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Demographic parameters of adults of *Pseudodiaptomus annandalei* (Copepoda: Calanoida): Temperature–salinity and generation effects

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ABSTRACT

The calanoid copepod *Pseudodiaptomus annandalei* is distributed exclusively in the Indo-Pacific regions from subtropical to tropical estuaries and shallow coastal waters. Its population dynamics is not well understood despite its ecological importance to natural ecosystems and potential applications to aquaculture. We studied the combined effects of temperature and salinity on survivorship and reproduction of *P. annandalei*. The experimental protocol included adult cohort life table analysis and observations on reproductive parameters of individual females (paired with males) in relation to 9 different temperature–salinity combinations. At salinity level 10–20, the average survival ($l_x = 0.5$) and life expectancy at moulting was significantly higher at 18 °C (38 days); however, at salinity 30, the survival was significantly higher at 25 °C (22.17 days) than either of those at 18 or 32 °C. The gross and net reproductive rates were higher (267 and 176 nauplii female^{-1} respectively) at salinity 10 and temperature 25 °C. Neither interclutch duration nor embryonic development time was affected by salinity; whereas, temperature had a significant effect on both parameters. The clutch size was significantly affected by salinity, but not by temperature. Across temperature–salinity combinations tested in the present study, the total lifetime fecundity was significantly correlated with adult generation time, but not with longevity. The population growth rate (Euler's r) was negatively related to the adult generation time across temperature–salinity levels tested. Continued production of viable fertile clutches by the female required remating with the male at frequent intervals. Our results suggest that the most appropriate temperature–salinity combination for this species is 25 °C at salinities 10–15 for reproduction, and 20 °C at salinity 10 for survival.

1. Introduction

The euryhaline calanoid copepod *Pseudodiaptomus annandalei* Sewell 1919 is found perennially in coastal, estuarine (Chen et al., 2006; Sarkar et al., 1985), and in brackish water ecosystems (Golez et al., 2004; Pillai, 1976; Reddy and Radhakrishna, 1982) in the subtropical and tropical Indo-Pacific region (Hwang et al., 2010; Madhupratap, 1987; Walter et al., 2006). This species is an important food component for many estuarine fish larvae in nature and is also being used commercially as live food in the aquaculture of grouper fish larva (Chen et al., 2006; Doi et al., 1997; Liao et al., 2001). Unlike many other calanoids, *P. annandalei* appears to be well suited for culture systems as it can tolerate a wide salinity range (3–30; Madhupratap, 1987; Chen et al., 2006, Hwang et al., 2010), heavy aeration, presence of sediment, suspended solids and high ammonia levels (Hwang et al., 2010). In nature, determinants of population structure of *P. annandalei* are fish larvae (predators), other copepods (competitors) and abiotic factors mainly salinity and temperature. The fluctuations in temperature and salinity influence metabolism and energy balance which in turn affect the growth and reproduction of a brackish water species (Beyrend-Dur et al., 2009; Devreker et al., 2009; Hall and Burns, 2001; 2002; Holste and Peck, 2006). The salinity stress in an organism may have energetic implications as the energy allocated for osmoregulation could be diverted to somatic growth and reproduction (Gonzalez and Bradley, 1994) at optimal salinities. We hypothesize, therefore, that the reproductive adult *P. annandalei* should realize higher reproduction and survival rates at optimum salinities. Temperature is another important abiotic factor, which

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affects the general metabolism and hence influences the survival and reproduction of copepods, and consequently, their biomass (Christou and Moraitou-Apostolopoulou, 1995; Isla and Perissinotto, 2004; Peterson, 2001; Siokou-Frangou, 1996; Sullivan et al., 2007). Temperature effects on embryonic development time, egg hatching success and frequency of clutch production have been demonstrated in many copepod species (Andersen and Nielsen, 1997; Ban, 1994; Castro-Longoria, 2003; Devreker et al., 2009; Jimenez-Melero et al., 2005).

In nature, temperature and salinity act in concert shaping the population structure of species. Temperature, through its effects on general metabolism, might also modulate the salinity effects while these two factors are acting in concert (Castro-Longoria, 2003; Devreker et al., 2009; Hall and Burns, 2001; 2002; Holste and Peck, 2006). Earlier studies on *P. annandalei* focussed either on salinity effects only (Chen et al., 2006) or on temperature effects only (Golez et al., 2004) but none on the combined effects of these factors. Nearly all the studies followed reproductive output for a short term instead of the entire lifespan. The short-term study on reproductive output would often lead to misinterpretation of the lifetime reproductive potential of the copepod. The assessment of the performance of the copepod should be made along its lifespan to estimate the overall reproduction of a species experiencing wide variations of salinity and temperature in its natural habitat. For example, the change in the clutch size is a function of either clutch order or age of the reproductive female (Devreker et al., 2009; Kumar, 2003; Kumar and Rao, 1999). The timing of processes like birth and death plays a critical role in age structure and temporal fluctuations of a population. Life tables are tables of data on survivorship and fecundity of individuals within a population. A standard method is to collect data on a cohort (dynamic or horizontal life table), which enable us to determine age- or stage-specific fecundity and mortality rates, survivorship, and basic reproductive rates (Kumar, 2003, Kumar and Rao, 1999). Life table experiments covering the entire lifetime allow us to obtain realistic information on life history traits such as the age at first reproduction, generation time, clutch size, age-specific survival and reproduction (Case, 2000; Charlesworth, 1980) which are sensitive indicators of environmental conditions (Ianora, 1998; Kumar, 2003; Kumar and Rao, 1999; Peterson, 2001) and can thus provide a clear picture of life history shifts in relation to salinity and temperature fluctuations. Though field studies provide insight into some of the life history variables such as sex ratio and generation time (Cryer and Townsend, 1989), laboratory evaluations permit us to quantify both the patterns of survivorship and reproduction in an age-specific manner (Carey, 1993; Kumar 2003; Kumar and Rao, 1999).

Relative to the studies on the life history traits of temperate and sub-temperate copepod species (Ianora, 1998), those of the tropical and subtropical copepods are poorly explored. More data on copepod life history attributes of tropical and subtropical species are needed for establishing a consistent global pattern of the copepod life cycle. The objective of our study was to examine the combined effects of temperature and salinity on the demographic responses of adult *P. annandalei* and to establish the optimal temperature–salinity levels for maximizing production under culture conditions. Two sets of common garden experiments were conducted separately: one with a cohort observation protocol and another with an individual observation protocol. Experimental temperatures and salinities tested in this study were representative of the range of temperature and salinity recorded in the natural habitat of *P. annandalei*.

2. Materials and methods

2.1. Stock culture

The copepod *Pseudodiaptomus annandalei* Sewell 1919 used in the present study was originally collected from a coastal brackish water pond (salinity ~20) in Tungkang (southern Taiwan). The copepod cultures were maintained in 20 L round plastic tanks at salinity 15–20 using as food the microalga *Isochrysis galbana* at the Biotechnology Center of the Fisheries Research Institute (Tungkang). *I. galbana* has a high content of polyunsaturated fatty acid (PUFAs) (Jeffrey et al., 1994) and is small enough (~3–6 μm) to feed all the developmental stages. The copepod culture was mildly aerated continuously for mixing and keeping the algae suspended. The culture medium was renewed with a mixture of filtered seawater (0.45 μm millipore filter) and purified freshwater once a week. The cultures were maintained at ambient temperature (annual range 20–30 °C) under photoperiod 12 L:12 D. The temperature was about 26 °C when the experiments were initiated in early spring.

2.2. Preconditioning of experimental animals

The effects of temperature and salinity on the adult demographic parameters of *P. annandalei* were studied in the laboratory in two consecutive experiments (experiments I and II) in sequence. Experiment I was on adult cohort life table analysis and experiment II was on individual reproductive parameters. To obtain the required number of CV stage (pre-adult stages) for both experiments I and II, sufficiently large number of copepods were collected from the stock culture and distributed in 9 different 2 L glass beakers containing 1.5 L culture medium. Three of these beakers were placed in a BOD incubator set at each of the three temperatures tested (Table 1). Each of the three beakers at particular temperature was assigned for experimental salinity levels (3 temperatures × 3 salinities). The desired salinity of the medium was obtained by gradually adding either millipore filtered freshwater or sea water at each of the three tested temperatures. Therefore desired temperature–salinity combinations for the acclimated stock cultures were achieved. To obtain the required numbers of individuals for experiments, ovigerous females were taken out from the temperature–salinity acclimated stock cultures and were placed inside a hatchery of a 1 L beaker covered by the aluminium foil to minimize evaporation. The nauplii obtained at each temperature–salinity level were reared from birth to pre-mature stage (CV) in batches before we started to observe their reproduction. For both experiments I and II, the same light regime (12 L:12 D; daytime light: 24 10^3 lx) and *ad libitum* food conditions (*I. galbana*) were maintained. In experiment II, the required number of male–female pairs (Table 1) were isolated immediately after they reached the CV stage, and corresponded to the first generation (labelled "F1"). The remaining individuals F1 were returned to the hatchery to obtain the second generation (labelled "F2"). Likewise when the individuals of F2 reached to the CV stage, the male–female pairs were selected for observations of individual reproduction (Table 1). Thus, separate observations were taken for F1 and F2 generation individuals. Therefore all CVI copepods used in both experiments I and II were prior exposed and acclimatized to the experimental temperature–salinity combinations.

2.3. Experiment I — adult cohort life table analysis

The experimental protocol included three temperatures (18, 25 and 32 °C) and three salinities (10, 20 and 30) making a total of 9 temperature–salinity combinations (Table 1). In the present experiment, the combinations of temperature (T)–salinity (S) are called T18–S10, T18–S20, T18–S30, T25–S10, T25–S20, T25–S30, T32–S10, T32–S20 and T32–S30. The standard life table approach (Begon et al., 1996, Chiang, 1984, Pianka, 1988) was adopted. The experiment was set up soon after the emergence of adults with the acclimated stock cultures, and was conducted in 250 mL beakers, each containing 200 mL medium in triplicate. Freshly moulted adults (CVI) of 10 females (F) and 10 males (M) were introduced into each beaker containing one of the 9 temperature–salinity combinations.