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Simulated growth and reproduction of green turtles (*Chelonia mydas*) under climate change and marine heatwave scenarios

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Abstract

Environmental conditions experienced by animals constrain their energy acquisition and its subsequent allocation to growth and reproduction, which ultimately contributes to population dynamics. Understanding how environmental conditions affect these physiological processes is therefore important for predicting how threatened species will respond to altered food and temperature conditions. Here we use a mechanistic modelling approach based on Dynamic Energy Budget (DEB) theory to demonstrate that changing food availability has a strong impact on growth and reproduction for a Western Australian population of green sea turtles (*Chelonia mydas*) particularly in scenarios with simulated marine heatwaves. Models predicted increasing time between nesting years in scenarios of decreasing food availability. Furthermore, increased frequency of marine heatwaves reduced reproductive output with the number of eggs a female produced in its lifetime predicted to be approximately 20% lower when heatwaves occurred every five years compared to every 20 years. Our predictions suggest that frequent marine heatwaves could have similar adverse effects to long-term decreases in food availability. In all scenarios, direct impacts of changes in temperature were less pronounced and suggest that the strongest impacts of the increasing temperatures of climate change will be mediated through food availability. The approach demonstrated here provides a strong foundation for understanding how the Ningaloo *C. mydas* population will respond to climate change, and can be refined as new physiological, behavioural, and environmental data become available.

Keywords: *Chelonia mydas*, Ningaloo Reef, climate change, life history, food availability, temperature, marine heatwave, Dynamic Energy Budget

1. Introduction

The acquisition and allocation of energy to processes such as growth and reproduction are key determinants of an animal's fitness, with limited resources resulting in trade-offs between life history traits (Congdon et al., 1982; Stearns, 1989). Individuals' growth and reproduction also drive population demographics, ultimately regulating population trends and persistence (McNab, 2002; Brown et al., 2004). Energy budgets are a valuable tool for quantifying an individual's energy acquisition and its subsequent allocation to physiological processes (Careau et al., 2014). Understanding the impact of environmental conditions on an individual's energy budget is of particular interest for threatened species, because in order to successfully manage and conserve populations, the ability to predict likely responses to the changing climate is critical (Hays, 2008; Tomlinson et al., 2014).

Globally, average surface air and sea temperatures have increased by approximately 1 °C between 1901 and 2012 with future projections estimating increases of up to 5 °C by 2100 (IPCC, 2013; CSIRO and BOM 2015; IPCC, 2019). Furthermore, extreme events such as marine heatwaves are predicted to occur more frequently (CSIRO and BOM 2015; Frölicher et al., 2018) meaning that ecosystems will face the compounding pressure of 'press and pulse' perturbations of both short term disturbances and long-term environmental change (Bender et al., 1984; Harris et al., 2018; Babcock et al., 2019). Many species are already experiencing negative impacts of altered conditions such as changes in abundance and breeding phenology (Walther et al., 2002; Hoegh-Guldberg and Bruno, 2010), with life history traits a likely factor contributing to a species' sensitivity to climate change (Dawson et al., 2011).

Sea turtles are a globally distributed group of threatened and endangered marine reptiles (Wallace et al., 2011). They display life history traits that make them vulnerable to a wide range of threats including climate change (Lutcavage et al., 1997; Poloczanska et al., 2009; Bolten et al., 2011). For most species, hatchlings emerge from their nests and swim offshore into oceanic currents where they spend several years. They then recruit to neritic areas where they continue to grow and mature until they reach sexual maturity, after which adults migrate periodically to nesting beaches to lay their eggs (Musick and Limpus, 1997; Bolten, 2003). This complex life cycle with life history traits such as slow growth and late maturation means that sea turtles are exposed to threats such as bycatch, boat strike, and plastic ingestion (Commonwealth of Australia, 2017) for up to 50 years before reaching sexual maturity

(Chaloupka et al., 2004), thereby risking mortality before reproducing (Bjorndal et al., 2013; Turner Tomaszewicz et al., 2015). Further, sea turtles are ectothermic and so variation in environmental temperature can have ecologically relevant effects on rates of physiological processes, for example altered growth rates (Hamann et al., 2007; Williard, 2013; Marn et al., 2017a). Long generation times limit adaptive capacity (Poloczanska et al., 2009) and mean that significant environmental changes are likely to occur within an individual's lifetime. Consequently, changes in temperature and food availability associated with climate change present a substantial threat to sea turtle populations (Davenport, 1997; Hamann et al., 2007; Hawkes et al., 2009; Wallace et al., 2011).

While information on sea turtles' energy acquisition and allocation is fundamental to understanding responses to changes in environmental conditions, major knowledge gaps exist (Hays, 2008; Wallace and Jones, 2008). Most research and monitoring of sea turtle populations is focussed on nesting environments and consequently less is known about their in-water biology, ecology and basic life history traits (Bjorndal, 1999; Hamann et al., 2010). This is due to the difficulties in studying these species within the marine environment and challenges in recapturing individuals. In addition to limited knowledge of the effects environmental conditions have on physiological processes of sea turtle species, inter- and intra-population differences in diet and thermal sensitivities exist (Wallace et al., 2006b; Arthur and Balazs, 2008; Weber et al., 2011b; Jones and Seminoff, 2013; Stubbs and Mitchell, 2018; Bentley et al., in prep) and can contribute to differences in growth and reproduction. Such intra-specific variation highlights the need to consider the specific conditions and physiology of a population when predicting responses to change.

For sea turtles, one physiological process that is particularly important to understand is allocation of energy to reproduction in different environmental conditions and how that translates to variation in reproductive output. Females of most sea turtle species lay several clutches of eggs per season but do not nest annually, with the time between nesting years (remigration interval) typically around 2 – 5 years (van Buskirk and Crowder, 1994; Broderick et al., 2003). Commonly, numbers of nesting females or their nests are used to infer abundances and population trends (Heppell et al., 2002; National Research Council, 2010; Esteban et al., 2017). This is problematic for two reasons, firstly, such monitoring relies on estimates of variables such as remigration intervals and numbers of clutches per female, which are often poorly resolved (Richards et al., 2011; Pfaller et al., 2013; Esteban et al., 2017). Secondly, sea turtles' late maturation means that any influences of environmental conditions on juveniles will not be immediately captured by such monitoring, and any effects on population trends will take many years to become apparent in the breeding population (Heppell et al., 2002; Mazaris et al., 2017). An understanding of how environmental conditions affect reproductive output in adult females will therefore fill a key knowledge gap in sea turtle ecology.

Modelling approaches that describe full life cycle energetics are useful for predicting physiological responses to future environmental conditions, especially for species that are difficult to study in the marine environment. Dynamic Energy Budget (DEB) theory (Kooijman, 2010) offers one such approach. DEB theory is based on first principles of mass and energy conservation and thermodynamics (Kooijman, 2010; Sousa et al., 2010; Nisbet et al., 2012; Jusup et al., 2017) and has been applied to a wide range of taxa (Marques et al., 2018; AmP, 2019), including sea turtles (Marn et al., 2017a; Marn et al., 2017b; Marn et al., 2019; Stubbs et al., 2019). DEB theory offers a quantitative framework that describes how an individual acquires energy and then allocates it to growth, maintenance, maturation and reproduction over its full life cycle as a function of its state and its environment (Kooijman, 2001; van der Meer, 2006; Kooijman, 2010). Its mechanistic nature means that ecological applications, such as quantifying growth and reproduction for the full life cycle of an individual under a varying environment, can be fully explored.

Green turtles (*Chelonia mydas*) are primarily herbivorous for most of their life (Bjorndal, 1997; Jones and Seminoff, 2013) and therefore factors that affect primary producers place them at particular risk (Broderick et al., 2001; Hamann et al., 2007; Hughes et al., 2009). Annual variation in the numbers of nesting *C. mydas* have been linked to the El Niño Southern Oscillation, and associated changes in food availability at foraging grounds (Carr and Carr, 1970; Limpus and Nicholls, 1988; Broderick et al., 2001). Ningaloo Reef, a World Heritage Area, is an important foraging ground for *C. mydas* in Western Australia (Preen et al., 1997; Limpus, 2008) yet little research has been conducted on resident *C. mydas* there. The area is prone to conditions of anomalously warm water temperatures (Ningaloo Niño) that have increased in frequency in recent years (Feng et al., 2015; Narayanasetti et al., 2016). Once such marine heatwave occurred along the Western Australian coast in the 2010/2011 summer, with nearshore water temperatures reaching up to 5 °C above average in some areas (Pearce and Feng, 2013). This heatwave had ecosystem-wide impacts that have been well studied at Shark Bay (approximately 350 km south of Ningaloo), where primary producers, such as seagrass suffered significant dieback, and body condition of *C. mydas* declined in the years following the heatwave (Wernberg et al., 2013; Thomson et al., 2015; Wernberg et al., 2016; Kendrick et al., 2019; Nowicki et al., 2019). Predicting the impact of such changes in environmental conditions for *C. mydas* foraging at Ningaloo will therefore be imperative in understanding how the population will respond to future environments. Here, we use a DEB model previously developed for Ningaloo *C. mydas* (Stubbs et al., 2019) to investigate the effects of food availability and temperature on life history traits, growth, and reproduction. We simulate different combinations of food availability and temperature and examine how variables such as size, age at puberty, and lifetime reproductive output respond. We focus on conditions that are realistic in regards to future climate change, in particular the 'press' disturbance of gradually changing food availability and temperature and the 'pulse' disturbance of an extreme event, in the form of simulated marine heatwaves.

2. Methods

2.1 Standard Dynamic Energy Budget model and its application to Chelonia mydas

The energetics of green turtles were modelled using the standard model of Dynamic Energy Budget (DEB) theory that describes the uptake, storage and use of energy by individuals for growth, maintenance, maturation and reproduction (Kooijman, 2010; Sousa et al., 2010; Nisbet et al., 2012; Jusup et al., 2017; Stubbs et al., 2019). In the standard DEB model, the life cycle consists of embryo, juvenile and adult stages, and individuals are characterised by the state variables structure V (cm^3), reserve E (J), maturity E_H (J), and a reproduction buffer E_R (J). Maturity (E_H) tracks energy invested into maturation, i.e. increasing the complexity of the individual, and life stage transitions occur when thresholds of maturity are met (e.g. E_H^b for birth and E_H^p for puberty; Table 1). The transition from embryo to juvenile is termed 'birth', and the transition from juvenile to adult is termed 'puberty'. In DEB theory, structure and reserve (and the reproduction buffer in adults) contribute to the weight of the individual, while structure is proportional to appropriately chosen (isomorphic) length measures (Kooijman, 2010; Sousa et al., 2010). Additionally, structure and maturity require maintenance, whereas reserve and the reproduction buffer do not (Kooijman, 2010; Sousa et al., 2010). The relationship between the state variables and the observed physical properties of the individual (e.g. length and weight) are described with auxiliary equations and are shown along with equations describing state variable dynamics and energy fluxes in Table

A.1. A standard DEB model has previously been developed for Ningaloo *C. mydas* (Stubbs et al., 2019), and these parameters were used in this study (Table 1).

Table 1: Standard Dynamic Energy Budget (DEB) model parameters for Ningaloo *C. mydas* described by Stubbs et al. (2019) used in this study. Parameters describing rates are given at the reference temperature (T_{Ref} = 20 °C).

Parameter	**Symbol**	**Value**	**Unit**
Maximum specific assimilation rate	$\{\dot{p}_{\mathrm{Am}}\}$	830.5	$\mathrm{J\ d^{-1}\ cm^{-2}}$
Energy conductance	$\dot{v}$	0.1006	$\mathrm{cm\ d^{-1}}$
Allocation fraction to soma	κ	0.7502	-
Volume-specific somatic maintenance	$[\dot{p}_M]$	12.3	$\mathrm{J\ d^{-1}\ cm^{-3}}$
Specific cost for structure	$[E_G]$	7845	$\mathrm{J\ cm^{-3}}$
Maturity maintenance rate coefficient	$\dot{k}_{\mathrm{J}}$	0.0011	$\mathrm{d^{-1}}$
Maturity at birth	E_H^b	$3.18\mathrm{x}10^4$	J
Maturity at puberty	E_H^p	$2.06\mathrm{x}10^8$	J
Shape coefficient (for curved carapace length)	δ_{CL}	0.3899	-
Arrhenius temperature	T_A	7680	K
Specific density of structure and reserve	d_V, d_E	0.3	$\mathrm{g\ cm^{-3}}$
Maximum specific searching rate	$\{\dot{F}_{\mathrm{m}}\}$	6.5	$\mathrm{l\ d^{-1}\ cm^{-2}}$
Digestion efficiency	κ_x	0.8	-
Reproduction efficiency	κ_R	0.95	-

This study focuses on juveniles and adult females. Juveniles and adults assimilate energy ($\dot{p}_A$) from food into reserve which is then mobilised ($\dot{p}_C$) for maintenance, growth, maturation and reproduction, where maintenance takes priority over growth and reproduction. A fraction (κ) of mobilised energy (i.e. $\kappa\ \dot{p}_C$) is allocated first to somatic maintenance ($\dot{p}_S$) and the remainder to growth ($\dot{p}_G$), while the fraction (1-κ) is allocated to maturity maintenance ($\dot{p}_J$) and the remainder to maturation in embryos and juveniles or reproduction in adults ($\dot{p}_R$) (Kooijman, 2010).

The effect of food availability is described by a scaled functional response $f = \mathrm{X}/(\mathrm{X_K} + \mathrm{X})$ where X is food density and $\mathrm{X_K}$ is the half saturation coefficient (i.e. the density of food that results in half the maximum ingestion rate; $\mathrm{X_K} = \{\dot{p}_{\mathrm{Am}}\}/(\kappa_x \ \mathrm{x}\ \{\dot{F}_{\mathrm{m}}\})$. The scaled functional response is 0 when food is unavailable and reaches a maximum of 1 when food is unlimited (Kooijman, 2010; Marn et al., 2017a). The effect of temperature is modelled as an effect on the rates of physiological processes (e.g. assimilation, mobilisation, somatic maintenance) described using the Arrhenius temperature relationship (Kooijman, 2010). Because this study focuses on juveniles and adults for which there is little species specific data on thermal tolerance limits and associated changes in physiological rates outside those limits, we use the simple version of the Arrhenius equation:

$$C_T(T) = \exp\left(\frac{T_A}{T_{Ref}} - \frac{T_A}{T}\right)$$

where C_T is the temperature correction at temperature T, T_{ref} is the reference temperature of 20 °C = 293.15 K, and T_A is the Arrhenius temperature. The effect of temperature is assumed to be the same for all physiological rates (Kooijman, 2010).

2.2 Simulation design

Simulations were run for 80 years from birth, as this was the lifespan assumed for parameter estimation (Stubbs et al., 2019). Individuals in all scenarios began (i.e. were born) with the same amounts of structure, reserve, and maturity. Green turtles typically change diet when they move from the oceanic to neritic habitat at approximately 20 – 50 cm curved carapace length (Hirth, 1997; Bolten, 2003; Reich et al., 2007; Arthur et al., 2008; Limpus, 2008) which is likely accompanied by changes in food availability and temperature. We did not, however, include these changes in our simulation (i.e. we simulate birth to 80 years in neritic environment conditions) as there is little information available regarding conditions experienced during the pelagic phase and the focus of this study is on the neritic environment at Ningaloo. Further, while any differences in the conditions experienced in the pelagic phase could be incorporated into this modelling framework, it would greatly increase the complexity of the model and interpretation of the outputs.

To investigate the effects of environmental conditions on reproduction, nesting was simulated to occur in years when energy in the reproduction buffer (E_R) reached a certain threshold. This threshold was assumed to be the energy required to allow the production of 400 eggs under current conditions (i.e. $400\times \mathrm{E}_0/\kappa_\mathrm{R}$, where E_0 is the initial reserve energy in an egg under current food conditions; 88 800 kJ). The threshold was based on 400 eggs because this is an approximation of the average number of eggs per nest multiplied by the average number of nests per season reported for *C. mydas* (Bjorndal and Carr, 1989; Limpus and Chaloupka, 1997; Broderick et al., 2003; Limpus, 2008; Guinea, 2009; Ekanayake et al., 2016). In our simulations, energy in the reproduction buffer (E_R) was assessed on the same day each year during the nesting season (January 1st for simplicity). If $E_R \geq 88\,800$ kJ then nesting occurred and the reproduction buffer was completely emptied, otherwise no nesting occurred and energy continued to accumulate in E_R until it was reassessed on the same date in the following year. We also took into account the maternal effect assumption of the standard DEB model that the initial reserve energy of eggs (E_0) varies with food availability such that an individual's reserve density (ratio of amounts of structure and reserve) at birth equals that of its mother at egg formation (Kooijman, 2009; Kooijman, 2010). E_0 was calculated using the 'initial_scaled_reserve' routine of the DEBtool software package (http://www.bio.vu.nl /thb/deb/deblab/debtool/DEBtool_M/manual/). Using this approach, we could investigate the effects of environmental conditions on the frequency of nesting by estimating the time between years when nesting occurred (i.e. remigration interval). Shorter remigration intervals result in more frequent nesting and therefore contribute to a larger amount of energy allocated to reproduction over an individual's lifetime. All simulations were performed in Matlab (R2017a) using modified "EVHR" simulation scripts provided with permission for use by L. Pecquerie (Institut de Recherche pour le Développement, Plouzané, France) that have previously been used for similar simulations in loggerhead turtles (Marn et al., 2017a).

To visualise the interacting effects of food and temperature on life history traits, a range of constant temperatures and food levels were simulated (i.e. food and temperature conditions remained the same for the entire 80-year simulation). The current availability of food for the Ningaloo population was inferred from a scaled functional response (f) value of 0.8, as was used for parameter estimation (Stubbs et al., 2019). Current food density (X) was then calculated using the equation $f = X/(X_K + X)$. Simulated conditions were based on this estimate such that food availabilities ranged between 50 – 150% of the current food density, simulated in 1% increments. Over a range of temperatures, juvenile or inactive adult *C. mydas* have body temperatures that closely match ambient water temperatures (Standora et al., 1982; Read et al., 1996). Therefore, we used sea surface temperature (SST) as a proxy for body temperature. A wide range of temperatures between 16 – 30 °C were simulated in 0.1 °C increments. Every combination of food and temperatures was simulated (14 241 scenarios in total) and eight life history traits; age at puberty, length at puberty, ultimate length, ultimate weight, energy content of each egg, mean number of eggs per season, number of nesting seasons and lifetime reproductive output were estimated and plotted.

While simulating constant temperature and food availability allows for visualisation of the combined effects of these conditions, wild *C. mydas* would not experience constant conditions throughout their lives. Therefore, more realistic varying food and temperature conditions were also simulated. Temperature data were acquired from NOAA Coral Reef

Watch 5-km Regional Virtual Stations for Ningaloo (NOAA Coral Reef Watch, 2019). Daily sea surface temperatures (SST) from 1986 – 2005 were used and temperatures for each calendar day were averaged over this period to generate an average year of temperatures (Figure A.1A). These averaged temperatures were then repeated 80 times to generate daily temperatures for a full lifetime simulation (i.e. for every year, the temperature on any particular day was the same). Then, to simulate realistic gradual increases in temperature (‘press’ disturbance) over the lifespan of a turtle, a gradient of different temperature increases consistent with climate change predictions were added to averaged temperatures. Sea surface temperatures near Australia’s coasts are predicted to rise by 0.5 – 4 °C by 2090 relative to 1986 – 2005 conditions (CSIRO and BOM 2015). Therefore, gradual increases of 0.5, 2, and 4 °C were applied over the 80-year simulation duration such that the temperature increase was 0 °C at the start of the simulation and 0.5, 2, or 4 °C at the end (Figure A.2D-F). Similarly, scenarios of gradual increases and decreases in food availability were simulated. Food levels either remained constant at the current food density or were gradually increased or decreased by 20% of the current food density (corresponding to a change of <5% in the scaled functional response, f) over the 80-year simulation (Figure A.2A-C). All combinations of these food and temperature conditions were simulated (nine scenarios in total).

In conditions of decreasing food density, it is possible that somatic maintenance requirements may not be covered by energy allocated from the reserve (E) to somatic processes (growth and somatic maintenance; $\kappa\ \dot{p}_C$). Therefore, for simulations of varying conditions, we included a starvation rule where in the case that somatic maintenance costs cannot be paid by energy mobilised from reserve to somatic processes ($\kappa\ \dot{p}_C$), they are paid using energy previously allocated to the reproduction buffer (E_R). This approach has previously been used in DEB modelling (Pouvreau et al., 2006; Pecquerie et al., 2009). To examine the effects of environmental changes for turtles born in the future when conditions have changed substantially, we modelled individuals that were born at the start (t = 0) and at year 40 (t = 40) of each 80-year simulation. Simulation outputs were summarised in terms of growth (Curved carapace length; CCL) and reserve energy (E) trajectories, and the number of eggs and remigration interval for each nesting event. Lifetime reproductive output (number of eggs) was also predicted for individuals born at t = 0.

Finally, to model the effects of major ‘pulse’ disturbance events, we simulated conditions that might occur under marine heatwaves. We based these on conditions reported during the marine heatwave that occurred along the Western Australian coast in the austral summer of 2010/2011 (Pearce and Feng, 2013). Temperature anomalies at Ningaloo increased to a peak of 3 °C in January then declined over the following few months (Pearce and Feng, 2013). Hence, to simulate heatwave conditions, temperatures were gradually increased by 3 °C during three months, then decreased by the same amount (i.e. to a 0 °C anomaly) during the following three months. These changes were applied on top of a baseline gradual warming of 1 °C during the 80-year simulation. During the 2010/2011 marine heatwave, seagrass and macroalgae cover decreased substantially (Smale and Wernberg, 2013; Wernberg et al., 2013; Wernberg et al., 2016; Kendrick et al., 2019). One of the most affected areas, Shark Bay, saw >90% declines of a habitat-forming seagrass (Thomson et al., 2015; Kendrick et al., 2019), with cover remaining low in the following three years (Nowicki et al., 2017). To model food availability during a heatwave, we simulated a conservative decrease of 20% below the current food density over three months, which gradually returned to current levels over the conservative timeframe of two following years (Figure A.3). Marine heatwaves are expected to occur more frequently in coming decades (Meehl and Tebaldi, 2004; Frölicher et al., 2018; Oliver et al., 2018). Hence we modelled marine heatwaves that occurred every 20, 10 or 5 years with the first heatwave peaking in the third year of the simulation (Figure A.3). Simulation outputs were summarised in terms of growth (CCL) and reserve (*E*) trajectories, the number of eggs and remigration interval for each nesting event, and lifetime reproductive output.

3. Results

3.1 Constant food and temperature scenarios

Food availability and temperature affected life history traits in different ways (Figure 1). Greater food availabilities resulted in larger length (CCL) at puberty up to 99 cm and younger age at puberty to a minimum of 14 years at 150% of current food availability (Figure 1A, B). Length at puberty was not affected by temperature, but lower temperatures resulted in a longer time taken to reach puberty because growth and energy allocation to maturation occur slower at lower temperatures (Figure 1A, B). When food availability was 75% of the current food density (or lower), puberty could not be reached. While ultimate weight was affected by temperature and food availability (adults predicted to be up to 84% heavier than under current conditions), ultimate length was affected mostly by food availability, and the effect of temperature was not discernible (Figure 1C, D). At warmer temperatures, rates of assimilation and energy allocation to the reproduction buffer (E_R) (which contributes to weight but not length) are higher, therefore at warmer temperatures, greater ultimate weight reflects a larger reproduction buffer (Figure 1D).

Food and temperature had an interacting effect on reproduction (Figure 1F-H). Greater food availability resulted in more energy available for reproduction, a slightly greater energy content of eggs (Figure 1E), a greater number of eggs produced per season (up to 758 eggs; Figure 1F), and higher lifetime reproductive output (up to 28 596 eggs, more than 4 times greater than under current conditions; Figure 1H), and these effects were more pronounced at higher temperatures. Higher temperatures mean that energy can be assimilated faster and egg formation occurs at a higher rate (Mrosovsky, 1980; Sato et al., 1998; Weber et al., 2011a). This meant that higher temperatures also generally resulted in a greater number of eggs produced per season (Figure 1F), a greater number of lifetime nesting seasons (Figure 1G), and higher lifetime reproductive output (Figure 1H) but only with sufficient food availability. The patterns of seasonal reproduction – more nesting seasons over the lifetime at higher temperatures and food availabilities, but sometimes with fewer eggs per season (Figure 1F, G) – can be explained because higher food availability and temperatures result in more energy accumulated between nesting seasons. Therefore with increasing food and/or temperature either more eggs were produced per season, or enough energy was accumulated earlier so that nesting could occur more frequently (i.e. higher number of nesting seasons over the lifetime), but with fewer eggs per season (Figure 1F, G). When food availability was between 75 and 76 – 80% of current levels (exact value depends on temperature), puberty was reached but the energy threshold for reproduction was not met and reproduction did not occur (Figure 1F-H).

3.2 Variable food and temperature scenarios

When scenarios of varying food availability and temperature were simulated (Figure A.2), effects of changes in food availability were more apparent than the effects of changes in temperature (Figure 2; Figure 3). Gradual increases in temperature (0.5, 2, and 4 °C) over the 80-year simulation had such a small effect on growth rate (i.e. time taken to reach a particular length) and reserve energy (*E*) that differences between the three scenarios of temperature increases were not evident (Figure 2). Temperature had a small effect on age at puberty, for example at current food availability, puberty occurred 0.4 years earlier in the scenario of 4 °C temperature increase than it did in the scenario of 0.5 °C increase. Similarly, the difference in age at puberty between the scenarios of the highest (4 °C) and lowest (0.5 °C) temperature increase was 0.5 years for increasing food availability or 0.6 years for decreasing food availability. Because puberty can occur at any time of year but reproduction only occurs at a particular time of year (in our simulations), these small differences in age at puberty did not affect the timing of the first nesting event in most scenarios. The differences in age at puberty were more apparent in simulations of turtles born at year 40 of the simulation, with differences between the highest (4 °C) and lowest (0.5 °C) temperature increases of 2.6, 2.3, and 3.5 years for scenarios of current, increasing, and decreasing food availability, respectively. Furthermore, the difference in the time between puberty and the first nesting event varied by 0.8 – 3.5 years (depending on the food availability scenario) when comparing scenarios of the highest (4 °C) and lowest (0.5 °C) temperature increases.

In scenarios where food availability increased, turtles grew larger (3% larger ultimate length than at current food availability) and reserve energy continued to increase throughout the lifetime to a maximum of 14% higher than current food availability (solid lines; Figure 2). In contrast, in scenarios with decreasing food availability (dotted lines; Figure 2), individuals grew to a smaller size (2% smaller ultimate length than at current food availability) and reserve energy increased to a maximum and then decreased for the remainder of the simulation to 11% lower than at 80-years under current food availability (Figure 2). Differences in length and reserve energy between scenarios were more pronounced for individuals born at year 40 of the simulations when conditions are more different to current conditions. Additionally, differences in length and reserve energy between the turtles born at year 0 and year 40 of the simulations were more pronounced in decreasing food availability scenarios (Figure 2).

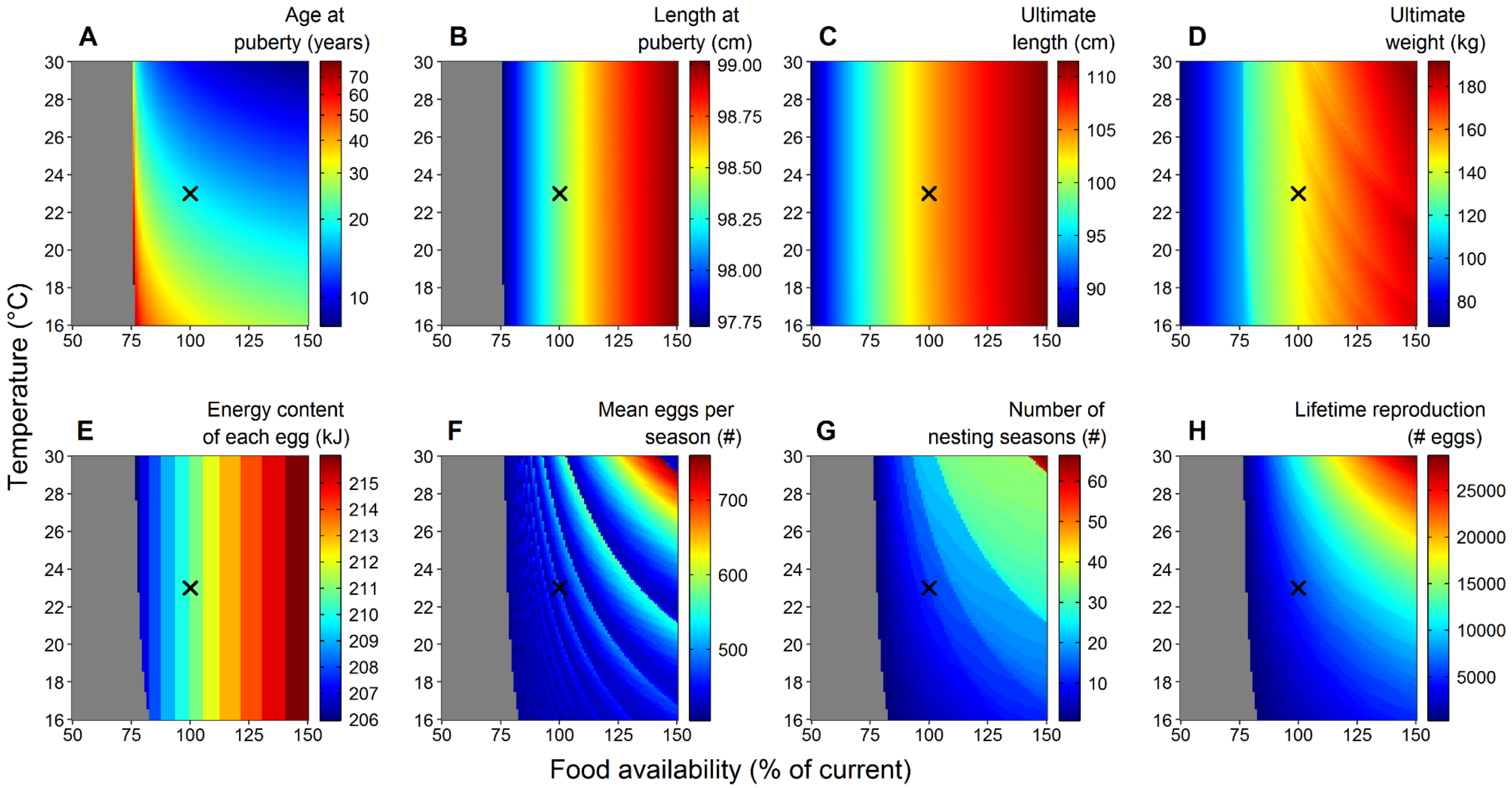

Figure 1: Effects of constant food and temperature on *C. mydas* at Ningaloo Reef over an 80-year simulation (see section 2.2 for simulation details). Values of age at puberty (A), length at puberty (B; curved carapace length), ultimate length (C; curved carapace length), ultimate weight (D), energy content of each egg (E), mean number of eggs per season (F), number of nesting seasons in an individual's lifetime (G), and total number of eggs produced in an individual's lifetime (H; lifetime reproduction) are represented by the colour scale adjacent to each panel. Current conditions experienced by Ningaloo *C. mydas* are marked with a black X. Grey shaded areas in panels A, B, E, F, G and H represent food availability scenarios where puberty is not reached and/or no reproduction occurs.

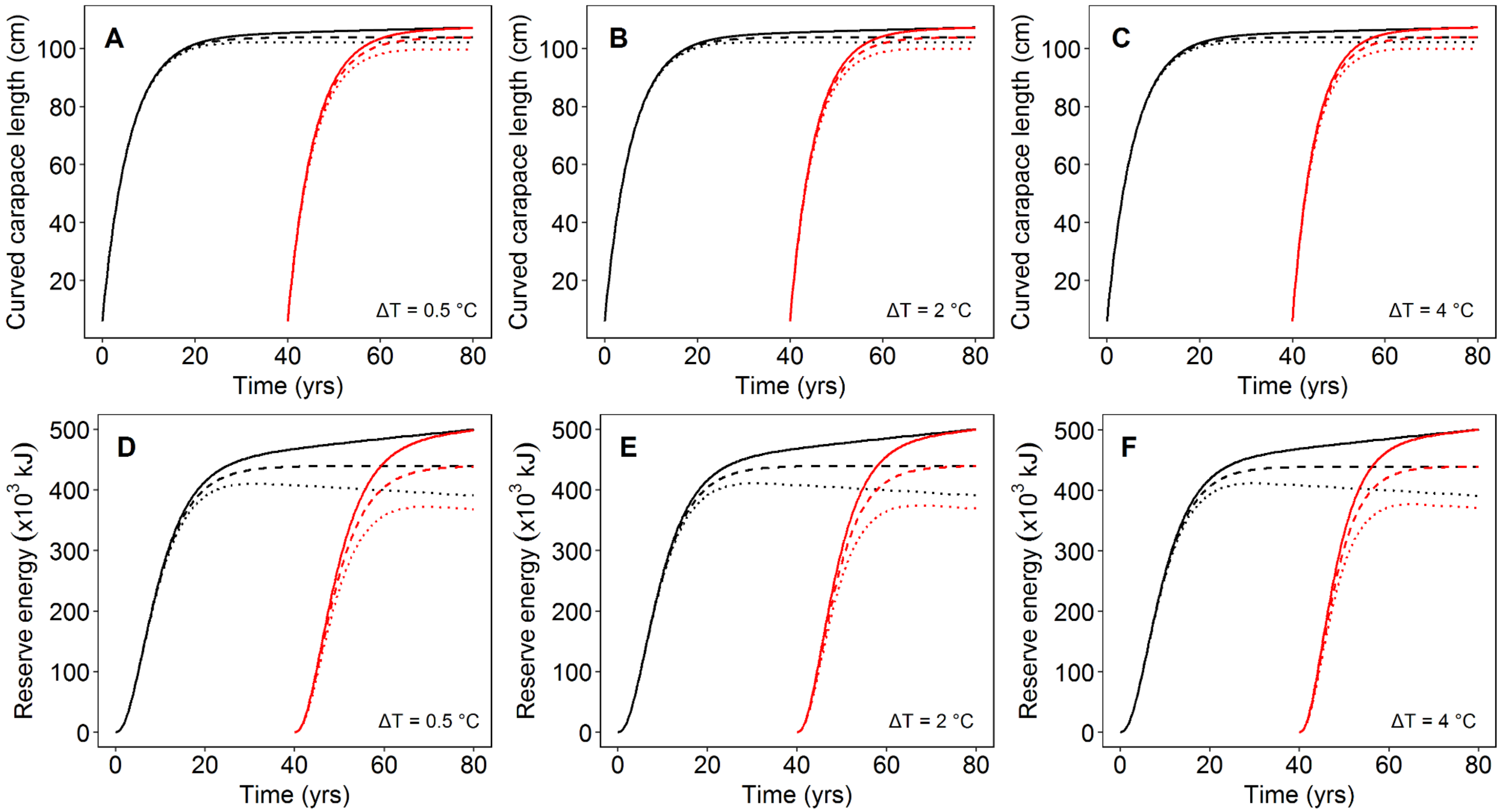

Figure 2: Effects of changing environmental conditions on growth of *C. mydas* at Ningaloo Reef as described by curved carapace length (A, B, C) and reserve energy (D, E, F). Simulations were run for 80 years with black lines representing individuals born at the start of the simulation and red lines representing individuals born after 40 years. Solid lines represent scenarios where food availability increased to 20% above current density over the simulation duration, dashed lines represent current food availability, and dotted lines represent a 20% decrease in food availability. The magnitude of the temperature increase (ΔT) over the 80-year simulation is shown on each panel (see section 2.2 and Figure A.2 for simulation details).

Reproduction was affected by food availability to a greater extent than by temperature (Figure 3) but their effect was synergistic. An increase in food availability results in more energy available for reproduction and an increase in temperature speeds up the processes of energy assimilation and allocation. In the scenarios with current (Figure 3D, E, F) and increasing (Figure 3A, B, C) food availability, the remigration interval decreased over time to a minimum of 3 and 2 years under current and increasing food availabilities respectively. Additionally, the number of eggs per season was more variable but tended to increase. Sharp decreases in the number of eggs per season coincided with a decrease in remigration interval. This decrease occurred when sufficient energy was accumulated in the reproduction buffer (E_R) shortly before the nesting season. This meant a smaller number of eggs but the female could nest in the current year rather than the following year (which would result in more eggs but a higher remigration interval). Females born at year 40 of the simulations showed similar patterns in numbers of eggs per season and remigration intervals, with the numbers of eggs per season quickly increasing to match those of females born at the start of the simulation (Figure 3A-F).

In all scenarios where food availability decreased, somatic maintenance costs could not be covered by the proportion of energy allocated to somatic processes (growth and somatic maintenance; $\kappa\, \dot{p}_C$), and the deficit was paid from the reproduction buffer. The effects of this were evident in measures of reproductive output where remigration intervals were longer and increased over time, while the number of eggs per season remained low, resulting in lower lifetime reproductive outputs compared to scenarios of increasing or current food availability (Figure 3G, H, I). For scenarios of decreasing food availability, turtles born at year 40 of the simulations required 2 – 5 years longer between puberty and the first reproduction event than turtles born at t = 0 and only one or two reproductive events occurred in the first 40 years of life (years 40 – 80 of the simulations) compared to 3 or 4 events in the first 40 years for individuals born at the start of the simulations (Figure 3G, H, I). Taken together, the changes in reproductive output show that *C. mydas* produce more eggs in warmer waters, but only if sufficient food is available.

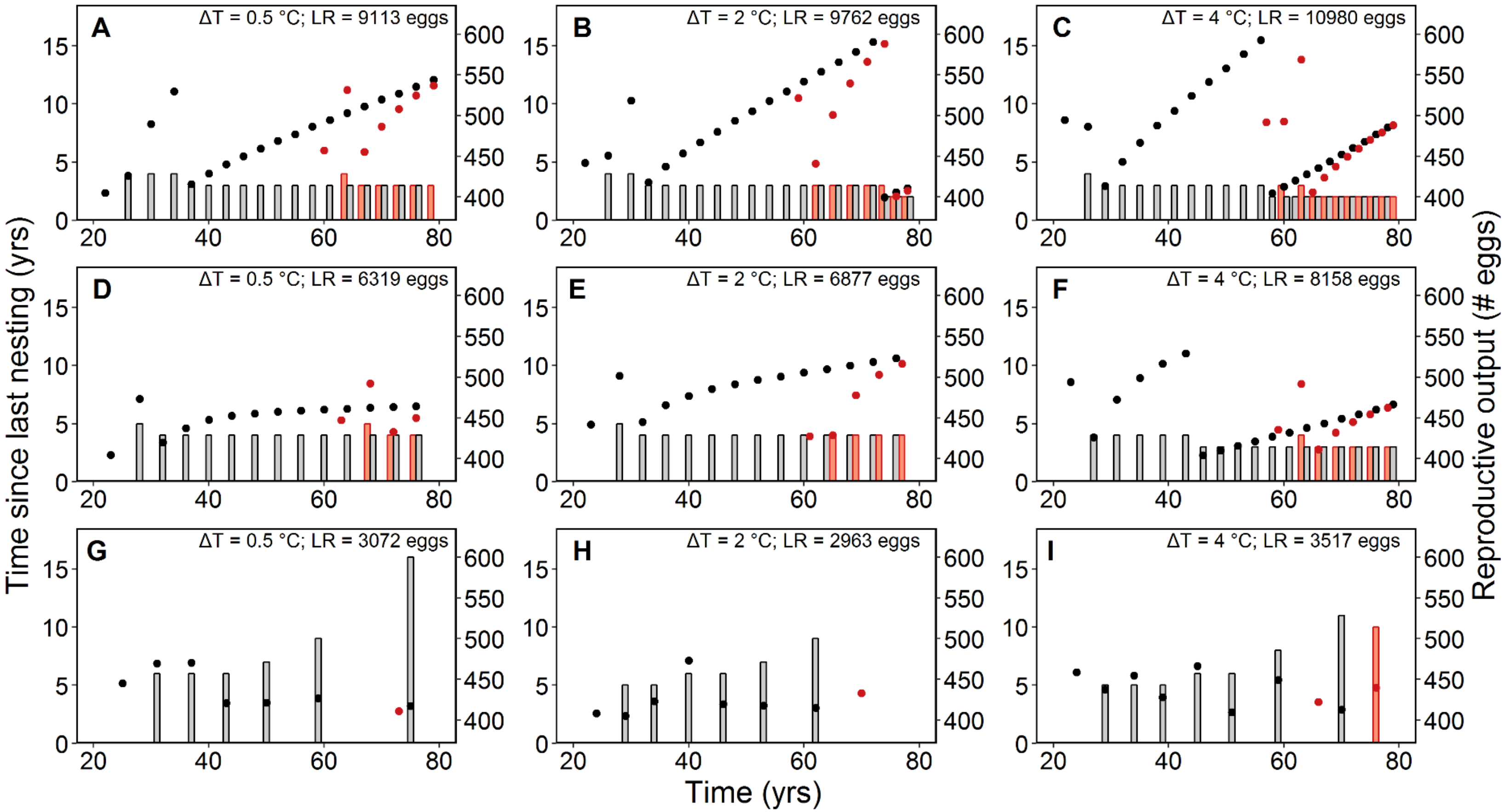

Figure 3: Effects of changing environmental conditions on reproductive output of *C. mydas* at Ningaloo Reef. Shaded bars represent the time since the previous nesting season (i.e. remigration interval; left y-axis) and filled circles represent the number of eggs per nesting season (right y-axis). Black circles and grey shaded bars represent females born at the start of the 80-year simulations, and red circles and shaded bars represent females born after 40 years. Panels A, B, and C show scenarios where food availability increases to 20% above current density over the simulation duration. Panels D, E, and F show current food availability, and panels G, H, and I show scenarios where food availability decreases to 20% below current availability. The magnitude of the temperature increase (ΔT) over the 80-year simulation is shown on each panel (see section 2.2 and Figure A.2 for simulation details). Lifetime reproductive output (LR; number of eggs) for individuals born at the start of the simulations are shown for each scenario on each panel.

3.3 Marine heatwave scenarios

Marine heatwaves (simulated as short term changes in food and temperature conditions on top of a long term 1 °C gradual temperature increase) also affected growth and reproduction. Length was affected to a small degree, with pauses in growth associated with heatwave events (Figure 4). These delays in growth result in puberty occurring approximately one year later for scenarios with heatwaves occurring every five years than scenarios with heatwaves every 20 years. The amount of energy that accumulated in the reserve was also influenced by heatwaves, with reserve energy decreasing during each heatwave event (Figure 5). The magnitude of these decreases was similar in all scenarios, but the frequency corresponded to the frequency of the heatwave (Figure 5). In all three heatwave scenarios, somatic maintenance costs could not be covered by the proportion of mobilised energy allocated to somatic processes, and the deficit was paid from the reproduction buffer.

The effect on reproduction of the short term changes in food availability and temperature during simulated heatwaves is shown in Figure 6. For scenarios with heatwaves every 20 years, remigration intervals were initially five years, then decreased to four years and remained at that level for several years, before increasing again to five years periodically. There was a general trend of increasing number of eggs per season over time (Figure 6A). Reproduction in scenarios with heatwaves every ten years followed a similar pattern, but the periods of time when remigration intervals were four years was shorter, with only one or two nesting events occurring before remigration intervals increased again to five years (Figure 6B). For scenarios with heatwaves every five years, the remigration interval was initially at six years, before decreasing to five years for the remainder of the simulation. After an initial decrease, the number of eggs per season increased steadily over the lifetime (Figure 6C). The lifetime reproductive output decreased with increasing heatwave frequency (Figure 6).

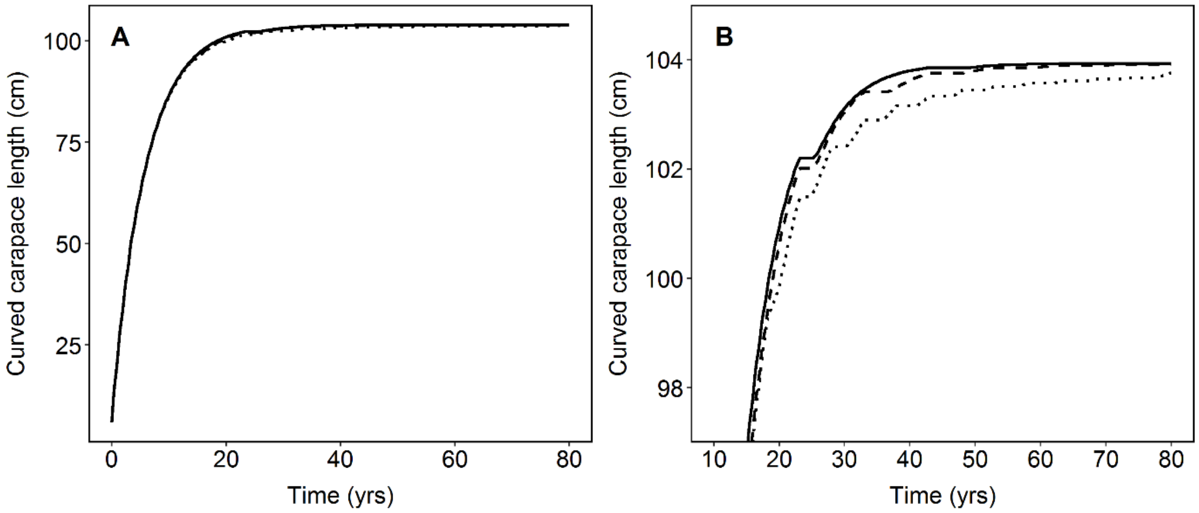

Figure 4: Effect of simulated marine heatwaves occurring at different frequencies on growth of *C. mydas* at Ningaloo Reef. Curved carapace length is shown in panel A, while panel B shows a subset of the same predictions enlarged to highlight differences. Solid, dashed and dotted lines represent simulations where heatwaves occur every 20, 10, and 5 years respectively (see section 2.2 and Figure A.3 for simulation details).

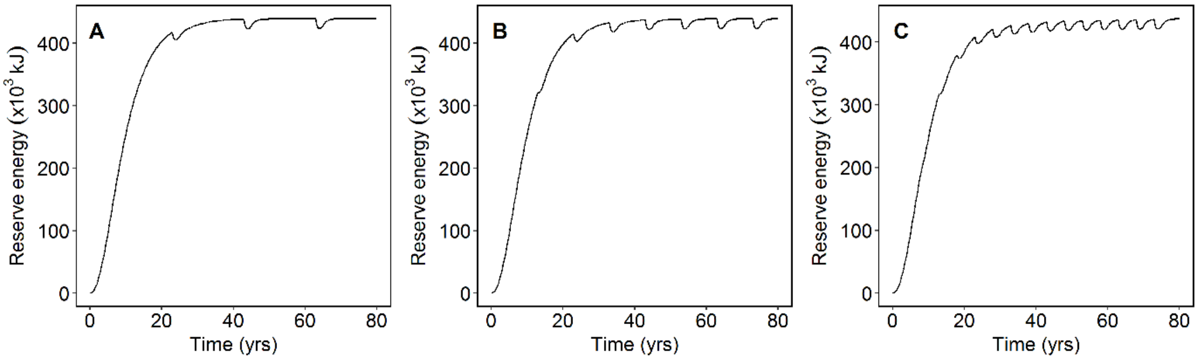

Figure 5: Effect of simulated marine heatwaves occurring at different frequencies on reserve energy of *C. mydas* at Ningaloo Reef. Panels A, B, and C represent simulations where heatwaves occur every 20, 10, and 5 years respectively (see section 2.2 and Figure A.3 for simulation details).

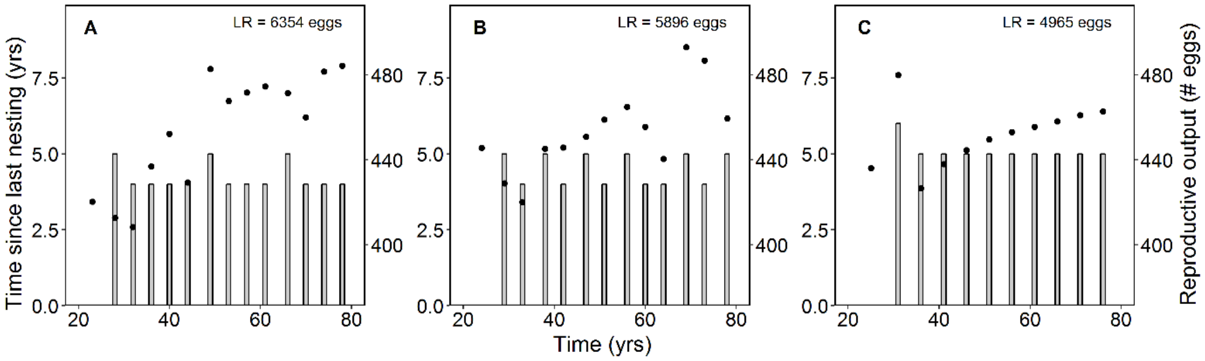

Figure 6: Effect of simulated marine heatwaves occurring at different frequencies on the reproductive output of *C. mydas* at Ningaloo Reef. Panels A, B, and C represent simulations where heatwaves occur every 20, 10, and 5 years respectively. Shaded bars represent the time since the previous nesting event (i.e. remigration interval; left y-axis) and filled circles represent the number of eggs per nesting season (right y-axis). Lifetime reproductive output (LR; number of eggs) for the 80-year simulation is shown on each panel (see section 2.2 and Figure A.3 for simulation details).

4. Discussion

Our simulations demonstrate the strong influence of changes in food availability on all reported aspects of energy acquisition and allocation for *C. mydas*, and show that ‘pulse’ disturbances in the form of frequent marine heatwaves could have similar detrimental effects to long-term decreases in food availability ('press' disturbance; Bender et al., 1984; Harris et al., 2018). Furthermore, our model simulations imply that indirect effects of increasing sea surface temperature – mediated through its influence on food availability (Duarte, 2002; Johnson and Marshall, 2007; Waycott et al., 2009) – will likely have a greater impact on *C. mydas* than direct effects such as higher physiological rates (Hamann et al., 2007; Saba et al., 2007; Saba et al., 2008; Fuentes et al., 2009; Poloczanska et al., 2009; Suryan et al., 2009; Bjorndal et al., 2017). Although our model is specific to Ningaloo *C. mydas* and other populations may require different parameters to be modelled accurately (as for North Atlantic and Mediterranean loggerhead turtles; Marn et al., 2019), – the scenarios we simulate here could easily be applied to other *C. mydas* populations to explore the generality of our predictions. Furthermore, our study highlights the utility of this DEB model simulation approach for understanding species with empirically challenging life cycles and their responses to the altered environmental conditions expected with climate change.

4.1 Environmental effects on growth and maturation

The way in which environmental conditions influence the growth of *C. mydas* at Ningaloo can be explained by the effects of energy inputs and temperature on the processes of assimilation, mobilisation and maintenance. The estimates of ultimate weight and age at puberty for different simulated scenarios clearly demonstrate an interacting effect of food availability and temperature. At higher temperatures, the rate of energy assimilation into the reserve (E) and subsequent allocation to the reproduction buffer (E_R) increases, resulting in larger energy content of E_R and greater ultimate weights. This only occurs at relatively high food availabilities when there is sufficient food to support the increase in assimilation rate. At lower food availabilities, the effect of temperature increasing the assimilation rate is countered by the effect of lower food decreasing the assimilation rate. The contribution of reserve (E) (and the reproduction buffer; E_R) to weight but not length (Kooijman, 2010; Sousa et al., 2010) means that body condition (measured as a ratio of weight to length) is a good indicator of the energy a female has in reserve (E), and therefore is a useful measure for monitoring the condition or nutritional status of females in a population (e.g. Bjorndal et al., 2000; Seminoff et al., 2003; Jessop et al., 2004; Heithaus et al., 2007; Bjorndal and Bolten, 2010).

Under scenarios of decreasing food availability, reserve energy reached a maximum and then declined for the remainder of the female's life. This is because individuals grew to reach a large size (with high maintenance costs) when food conditions were close to current levels. Then, when food availability further decreased (limiting assimilation), somatic maintenance costs remained high, resulting in a decreasing amount of energy in the reserve, while the assimilation rate was too low to fully replenish the reserve. Conversely, under scenarios of increasing food availability, the higher food availability over time continuously increased the energy assimilated, and reserve energy increased over a female's lifetime. The comparisons of length and reserve energy for females born at the start of simulations ($t = 0$) to those born after 40 years ($t = 40$) revealed different magnitudes of variation between scenarios. When comparing 40 year old individuals, females born at $t = 40$ had similar length and reserve energy to those born at $t = 0$ for scenarios of current or increasing food availability but had slightly smaller (~2%) lengths and lower (~10%) reserve energy for scenarios of decreasing food availability. Critically, this suggests that a combination of increasing temperatures and decreasing food availability will have a more pronounced impact on growth (at least in the first 40 years of life) than would increasing temperatures and increasing food.

The variation in ultimate length across all evaluated scenarios was similar to the variation observed in adult female length in the Ningaloo population (~85 - 115cm CCL; Prince, 1993 CSIRO unpublished data; R. Prince, pers comm. 15 November 2017). While there are no estimates of the age at puberty for *C. mydas* from Ningaloo, estimates for other *C. mydas* populations range from 8 years for captive turtles experiencing consistent favourable conditions (Bjorndal et al., 2013) to 50 years on the Great Barrier Reef (Chaloupka et al., 2004). This very broad range is similar to that predicted here (Figure 1A). A DEB model describes a single female individual, and does not incorporate individual differences in parameter values, so the fact that variation comparable to empirical data can be recreated using a single set of physiological parameters suggests that much of it can be attributed to environmental conditions (Marn et al., 2017a). By varying food availability, only changes in food quantity are being considered. However, if females have different diets, they are likely to experience differences in food quality, such as its digestibility and protein content (McDermid et al., 2007; Amorocho and Reina, 2008). Changes in food quality will influence assimilation rates, and could have similar and compounding effects to changes in food availability, causing greater variation in observed life history traits than those reported in our simulations.

4.2 Environmental effects on reproduction

Temperature had an appreciable effect on reproduction, especially when food was relatively abundant. Changes in reproductive outputs (i.e. number of eggs and remigration intervals) across simulations suggest that the reproductive potential of *C. mydas* at Ningaloo is not being fulfilled under current conditions, but under conditions of warmer waters and higher food availability, reproduction might increase. Yet, if food availability decreases in the future, our simulations suggest this would substantially reduce the reproductive output of females, with an approximate 50% decrease in the number of eggs produced over a female's lifetime predicted for scenarios of a 20% decrease in food availability over 80 years (Figure 3). Specifically, simulations of scenarios of decreasing food availability showed that somatic maintenance costs could not be paid entirely from energy allocated to growth and somatic maintenance ($\kappa\, \dot{p}_C$ flux), resulting in the remainder being paid from the reproduction buffer. This, combined with the lower energy available due to decreasing food resulted in slower accumulation of energy in the reproduction buffer, which translated to longer remigration intervals and fewer eggs produced per nesting season. These effects were more pronounced in females born at t = 40. In these simulations, the time between puberty and the first reproductive event was extended and the number of eggs produced in the first 40 years of life was 50 – 70% lower (depending on the temperature scenario) than for individuals born at t = 0. This shows that compounding effects of increasing temperatures and decreasing food availability could markedly reduce the reproductive output (number of eggs) of Ningaloo *C. mydas*. Reductions in reproductive output of the magnitude predicted in this study would have substantial consequences for population viability (Mazaris et al., 2005; Wallace et al., 2006a). Further, when considering predictions of lifetime reproductive potential in our simulations, it is important to note that while we assumed an 80-year lifespan in all scenarios, temperature also affects lifespan in ectotherms (Munch and Salinas, 2009). Unfortunately there is no information on how temperature influences lifespan in *C. mydas* but any temperature-mediated reduction in lifespan would further contribute to reduced lifetime reproductive output.

Empirical data on remigration intervals in *C. mydas* range from two years in Costa Rica (Troëng and Chaloupka, 2007) to seven years at Heron Island (Limpus, 1993). The remigration intervals predicted in our simulations fell within this range (Figure 3, Figure 6) except in the last 30 years of decreasing food availability scenarios. In these low food conditions, it is likely that individuals could nest with less energy in the reproduction buffer than the threshold we set for our simulations, thereby nesting earlier (but laying fewer eggs) and avoiding excessively long remigration intervals. Notably, variation in remigration intervals with changes in food availability is supported by empirical data (Broderick et al., 2001; Reina et al., 2009; Hatase et al., 2013). The threshold energy required in the reproduction buffer for nesting in our simulations (88 800 kJ) was based on average numbers of nests per season and eggs per clutch. This threshold is comparable to the energy requirements estimated for egg production in Tortuguero and Surinam *C. mydas* (87 400 kJ and 104 000 kJ respectively) (Bjorndal, 1985), Accurate quantification of this threshold for Ningaloo *C. mydas* would be useful for refining future predictions of reproductive output.

Our model represents a simplification of sea turtle reproduction with a nesting event simulated as all eggs being released from the reproduction buffer (i.e. laid) at once. We did not incorporate the complexities of producing and laying individual clutches separately, nor did we constrain the time period to include only the time periods when incubation temperatures at the nesting beach are suitable. Additionally, simulations did not include the energy required for breeding migrations (Bjorndal, 1985; Hatase and Tsukamoto, 2008), or the fact that females may fast during the breeding season, as has been observed in some populations (Hochscheid et al., 1999; Hays et al., 2002a; Hays et al., 2002b). Migration distances for green turtles can range from non-migration breeding (e.g. Whiting et al., 2008) to up to 2 850 km for *C. mydas* nesting at Ascension Island (Hays et al., 2002a). If the energy needed for migration was considered, the energy required in the reproduction buffer to meet the threshold to nest and migrate would be greater and females would take longer to accumulate this energy (i.e. have longer remigration intervals) than predicted in our simulations. Further, the DEB model represents a female *C. mydas*, but males have lower energetic costs of reproduction (Hays et al., 2010) and may respond differently to environmental conditions. All these aspects of sea turtle breeding could be incorporated into the models we present here (for example by modelling the production of eggs as separate clutches; see Pecquerie et al., 2009) and would increase the realism of predictions.

4.3 Impacts of marine heatwaves on life history traits in C. mydas

Extreme events such as marine heatwaves are characterised by rapid, short-term changes in environmental conditions. In this study, the long term responses of female *C. mydas* to simulated heatwave events were similar to those predicted for gradually changing conditions over the 80-year simulation. Similarly to scenarios of gradual decreasing food availability, during heatwaves somatic maintenance costs could not be paid entirely from energy allocated to growth and somatic maintenance ($\kappa\ \dot{p}_C$ flux), and therefore energy from the reproduction buffer was used for somatic maintenance. When baseline conditions returned, females could build up their reserve and cease taking energy from the reproduction buffer, which could then build up more quickly and reproductive output increased. The responses to marine heatwave conditions predicted in our simulations are supported by observations of the body condition of *C. mydas* recorded before and after a marine heatwave that occurred off the Western Australian coast over the 2010/2011 summer. Thomson et al. (2015) reported that body condition (measured using indices based on length and weight) of *C. mydas* in Shark Bay declined in the two years following the heatwave, with turtles more likely to be classified in a lower condition category after the heatwave than before. Abundance and density of *C. mydas* also decreased following the heatwave (Kendrick et al., 2019; Nowicki et al., 2019), coinciding with significant seagrass dieback (Thomson et al., 2015). Marine heatwaves are predicted to become more frequent and more intense in future climates (Meehl and Tebaldi, 2004; Frölicher et al., 2018; Oliver et al., 2018) and our simulations suggest that if they become frequent (e.g. every 5 years), extended remigration intervals and reduced lifetime reproductive output may be a consistent response. This highlights why considering the effects of both ‘press’ and ‘pulse’ disturbances is important when predicting the impact of future climates on vulnerable species (Bender et al., 1984; Harris et al., 2018).

4.4 Ecological implications and future research directions

The starvation rule applied in our simulations – where starving individuals pay somatic maintenance costs from the reproduction buffer – may not be sufficient to cover maintenance costs in periods of prolonged starvation. In extreme conditions, further changes to the energy allocation rules may be necessary, such as changing the proportion of energy allocated to somatic maintenance and growth (κ), or paying only somatic maintenance costs (Pecquerie et al., 2009; Kooijman, 2010; Desforges et al., 2019). These dynamics could allow individuals to survive prolonged periods of poor conditions and could be explored with a more complex version of the DEB model. Another likely avenue for *C. mydas* to survive prolonged periods of low food is to move to another feeding area or switch to a more available food type as some *C. mydas* populations display an opportunistic foraging strategy (Garnett et al., 1985; Amorocho and Reina, 2008; Russell and Balazs, 2009).

The patterns of growth and reproduction presented here indicate that food availability has a stronger influence on the energy budgets of Ningaloo *C. mydas* relative to the direct effects of temperature. If temperature increases, but food availability is unchanged, then rates of growth and reproduction will increase but the ultimate length of females will remain stable. A more likely scenario is that temperature will indirectly affect female *C. mydas* by changing food quantity and/or quality (Hamann et al., 2007; Hawkes et al., 2009; Poloczanska et al., 2009). Hence if temperature increases, but food availability decreases slightly, growth rates similar to current values can be expected, as increases in physiological rates due to temperature offset the decrease in rates of energy assimilation due to lower food availability, but ultimate length and reproductive output would be smaller. This means that temperature increases could mask the effects of marginal decreases in food availability when growth rates are measured empirically (Marn et al., 2017a). However, if food availability declines markedly the effects of increased temperature would be overridden, and growth rates would decline.

The effects of environmental conditions on *C. mydas* growth have been observed in the Western Atlantic, where declining growth rates from 1973 – 2015 were attributed to an ecological regime shift (Bjorndal et al., 2017). As green turtles are herbivores, they are sensitive to changes in primary production that alter food availability (Broderick et al., 2001; Hamann et al., 2007). While the diet of *C. mydas* is well characterised (reviewed by Bjorndal, 1997; Jones and Seminoff, 2013), differences between and within populations exist (e.g. Arthur and Balazs, 2008; Burkholder et al., 2011). Globally, the biomass of seagrass is expected to be negatively impacted by climate change (e.g. Duarte, 2002; Waycott et al., 2009; Rasheed and Unsworth, 2011; Chefaoui et al., 2018), but the response of macroalgae is uncertain; some species are predicted to decline while others may become more abundant (Diaz-Pulidio et al., 2007; Wernberg et al., 2016). Simulated scenarios of food availability had a marked effect on *C. mydas* growth and reproduction, and with the contrasting predictions for changes in two major primary producers, it is critical to identify important diet items for *C. mydas* at Ningaloo, to be able to forecast future food availabilities, and turtles' responses.

Our modelled responses in reproductive output showed that the number of eggs produced per season and the remigration interval vary over time, and that each depends on food availability and temperature. Hence, monitoring programs that record annual numbers of nests or nesting females and estimate abundance using population or species averages of reproductive output (e.g. Troëng and Rankin, 2005; Whiting, 2016) may not accurately reflect trends in population size (Hays, 2000; Richards et al., 2011; Esteban et al., 2017). Further, egg quality (initial energy content; E_0) is influenced by food availability, with E_0 decreasing with lower food availability. While not explored here, this has consequences for hatchling survival, as hatchlings will be smaller and will have less energy in reserve to swim into the pelagic environment and to begin feeding (Stubbs et al., 2019). This shows that environmental conditions not only impact individual females, but have flow-on consequences for their offspring.

The direct effects of temperature on processes of maintenance, growth, maturation and reproduction were subtler than the effect of food. We used sea surface temperature as a proxy for body temperature in our simulations, but active adult sea turtles can have body temperatures several degrees higher than ambient water temperatures (Standora et al., 1982; Read et al., 1996). Similarly, individual turtles can seek out cooler or warmer water temperatures; for example juvenile *C. mydas* may overwinter in deep, cold waters (Williard et al., 2017), which lowers physiological rates (including maintenance) and thereby conserves energy. Conversely, nesting female loggerhead turtles select warm microhabitats during the nesting season (Schofield et al., 2009), which speeds the process of egg formation and allows clutches to be laid over a shorter timeframe. These types of behaviours may result in different body temperatures to those we simulated, and would thereby impact growth and reproduction. Further, our simulations assumed that all temperatures experienced would be tolerated by juvenile and adult *C. mydas* (i.e. we used an Arrhenius equation that did not specify a thermal tolerance range). This assumption is reasonable, as *C. mydas* are active in water temperatures of ~15 – 34 °C (Mendonça, 1983; Read et al., 1996). However, when temperatures exceed this range, as they may under climate change and extreme events, the impact of temperature may be more marked than is represented here.

The environmental changes simulated in this study are small, but realistic. A change in food availability of 20% over the 80-year lifespan of a green turtle represents a change of <5% in the scaled functional response (*f*). Despite this small change in *f* we show appreciable differences in several aspects of growth and reproduction in *C. mydas*. Other food-related factors likely to impact how individuals respond to environmental conditions such as variation in forage quality, searching rate, ingestion rate, and digestion rate were not considered here but can be fully explored within a DEB modelling framework, and can include compounding threats such as ingestion of marine debris (e.g. Marn et al., *in review*). Additionally, the early pelagic phase of a green turtle’s life is unlikely to have been modelled realistically, as food availability and temperature in pelagic environment differs to that in neritic habitats (Dalleau et al., 2014; Mansfield et al., 2014), but was a reasonable simplification in this study which focussed on the portion of the life cycle spent at Ningaloo. The great value of the full life cycle approach of a DEB model is that it allows for the inclusion of different conditions in different life stages (e.g. Pecquerie et al., 2009), and so future research could integrate the model developed here with individual-based population models, to gain insights into population level responses to changing environments.

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Appendix A

Table A.1: Standard Dynamic Energy Budget model equations. Energy fluxes, state variables and auxiliary equations that relate state variables to physical properties of the individual are described. Parameters and energy fluxes are described in Table 1 and the methods section of the main text.

	Equation
Energy Fluxes	
Assimilation	$\dot{p}_A = f\{\dot{p}_{Am}\}V^{\frac{2}{3}}$
Reserve mobilisation	$\dot{p}_C = E\left(\frac{[E_G]\dot{v}V^{\frac{2}{3}} + \dot{p}_S}{\kappa E + [E_G]V}\right)$
Somatic maintenance	$\dot{p}_S = [\dot{p}_M]V$
Growth	$\dot{p}_G = \kappa\dot{p}_C - \dot{p}_S$
Maturity maintenance	$\dot{p}_J = \dot{k}_J E_H$
Maturation then reproduction	$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$ OR in the case when somatic maintenance can't be paid from the $\kappa\dot{p}_C$ flux, then $\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J - (\dot{p}_S - \kappa\dot{p}_C)$
State Variable Dynamics	
Structural volume	$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$
Reserve energy	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$
Maturity	$\frac{dE_H}{dt} = \begin{cases} \dot{p}_R, if\ E_H < E_H^p \\ 0, otherwise \end{cases}$
Reproduction buffer	$\frac{dE_R}{dt} = \begin{cases} 0, if\ E_H < E_H^p \\ \dot{p}_R,\ otherwise \end{cases}$
Auxiliary Equations	
Physical length	$L_w = \frac{V^{\frac{1}{3}}}{\delta_{CL}}$
Weight	$W_w = w\left(Vd_V + \frac{w_E(E + E_R)}{\mu_E}\right)$
Fecundity (number of eggs)	$\dot{R} = \frac{\kappa_R\dot{p}_R}{E_0}$

w_E = 23.9; molecular weight of reserve (g mol^{-1}), μ_E = 5.5x10^5; chemical potential of reserve (J mol^{-1}), w = 3.33; dry to wet weight conversion factor.

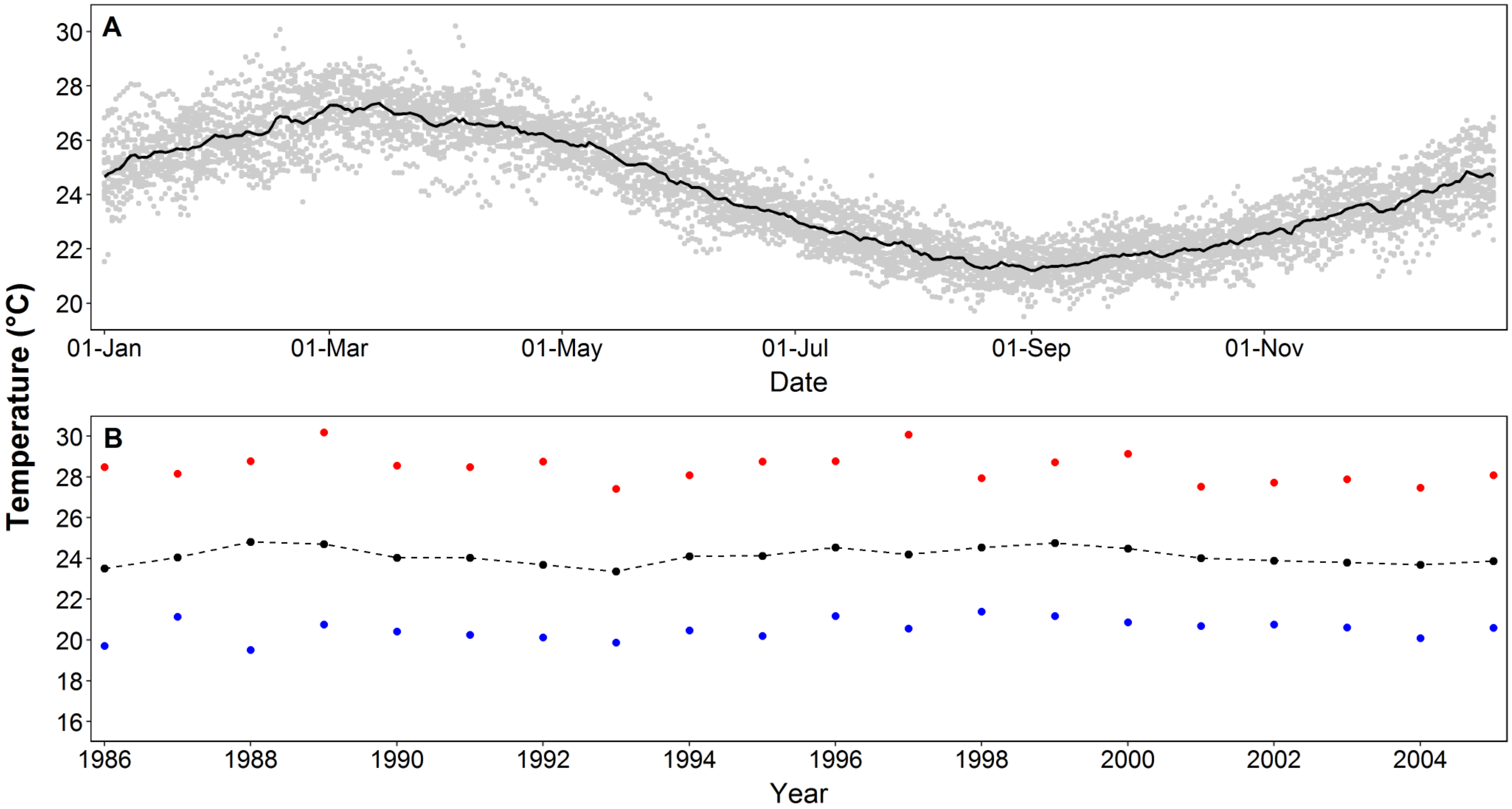

Figure A.1: Temperatures from NOAA Coral Reef Watch 5-km Regional Virtual Stations for Ningaloo (NOAA Coral Reef Watch, 2019), used to generate simulation temperatures for varying conditions. Panel A shows the daily sea surface temperature (SST) on each day of the year from 1986 – 2005 in grey dots, while the solid line shows the mean daily SST averaged over the same period. Panel B shows the annual average (black points), minimum (blue points), and maximum (red points) temperature for the period 1986 – 2005.

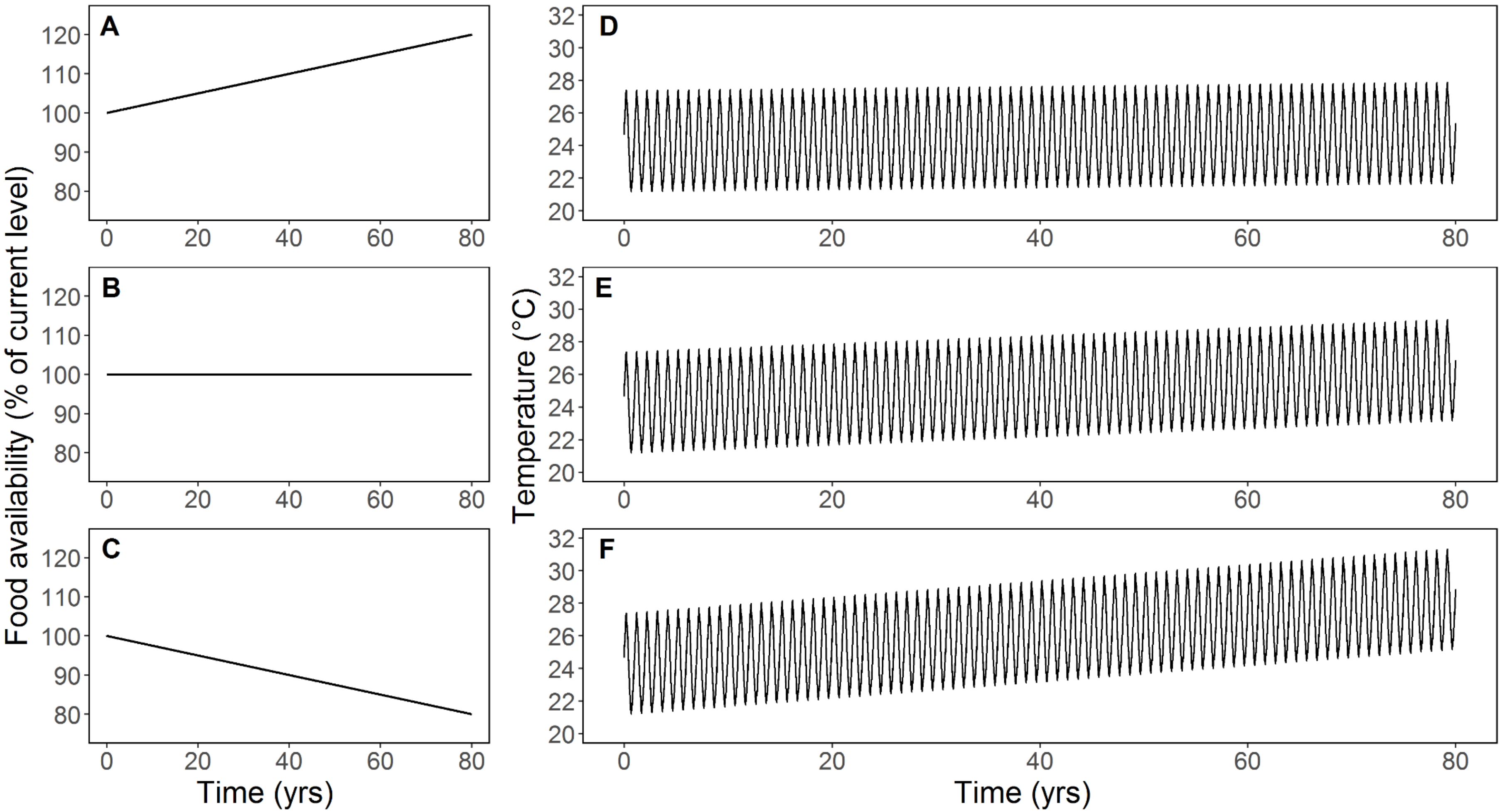

Figure A.2: Food availability (A, B, C) and temperatures (D, E, F) for simulations of varying conditions. Each combination of food and temperature conditions were simulated (nine scenarios in total). Food availability was increased by 20% (A), 0% (i.e. current conditions; B), or decreased by 20% (C) over the 80-year simulation. Temperature was increased by 0.5 °C (D), 2 °C (E), or 4 °C (F) over the 80-year simulation (see the methods section of the main text for details).

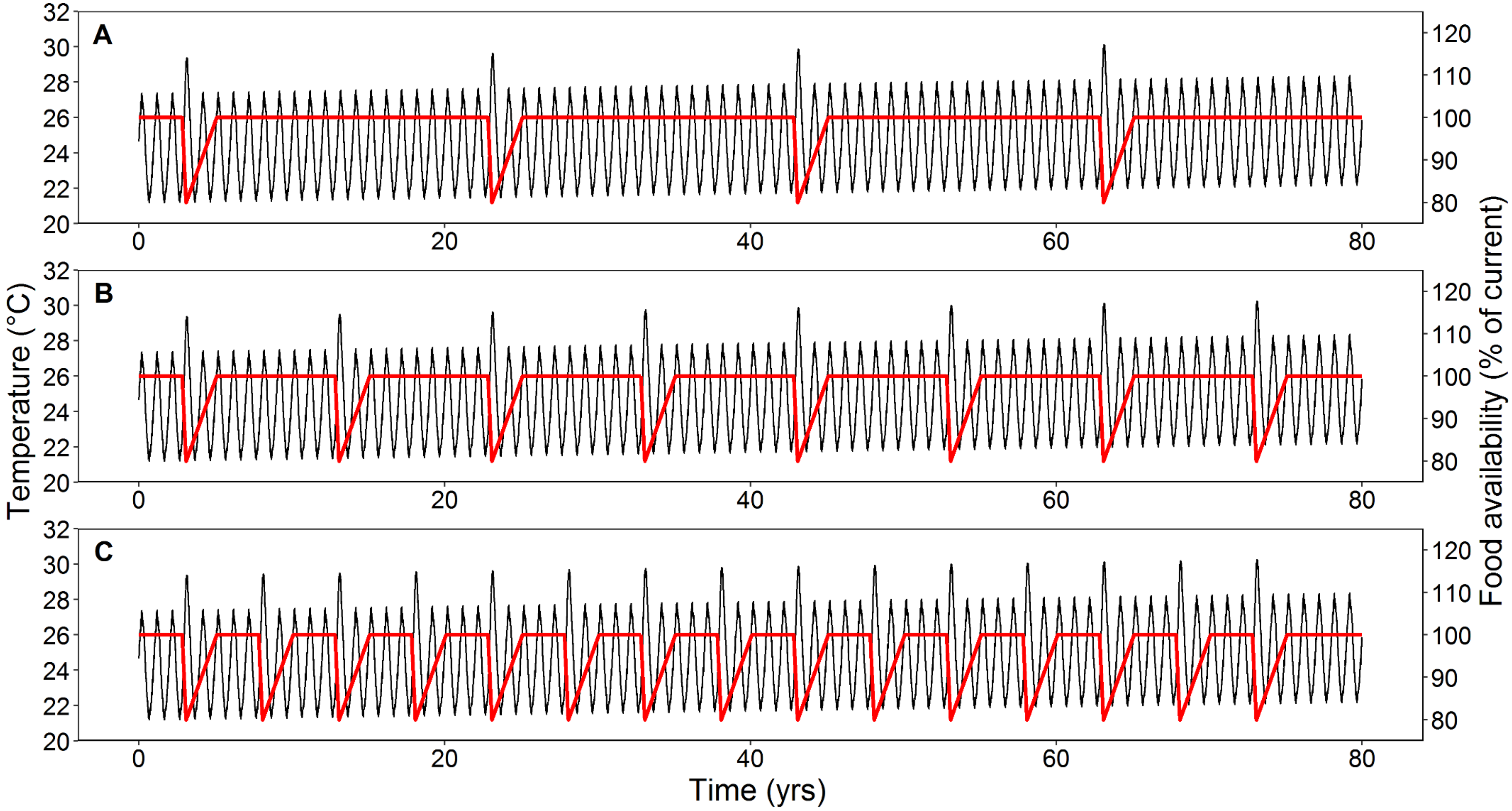

Figure A.3: Temperature (black lines; left y-axis) and food availability (red lines; right y-axis) for simulated marine heatwave scenarios. Heatwaves were simulated to occur every 20 (A), 10 (B), or 5 (C) years (see the methods section of the main text for details).

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