ. Res. 79, 1–15.
Srinivasan, U., Elsen, P.R., Tingley, M.W., Wilcove, D.S., 2018. Temperature and competition interact to structure Himalayan bird communities. Proc. R. Soc. B Biol. Sci. 285 (1874), 20172593.
Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., Osman, R.W., 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proc. Natl. Acad. Sci. 99 (24), 15497–15500.
Steeves, L.E., Filgueira, R., Guyondet, T., Chassé, J., Comeau, L., 2018. Past, present, and future: performance of two bivalve species under changing environmental conditions. Front. Mar. Sci. 5, 1–14.
Tan, L.S., 2019. Impact of Climate Change on the Future Life History Traits of Economically Important Bivalves along the China Coast HKU Theses Online (HKUTO).
Tan, K.S., Tay, T., 2018. The invasive Caribbean *Mytilopsis sallei* (Bivalvia: Dreissenidae): a short review. ASEAN J. Sci. Technol. Development 35 (1–2), 133–139.
Thomas, Y., Mazurie, J., Alunno-Bruscia, M., Bacher, C., Bouget, J.F., ... Gohin C., F.Struski, 2011. Modelling spatio-temporal variability of *Mytilus edulis* (L.) growth by forcing a Dynamic Energy Budget model with satellite-derived environmental data. J. Sea Res. 66, 308–317.
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.
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 (3), 145–165.
Valdizan, A., Beninger, P.G., Decottignies, P., Chantrel, M., Cognie, B., 2011. Evidence that rising coastal seawater temperatures increase reproductive output of the invasive gastropod *Crepidula fornicata*. Mar. Ecol. Prog. Ser. 438, 153–165.
van der Meer, J., 2006. An introduction to Dynamic Energy Budget (DEB) models with special emphasis on parameter estimation. J. Sea Res. 56, 85–102.
Xu, H., Ding, H., Li, M., Qiang, S., Guo, J., Han, Z., ... Wan, F., 2006. The distribution and economic losses of alien species invasion to China. Biol. Invasions 8 (7), 1495–1500.
Zhang, Y., Xu, Y., Dong, W., Cao, L., Sparrow, M., 2006. A future climate scenario of regional changes in extreme climate events over China using the PRECIS climate model. Geophys. Res. Lett. 33 (24).