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Preliminary Observations of the Effect of Temperature and Food Concentration on the Egg Production Rate and Hatching Success of *Acartia amboinensis* from the Central Red Sea

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The effects of temperature and food concentration on the egg production rate (EPR) of the tropical calanoid copepod *Acartia amboinensis* were studied from the coastal waters of the central Red Sea in March 2017. In the first experiment, adult females were incubated in glass bottles that were pre-filled with screened seawater containing a natural assemblage of phytoplankton. In the second experiment, the species were incubated in glass bottles that were enriched with different concentrations of *Chaetoceros muelleri* along with natural assemblages of phytoplankton. Both the experimental setups were then exposed to different temperatures (21, 24, 27, 30 and 33°C). The daily EPR varied significantly across different temperatures and the various food concentrations ($p < 0.05$). Within the natural food assemblage (Exp. 1), the EPR increased gradually to a peak mean of 13.7 eggs female^{-1} d^{-1} at 27°C, then declined as temperatures increased (at 30 and 33°C). In the second experiment when the water was enriched with algal culture, EPRs were significantly greater (maximum EPR: 63.9 eggs female^{-1} d^{-1} at 27°C) than those incubated in ambient water with natural food (maximum EPR: 17.4 eggs female^{-1} d^{-1} at 21°C). The hatching rate fluctuated between 42.4% and 88.6%. The present study revealed that the EPR of *Acartia amboinensis* responded rapidly to changes in food availability, suggesting an extreme food limitation in the central Red Sea.

Key words: *Acartia amboinensis*, Copepods, Egg production rate, Hatching rate, Red Sea.

BACKGROUND

In the marine ecosystems, copepods function as the key primary consumers, playing a crucial role in the proper functioning of various biogeochemical cycles and helping transfer energy from the producers to the secondary consumers (Harris et al. 2000). The population dynamics of these organisms are mainly affected by their ability to produce eggs and successfully hatch (Kimmerer et al. 2005; Nakajima et al. 2019). Several studies have focused on the variation in the reproductive potentiality of copepods, and have showed that fecundity is strongly influenced by the availability of various food sources (Durbin et al. 1983; Rodriguez et al. 1995; Calbet et al. 1999; Ara 2001; Burdloff et al. 2002), as well as various physico-chemical conditions such as temperature (Ambler 1986; Landry 1978; Sekiguchi et al. 1980; Kim 1995; Milione and Zeng 2008), salinity (Castro-Longoria 2003; Milione and Zeng 2008; Holste and Peck 2006) and wind speed and

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turbulence (Gómez-Gutiérrez et al. 1999). It is thus necessary to study the influence of such environmental factors on the egg production rate (EPR) of copepods in order to predict their pattern of reproduction and population dynamics within various natural environments. In general, many studies on the temperate regions have dealt with the egg production and feeding habits of many *Acartia* species (*e.g.*, White and Roman 1992; Rodriguez et al. 1995; Calbet and Alcaraz 1996; Gómez-Gutiérrez et al. 1999; Dvoretsky and Dvoretsky 2014; Nogueira et al. 2018; Cruz et al. 2020), while the similar studies from tropical and subtropical regions are comparatively low (*e.g.*, Hopcroft and Roff 1998; Ara 2001; Palomares-García et al. 2003; Yoshida et al. 2012b; Jo et al. 2019). Most importantly, there are hardly any studies on any of the copepod species from the Red Sea waters. As a complex ecosystem that consists of hot and high saline waters, the Red Sea acts as a perfect platform for studying the impact of global warming on various aquatic habitats on the earth (Chaidez et al. 2017). Moreover, the oligotrophic nature of the system provides more challenges to the inhabitants in terms of limited food availability (Sommer 2000; Devassy et al. 2017).

Acartiid copepods are known to be the most common inhabitants of the coastal and estuarine environments in the marine ecosystems worldwide (Liu et al. 2010; El-Sherbiny and Al-Aidaroos 2014). From the Red Sea, until now about nine species of the genus *Acartia* have been recorded (Al-Aidaroos et al. 2019b): *Acartia* (*Acanthacartia*) *fossae*, *A.* (*Acartia*) *danae*, *A.* (*Acartia*) *negligens*, *A.* (*Acartiura*) *clausi*, *A.* (*Acartiura*) *longiremis*, *A.* (*Odontacartia*) *centrura*, *A.* (*Odontacartia*) *erythraea*, *A.* (*Odontacartia*) *amboinensis* and *A.* (*Odontacartia*) *bispinosa*. Among them, the present experimental species, *Acartia* (*Odontacartia*) *amboinensis*, which was recorded recently in the Red Sea (Al-Aidaroos et al. 2016), has a common distribution in the tropical and subtropical waters (*e.g.*, Achuthankutty et al. 1989; Naz et al. 2012; Rezai et al. 2004; Revis 1988; Salakij et al. 2008; Tanaka 1965; Zuraire et al. 2018). This species is recorded in the coastal waters of the Arabian Sea and the Indian Ocean with affinity towards high saline and warm waters (Achuthankutty et al. 1989; Revis 1988; Zuraire et al. 2018). Furthermore, no investigation on the egg production rate has been carried out anywhere in the world for *A. amboinensis*. Hence, the present study was designed to understand the effects of temperature and food concentration on the EPR and hatching success of the *A. amboinensis* in the laboratory. The results obtained in this study can be considered as a model for predicting the abundance of *A. amboinensis* in tropical seas, which will experience hotter surface waters in the future due to global warming.

MATERIALS AND METHODS

Live specimen collection

Live copepod samples were collected during the early morning from the coastal waters of the central Red Sea, Saudi Arabia (21°42'32.45"N, 39°5'41.76"E) in March 2017 by vertical tows from a depth of 25 m to surface with a WP2 plankton net (150 µm mesh size) fitted with a 20 L non-filtering plastic bag as cod end to minimize damage to organisms. After collection, the plastic bags with the plankton were kept in an isothermal cooling box that was filled with ambient seawater and transferred to an environmental chamber (ESPEC walk-in) within 15 minutes, where they were gently aerated to minimize oxygen deficiencies. Meanwhile, surplus subsurface seawater was collected from the same area and gently sieved (to prevent deterioration of microzooplankton) through a 45 µm mesh sieve to remove metazoan zooplankton and other copepod eggs. The temperature of the environmental chamber was set to that observed in the coastal waters (26.4–27.1°C). For each experiment, about 300 individuals of *A. amboinensis* were sorted under a stereoscopic microscope with a wide-mouth sterilized Pasteur pipette, and maintained in 2 L glass beakers with proper aeration until the beginning of the experiment.

Experiment 1: Effects of temperature on egg production rates of *A. amboinensis* in March (with natural food assemblage)

We evaluated the effect of different temperatures [21, 24, 27, 30 and 33°C, which is comparable to seasonal variations observed by Alsaafani et al. (2017)] on the egg production rate of female *A. amboinensis* in March during their high abundance period. To do that, sets of copepods were acclimatized for 24 h through by increasing the temperature from *in situ* (~27°C) by 3°C every 3 h until it reached the target experimental temperature in 2 L jars filled with seawater. Lower treatments (21 and 24°C) were obtained through a gradual acclimation to the laboratory room conditions (ca. 21°C). After 24 h of acclimation, 10 intact and healthy adult females and two males (to ensure the natural fertilization processes) from each group were transferred to 1 L screw-capped glass bottles filled with pre-screened (45 µm) natural seawater collected in the field, containing the natural food assemblage, and kept at the corresponding temperatures for another

24 h. All the bottles were then carefully closed by placing a plastic film over their mouth to prevent bubble formation. Groups of four bottles were incubated at each of five different temperatures (21, 24, 27, 30 and 33°C) for a period ~24h; four additional bottles, with only the pre-screened water, were set at each temperature as controls. Light in the experimental chamber was kept at a 12 h light:12 h dark pattern throughout the experiment period. To prevent the settling of the natural food present in the seawater, the bottles were turned upside down several times every 4 h. At the end of the experiment, EPRs (eggs female^{-1} day^{-1}) were calculated as the sum of eggs and nauplii divided by the total number of females in each bottle subtracted the number of eggs and nauplii in control ones. In our experiment, the average cannibalism rate was 0.9% after adjusting by including the crumpled membranes in the egg counts.

Experiment 2: Effects of food concentration and temperature on egg production rates of *A. amboinensis*

This experiment was designed to study the influence of different food concentrations on the egg production rates of *A. amboinensis* at different temperatures. The copepod individuals were fed with either the natural food assemblage or with suspensions of the diatom *Chaetoceros muelleri* at different carbon concentrations (108, 231 and 492 µg C l^{-1}). The range of *C. muelleri* concentrations used was determined assuming *Acartia* becomes satiated at ~500 µg C L^{-1} (Kiørboe et al. 1985). For comparative purposes, we assumed a carbon-chlorophyll ratio of 51 (White and Roman 1992) to estimate from chlorophyll the equivalent carbon concentration in the natural food assemblage. The diatom *C. muelleri* used in this experiment was inoculated from starter cultures supplied by the National Aquaculture Group (NAQUA), Al-Lith, Saudi Arabia. This diatom species was grown in f/2 medium (Guillard and Ryther 1962), with added silicate supplements, and maintained at a temperature of 25 ± 1°C and a salinity of 39–40. The cultures were grown with continuous aeration and a light intensity of 5000 lx, 12 h light: 12 h dark photoperiod. The algal culture was maintained in the exponential growth phase by diluting ca. 30% every other day. Before the start of each experiment, the cell abundance of the diatom stock culture was determined using a Sedgwick-Rafter counting chamber under an inverted microscope (Leica DMI 3000B). The carbon content of *C. muelleri* was estimated from biovolume [according to geometric shape and corresponding equation proposed by Olenina et al. (2006)] using the equation provided by Montagnes et al. (1994): Cell carbon (pg) = 0.109 [cell biovolume (µm^3)]$^{0.991}$. The diatom stock culture was then diluted with 0.2 µm filtered seawater to make the various food concentrations required for the experiment (see above). Experimental bottles 1 L were then filled with the corresponding algal suspensions. Before starting this experiment, groups of the target species were acclimatized for 48 h at each temperature (21, 24, 27, 30 and 33°C) with different food concentrations of *C. muelleri*. After 24 h, the bottles contents were gently filtered, and animals were transferred to a new algal suspension previously adjusted to the corresponding concentrations. In case of using natural food assemblages, the copepods were acclimatized as in experiment 1. After transferring the preconditioning copepods to the experimental bottles 1 L they were incubated for 24 h in the environmental chambers at the five mentioned temperature regimes with a 12 h dark:12 h light photoperiod. Five replicates were set for each combination of food concentration and temperature. For each treatment, five additional bottles containing only screened seawater (without copepods) were used as controls. At the end of the experiment, bottle contents were sieved through a 45 µm sieve. The retained eggs were then transferred into a Petri dish and counted under a stereoscopic microscope.

Experiment 3: Egg hatching success experiments

To study the hatching success of the eggs produced by *A. amboinensis*, about 20–30 groups of females were transferred to sets of screw-capped 1 L glass bottle filled with the 45 µm pre-sieved seawater (maintained at 27°C). The eggs that were obtained within the first 2–3 hours (approximately 100–150) were collected using a sieve (45 µm mesh), and then transferred to 6-well plates (five replicates) filled with about 15 mL of filtered seawater and maintained at different temperatures (21, 24, 27, 30 and 33°C; one plate for each temperature). For each temperature, the hatching rate of the eggs was checked and counted under a Wild stereoscopic microscope after 48 h. The egg hatching success rate (%) for each replicate well was then calculated as the percentage in relation to the initial number of eggs introduced in each replicate well. Hatched eggs were calculated as the difference between the initial number of eggs and the number of eggs unhatched after 48 h.

Statistical analysis

One-way ANOVA was used to determine the differences in the effects of various temperatures on egg production rates with the natural food assemblage

(Exp. 1) and on egg hatching success (Exp. 3). For the egg hatching success, the data were arcsine transformed prior to analysis. Two-way ANOVA was used to study the combined effects of temperatures and food concentrations on egg production rate (Exp. 2). Tukey's post-hoc tests were conducted to assess differences between treatments. All data were statistically analyzed at confidence levels of 95% using CoStat (Version 6.303, CoHort, USA, 1998–2004). All values are presented as mean ± standard deviation (SD). A multiple regression model was used to predict egg production rate as a function of food concentration and temperature. The regression analysis was carried out using XLSTAT. Also, the functional response data were fitted to Holling type II models (equation 1) using nonlinear regression by the MATLAB Statistics toolbox:

$$EPR = aC/1+haC \quad \text{Eq. (1)}$$

where EPR is the egg production rate (eggs female^{-1} d^{-1}), a is the searching or attack coefficient and h is the handling time, and C is the food concentration (µg C l^{-1}).

Estimates of food concentration at which 90% of the maximum EPR was reached (C_{90}), maximum egg production (EPR_{max}), a and h were obtained directly from the Holling Type II model.

RESULTS

Exp. 1: Effects of temperature on EPR

The daily egg production rate (EPR) of *A. amboinensis* in the various experimental temperatures varied significantly (*d.f.* = 4, f = 135.92, $p < 0.05$) from 3.2 to 15.7 eggs female^{-1} d^{-1}. The average EPR values showed a gradual increase from 4.4 ± 0.9 eggs female^{-1} d^{-1} at 21°C to the highest value of 13.7 ± 2.5 eggs female^{-1} d^{-1} at 27°C. Then, it showed a substantial decrease in their mean values at 30°C and 33°C (9.4 ± 1.4 and 6.3 ± 0.9 eggs female^{-1} d^{-1}, respectively). Due to the non-linear response of such biological processes with changing environmental factors, the relationship between the egg production and temperature was better represented by a polynomial function (Fig. 1). The obtained relationship was expressed as:

$$EPR = -0.1841\ T^2 + 10.122\ T - 127.52$$
$$(R^2 = 0.645,\ p < 0.0001,\ n = 20)$$

where EPR is the egg production rate (eggs female^{-1} d^{-1}) and T is the temperature (°C).

Exp. 2: Effects of food concentration and temperature on EPR

In the second experiment, *A. amboinensis* was fed with both the natural food assemblage (estimated as 10 µg C l^{-1}) as well as different concentrations of *C. muelleri* (108, 231 and 492 µg C l^{-1}). The EPR generally increased with increasing food concentration and varied from a minimum of 3.7 eggs female^{-1} d^{-1} at 21°C with a food concentration of 10 µg C l^{-1} (natural food) to a maximum of 63.9 eggs female^{-1} d^{-1} at 27°C with a food

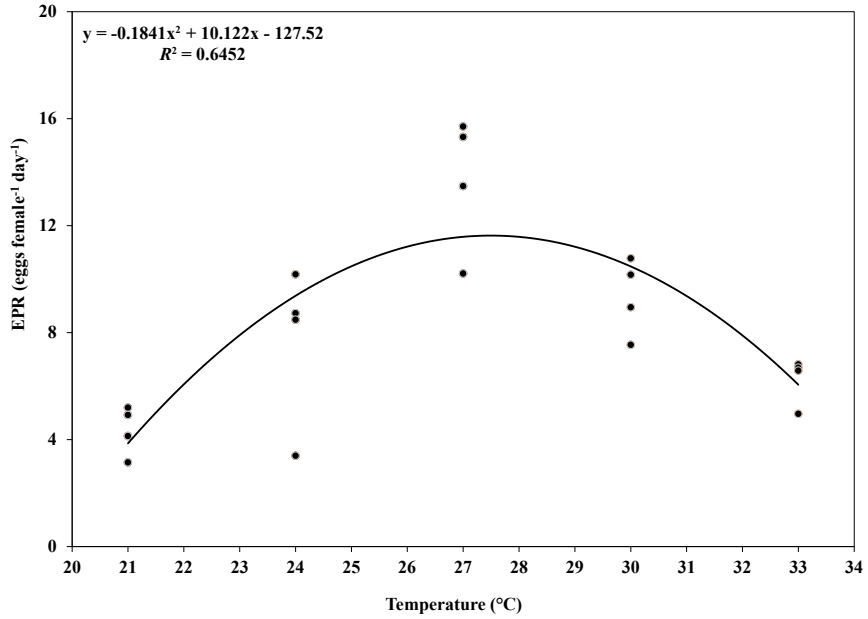

Fig. 1. Egg production rate (eggs female^{-1} d^{-1}) of *Acartia amboinensis* at different water temperatures.

concentration of 492 µg C l^{-1}. During this experiment, at the highest food concentration of 492 µg C l^{-1}, the maximum EPRs were recorded at all experimental temperatures (Fig. 2). The maximum EPRs observed at 21, 24, 27, 30 and 33°C were 22.4, 55.0, 63.9, 51.5 and 26.9 eggs $female^{-1}$ d^{-1}, respectively (Fig. 2). On the other hand, the lowest EPRs were recorded when the copepods were fed with the natural food assemblages. The functional response analysis (Holling type II) proved that EPRs varied significantly with increasing food concentrations at different temperatures ($p < 0.001$) with significant positive correlations (R^2 = 0.890, 0.906,

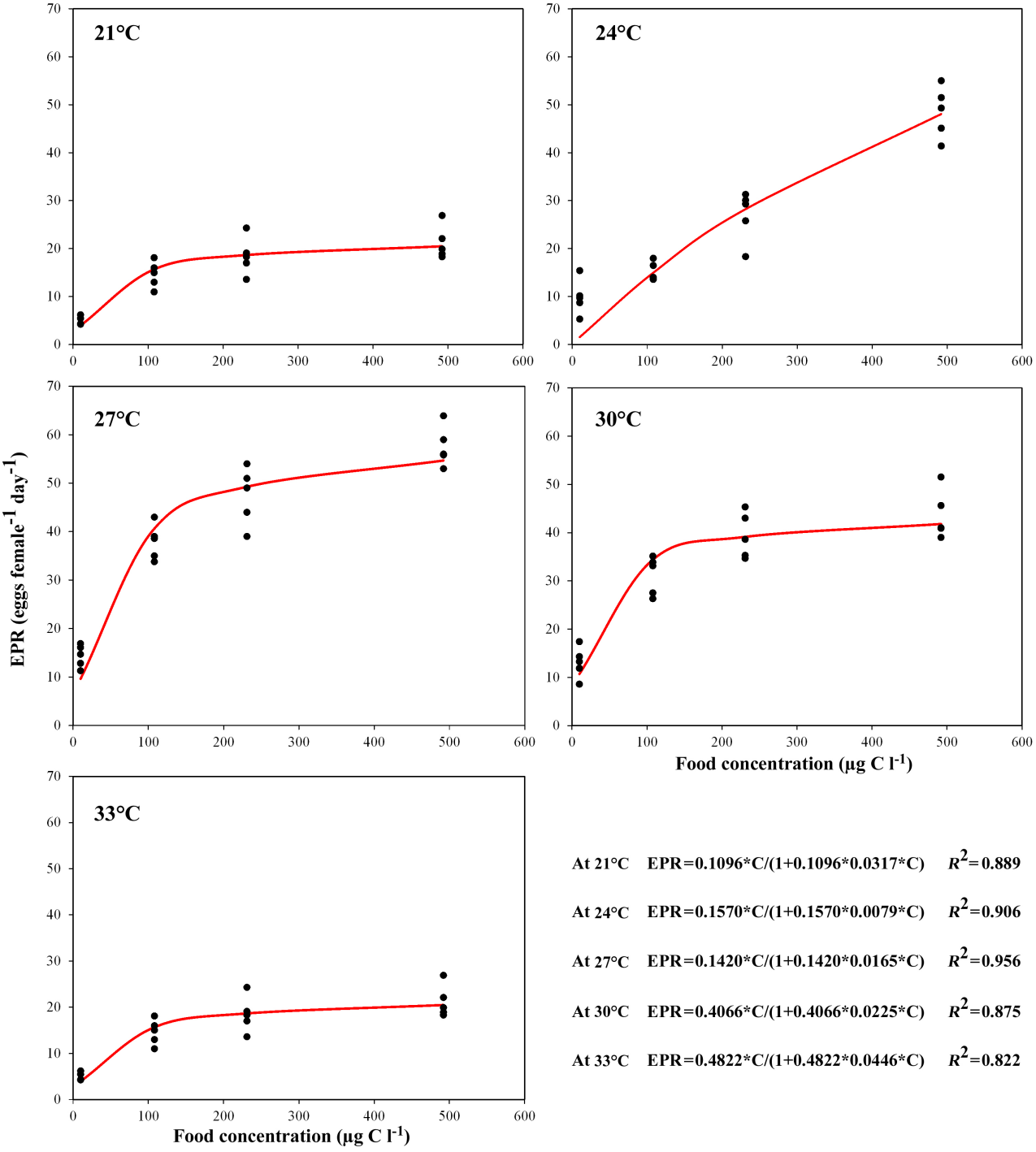

Fig. 2. Egg production rate (EPR) of *Acartia amboinensis* fed with natural food and different concentrations of *C. muelleri* at different temperature regimes. Data from all five replicates are shown. The curves represent the best-fitting functional response model (Holling type II).

0.956, 0.875 and 0.822 at 21, 24, 27, 30 and 33°C, respectively). Moreover, it was clear that the searching or attack rate (*a*) was generally higher at 27°C and 30°C (0.142 and 1.407, respectively), while lower rates were observed at 33°C and 21°C (0.045 and 0.032, respectively) (Fig. 2). This resulted in nearly three-fold higher maximum EPR at 27°C than 21°C. Meanwhile, maximum EPR decreased at the highest temperature of 33°C (Fig. 2). The estimated food concentrations at which 90% satiation occurred were 402 µg C l^{-1} at 21°C, 422.8 µg C l^{-1} at 24°C, 286.6 µg C l^{-1} at 27°C, 253.4 µg C l^{-1} at 30°C and 267.3 µg C l^{-1} at 33°C.

Statistically, two-way ANOVA confirmed the significant effects of food concentrations and temperatures on the egg production rate of *A. amboinensis* as well as the possible interactions between these two parameters (Table 1). We built a predictive model for EPR using temperature and food concentrations variables (regressors) for stepwise multiple regression. The effects of temperature and interaction (food concentration × temperature) were not significant ($p > 0.05$) and were eliminated from the model. Consequently, the best model included only one regressor (food concentrations), which was proven significant ($p < 0.0001$).

Exp. 3: Egg hatching success

Egg hatching rates varied significantly (*d.f.* = 4, $f = 140.1$, $p < 0.05$) at different temperatures and were considerably lower at 21°C and 33°C (averages: 42.4 ± 5.6% and 45.2 ± 5.8%, respectively). At other temperatures, the mean hatching rates varied between 58 ± 4.7% and 88.6 ± 2.1% at 24°C and 27°C, respectively. Statistically, a non-linear relationship between the temperature and the hatching rate was evident during the study (Fig. 3); the values are expressed in the following equation:

$$\text{Hatching rate} = -1.1238\ T^2 + 61.659\ T - 762.15$$
$$(R^2 = 0.822,\ p < 0.0001,\ n = 20)$$

DISCUSSION

In the current study, the instantaneous egg production rates of *A. amboinensis* were assessed experimentally for the first time from the oligotrophic warm waters of the Red Sea. The EPR obtained from the first experiment (range: 3.2 and 15.3 eggs $female^{-1}$ day^{-1}) are analogous with those obtained from other warm water *Acartia* species (Table 2). In comparison to the ecosystems, where all those above-mentioned studies happened, the Red Sea was unique in terms of having higher sea surface temperatures and lack of surplus food availability. This in turn may result in a low egg production rate when compared with temperate *Acartia* species. Moreover, most subtropical waters, including the Red Sea, are expected to have low food quality (Kleppel and Hazzard 2000), although in such an oligotrophic environment the heterotrophic component can be important (Saiz and Calbet 2011). Our observation that egg production was lowest at the lowest temperature of 21°C may be due to the loss of costly metabolism and lower production activity (Holste and Peck 2006). The pattern increased until the temperature reached to 27°C, after which it declined, indicating a suitable range of temperature for the Red Sea species. EPR declined gradually after 30°C, reaching a lower value of EPR at 33°C, following a dome-shaped pattern. Such dome-shaped patterns are the result of the optimal temperature thresholds driven by various copepod species-specific physiological tolerance towards the temperature (*e.g.*, Almeda et al. 2010; Ara 2001; Møller et al. 2012), which is apparent in many *Acartia* species where the EPR peaks at a particular temperature, then declines sharply as the temperature increases—*e.g.*, *A. tonsa* (White and Roman 1992; Holste and Peck 2006; Castro-Longoria 2003), *A. clausi* (Uye 1981, Sekiguchi et al. 1980; Castro-Longoria 2003), *A. bifilosa* (Uriarte et al. 1998), *A. hudsonica* (Sekiguchi et al. 1980), *A. lilljeborgi* (Ara 2001), *A. tsuensis* (Takahashi and Ohno 1996), *A. discaudata* and *A. margalefi* (Castro-Longoria 2003) and *A. steueri* (Uye 1981; Jo et al. 2019). Our study revealed that the optimal temperature for successful egg production for *A. amboinensis* in

Table 1. Two-way ANOVA for egg production rate of *Acartia amboinensis* at different food concentrations and different temperature regimes

Source	*d.f.*	Sum of squares	Mean squares	*f*	Pr > F
Food	3	11029.239	3676.413	299.738	< 0.0001
Temperature	4	10503.036	2625.759	214.078	< 0.0001
Food*Temperature	12	2578.296	214.858	17.517	< 0.0001
Error	76	932.171	12.265		

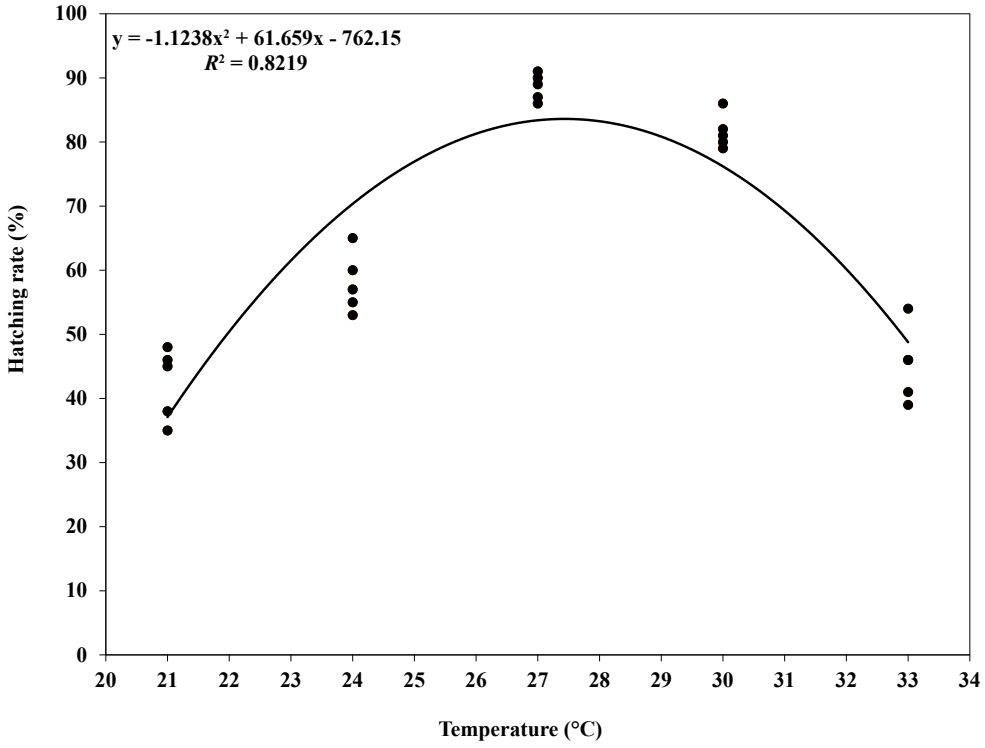

Fig. 3. Egg hatching rate (%) of *Acartia amboinensis* at different temperatures.

Table 2. Comparison of egg production rates (eggs female^{-1} day^{-1}) for different *Acartia* species. (Temp = Temperature and Chl *a* = Chlorophyll-*a*)

Species	Region	Temp (°C)	Range of EPR (mean)	Chl *a* (mg m^{-3})	References
Acartia pacifica	Malacca Strait, Malaysia	27	6.2 ± 2.4	0.23–2.89	Yoshida et al. (2012b)
Acartia pacifica	Tioman Island, Malaysia	29.3–31	6.5–13.3 (10.3)	0.24–0.26	Nakajima et al. (2019)
Acartia pacifica	Inland Sea of Japan	22	9	1.5	Checkley et al. (1992)
Acartia fossae	Exmouth Gulf, Australia	21–23	2–9	0.15–0.35	McKinnon and Ayukai (1996)
Acartia erythraea	Inland Sea of Japan	26	12.9	1.5	Checkley et al. (1992)
Acartia erythraea	Tioman Island, Malaysia	29.3–31	7.9–22 (14.7)	0.24–0.26	Nakajima et al. (2019)
Acartia lilljeborgi	Bahia Magdalena, Mexico	19.8–21	2.0–13.0 (6.2)	0.00–5.80	Gómez-Gutiérrez et al. (1999)
Acartia lilljeborgi	Jamaican waters (Hunt's Bay, Kingston Harbour, Lime Cay and offshore)	~28	10.4–88 (69)	1.63	Hopcroft and Roff (1998)
Acartia lilljeborgi	Cananéia Lagoon, Brazil	25.5	13.8–66.8	1.4–13.3	Ara (2001)
Acartia sinjiensis	North Queensland, Australia	23.2	1.3–14.9	1.63	McKinnon and Klumpp (1998)
Acartia steueri	Onagawa Bay, Japan	2.5–22.5	4.1–64.8	-	Uye (1981)
Acartia steueri	Ilkwang Bay, Korea	3.5–24	4.1–13.7	1–9.32	Kang (1997)
Acartia steueri	Busan bay, Korea	8.7–35	10–26	-	Jo et al. (2019)
Acartia steueri	Ilkwang Bay, Korea	12–26	4–10 (7.3)	0.99–11.63	Jung et al. (2004)
Acartia hongi	Kyeonggi Bay, Korea	1.6–26.5	0.8– 35	> 1–36.6	Youn and Choi (2007)
Acartia clausi	Ebrie lagoon, Gulf of Guinea	10–28	10–60	7–31	Pagano et al. (2004)
Acartia tonsa	Long Island Sound, U.S.A.	24	0–53.2	ND	Kim (1995)
Acartia tonsa	East Lagoon, U.S.A.	16–30	23–105 (56)	ND	Ambler (1985)
Acartia tonsa	Hunt's Bay, Jamaica	~28	(69.8)	1.63	Hopcroft and Roff (1998)
Acartia tonsa	Narragansett Bay, U.S.A.	20	1.6–51.6 (25.3)	1–52.4	Durbin et al. (1983)
Acartia amboinensis	Central Red Sea, Saudi Arabia	27	10.2–16.9 (14.1)	0.2	This study

the Red Sea waters lies in between 27–30°C, where we observed the maximum EPRs (15.7 eggs female^{-1} day^{-1}). This particular temperature range for the same species was found to be suitable for its successful proliferation in the current study as well as Kenyan and Malaysian waters of the Indian Ocean (Revis 1988; Zuraire et al. 2018).

In the second experiment, our results showed a significant relationship between food concentration and EPRs of *A. amboinensis* at each temperature (after acclimation). The increasing pattern of EPRs at 27°C and a food concentration of 492 µg C l^{-1} suggests that the EPRs of *A. amboinensis* can be increased by providing surplus food along with an ambient temperature, as seen in other *Acartia* species *in situ* or experimentally (Saiz et al. 1997; Gusmão and McKinnon 2009 2011; Camus and Zeng 2010; Nogueira et al. 2018; Zhang et al. 2015; Besiktepe and Dam 2020). The average EPR obtained in the present study (with *C. muelleri* as the feed) is comparable to that recorded for *Acartia clausi* (Pagano et al. 2004) and *A. tonsa* (Ambler 1985; Durbin et al. 1983; Kim 1995; Hopcroft and Roff 1998; Pagano et al. 2004). However, it is higher in comparison to those observed by Gusmão and McKinnon (2009 2011), Isari et al. (2013) and Nogueira et al. (2018 2019) for *A. grani*, as well as by Gusmão and McKinnon (2009 2011) for *A. sinjiensis* and by Jo et al. (2019) for *A. steueri.* These inter-specific differences in terms of EPR may be due to the increase of temperature as reported by Durbin and Durbin (1992), Durbin et al. (1983), Lincoln et al. (2001) and Jung et al. (2004) under both natural and experimental conditions and/or the quantity as well as the nutritional quality of the feed used.

In this study, the examined species showed a strong response to food availability during the 48 h. The maximum egg production rates were nearly three times higher 21°C than at 27°C at the highest food concentration of 492 µg C l^{-1}. This indicates that in the central Red Sea, the EPR of *A. amboinensis* females was extremely limited by the availability of food. This conclusion is based on the observation that the copepods enriched with lots of food for 48 h had significantly greater EPRs than did copepods kept in ambient Red Sea water (with natural food assemblage) during the same period. Several previous studies demonstrated that the availability of *in situ* surplus food is a pivotal factor in the EPRs of various copepods, which in turn showed positive relationships between the egg production rates and the phytoplankton biomass (*e.g.*, Durbin et al. 1983; Kiørboe et al. 1988; Calbet and Alcaraz 1996; Gómez-Gutiérrez and Peterson 1999). Our results further indicated that the increasing concentrations of *C. muelleri* had a clear positive effect on the EPR of *A. amboinensis*, which is strongly supported by the studies of Gusmão and McKinnon (2009 2011) and Zhang et al. (2015) for different *Acartia* species as well as the studies of Buttino et al. (2009), Santhanam et al. (2013) and Zhang et al. (2015) for other calanoid species. In the coastal waters and shallow embayment of the study area there is some evidence that the oligotrophic status is changing toward mesotrophic due to anthropogenic effects such as sewage effluents and other coastal developmental activities (Al-Aidaroos et al. 2019a; Al-Amri et al. 2020, El-Sherbiny et al. 2021), which may in turn influence copepod egg production rate. Finally, our EPRs with natural food assemblages were not saturated, since they improved when supplementary food of *C. muelleri* was provided, which suggests that egg production in the ambient water was limited by food quantity.

Results of the present study are very similar to other acartiid species (*e.g.*, Laabir et al. 1995; Castro-

Table 3. Egg hatching rates (HR) of different *Acartia* species in different parts of the world

Species	Region	HR (mean)	References
Acartia tonsa	East Lagoon, U.S.A.	65–98 (84.3)	Ambler (1985)
Acartia tonsa	Long Island Sound, U.S.A.	0–78 (21.1)	Kim (1995)
A. tonsa	Solent-Southampton Water, UK	86–79.3	Castro-Longoria (2003)
Acartia tonsa	Long Island Sound, U.S.A.	0–78 (21.1)	Kim (1995)
Acartia spinicauda	Malacca Strait, Malaysia	11–100 (52.8)	Yoshida et al. (2012a)
A. erythraea	Malacca Strait, Malaysia	10–86 (66.8)	Yoshida et al. (2012a)
A. pacifica	Malacca Strait, Malaysia	18–100 (75.2)	Yoshida et al. (2012a)
Acartia margalefi	Solent-Southampton Water, UK	45.3–54.6	Castro-Longoria (2003)
A. discaudata	Solent-Southampton Water, UK	88–96.6	Castro-Longoria (2003)
A. clausi	Solent-Southampton Water, UK	97.3–98.6	Castro-Longoria (2003)
Acartia lilljeborgi	Cananéia Lagoon, Brazil	69–92 (82.2)	Ara (2001)
Acartia longiremis	Off Newport, U.S.A.	20–60	Gómez-Gutiérrez and Peterson (1999)
Acartia amboinensis	Central Red Sea, Saudi Arabia	42.4–88.6 (67.7)	This study

Longoria and Williams 1999; Ara 2001; Castro-Longoria 2003; Chinnery and Williams 2003), in which temperature served as a controlling factor for the successful hatching of the eggs of *A. amboinensis*. Although we recorded lower hatching rates at low temperatures, similar to other studies (*e.g.*, Uriarte et al. 1998; Ara 2001; Yoshida et al. 2012a; Jo et al. 2019), the low hatching success in our study at 21°C may be related to the short incubation duration. The low EPR obtained in this study at 24°C and 33°C along with a potential delay in the egg development could partially elucidate why *A. amboinensis* in the central Red Sea waters have lower densities during the winter and summer months. The maximum hatching rate (88.6%) obtained in the current experiment at 27°C is similar to the results obtained for other warm water *Acartia* species (Yoshida et al. 2012a; Jo et al. 2019; Table 3).

The Red Sea is considered as one of the warmest ecosystems on earth, and it is quickly becoming even warmer (Chaidez et al. 2017). This may hurt its organisms, including copepods, which may already lies at their thermal threshold. In this study, even at higher food concentrations, egg production is negatively affected by temperature. Moreover, in a future warming scenario, the production of *A. amboinensis* will probably be affected even with high primary production in the coastal waters of the Red Sea since the nearshore tropical copepods are relatively close to their upper thermal threshold. In addition, different responses to temperature increase can also cause a trophic mismatch within the ecological community (Richardson 2008) that in turn leads to periods of food shortage for marine copepods and other species.

CONCLUSIONS

This study assessed for the first time the effects of temperature and food concentration on the egg production rate of the tropical calanoid copepod *Acartia amboinensis* collected from the central Red Sea. EPR and hatching rate for *A. amboinensis* increased with temperature from 21 to 27°C but then decreased with a further increase in temperature from 30 to 33°C, peaking at approximately the *in situ* ambient water temperature (26.4–27.1°C) on the sampling date. Results confirmed that the food concentration also plays an important role in the egg production rate of this particular species. During this study, the ambient food concentration was extremely limited, since it improved when supplementary food of *C. muelleri* was provided; this suggests that egg production in the oligotrophic water of the Red Sea is limited by food quantity. Moreover, this work underlines the need for further studies to increase our knowledge about the effect of different biotic and abiotic variables on the egg production of *A. amboinensis*.

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