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Demography of *Thiara riqueti* (Grateloup) (Mesogastropoda, Thiaridae) in Response to Temperature and Salinity

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Research Article

ABSTRACT

Both temperature and salinity significantly affected the demographic traits of the snail *Thiara riqueti* (Grateloup) (Mesogastropoda, Thiaridae). At 5% salinity, snails survived less than a week and no reproduction occurred. At 10°C, the mean longevity of the snail was about 10 days and no reproduction was observed. At 18°C, total longevity ranged from 4.1 to 19.8 weeks, and only minor reproduction was observed at 1% salinity. The longevity at 10 and 18°C, however, is sufficient for the snail to survive the short, mild winter period in Taiwan. At 25°C and 30°C, reproduction was observed at all salinities (except at 25°C and 0.2% salinity). At 30°C, the intrinsic rates of increase were 0.1236, 0.1502, 0.1081 and 0.0946 d^{-1} for salinity 1.0%, 2.0%, 2.5% and 3.0%, respectively. The net reproductive rate at 30°C ranged from 0.92 to 56.3 offspring per individual. Although *T. riqueti* was reported as a freshwater snail, our results indicate that it is euryhaline in Taiwan.

INTRODUCTION

Snails play important roles in aquatic ecosystems. Hall [1] reported that the exotic freshwater snail (*Potamopyrgus antipodarum*) consumed 75% of gross primary productivity, and their excretion accounted for two-thirds of ammonium demand in a highly reproductive stream in Wyoming, US. Gutiérrez [2] pointed out that shells of snails are substrata for attachment of epibionts, provide refuges from predation, and control transport of solutes and particles in the benthic environment, and thus changes in shell production have important consequences for other organisms.

Thiara (*Sermyla*) *riqueti* (Grateloup, 1840) (Mesogastropoda, Thiaridae) is distributed from the western coast of India, southeast Asia, Malaysia, Australia, the Philippines, China, Taiwan and the Ryukyu Islands[3]. Although Pace [3] reported it as an inhabitant of freshwaters, Cheng [4] found it to be the most abundant species in the saline environment of Su-Tsao estuary, Tainan, Taiwan. It is one of the major prey species of several birds, including the black-winged stilt (*Himantopus himantopus* [Linnaeus, 1758]) and the pied avocet (*Recurvirostra avosetta* [Linnaeus, 1758]) (Ueng, personal communication).

The population dynamics of aquatic organisms is under the influence of diverse environmental factors; among them, water salinity and temperature are generally considered as the dominant "ecological master factors" [5-8]. Because the survival and fecundity of *T. riqueti* vary with the age, its population dynamics cannot be properly described or analyzed by using the exponential model or logistic model. For an age-structured population, the cohort life table gives a detailed and complete description of the survivorship, development, and reproduction of a population. For a comprehensive understanding of the effect of temperature and salinity on population dynamics of *T. riqueti*, life table study is of prime importance. However, due to the difficulty, tediousness

and time-consuming work in collecting the age-specific survival rate and fecundity in a life table study, only a few data were available for snails.

The traditional life history theories [9-12] deal only with the female age-specific survival rate and fecundity and ignore the male population and the variable developmental rate that occurs among individuals. Chi and Liu[13] and Chi [14] demonstrated that age-specific life tables could not properly describe the stage differentiation of a population. They developed an age-stage, two-sex life table to present an age-stage description for the complete life history and to incorporate variable developmental rates occurring among individuals. Yu et al. [15] and Chi and Su [16] gave mathematical proofs on the relationship between female fecundity, preadult survival rate, and the gross reproductive rate.

In Taiwan, aquaculture of oyster, fishes, and eels significantly affected the costal and estuary habitats. For an integrated conservation and habitat restoration, we need urgently the ecological information for most costal organisms. Among many ecological studies, life table are the most basic and important, though very difficult, subject. For a preliminary understanding of the population ecology, we studied the field dynamics for two years. In accompany with the field study, we studied the cohort life table of *T. riqueti* at different temperatures and salinities in the laboratory and analyzed the raw data by using the age-stage, two-sex life table.

MATERIALS and METHODS

Life Table Study:

Thiara riqueti (Grateloup) were hand collected from the Su-Tsao estuary. The snails were transferred to 9-cm diameter Petri dishes containing sea water and kept in growth chambers at different temperatures ($10 \pm 1°C$, $18 \pm 1°C$, $25 \pm 1°C$ and $30 \pm 1°C$) for 2 d. A total of 28 treatment conditions, i.e., seven salinities (0.2%, 1.0%, 2.0%, 2.5%, 3.0%, 4.0%, 5.0%) and four temperatures (10°C, 18°C, 25°C, 30°C), were used in this study. Forty-eight newborn snails laid within a two day period were used for the life table study at 18°C and 25°C, 36 newborns for 10°C, 48 to 72 newborns for 30°C (Table 1). Because snails did not reproduce at 10°C, newborns collected from 18°C were used for the 10°C life table study. Each newborn snail was kept in an individual well of a 24-well cell culture cluster (cell diameter 1.5-cm) (Becton Dickinson Labware) filled with varying rearing solutions. The rearing solutions of different salinities were prepared from seawater and reverse osmosis water. The salinity of seawater was measured by using a conductivity meter (Model LF 330, WTW Wissenschaftlich-Technische Werkstatten, Weilheim, Germany). Commercial sea salt was used for preparing rearing solution of higher salinities. Rearing solutions were replaced weekly. Three species of algae, including the two predominant species *Ulothrix flacca* (Dillwn) Thuret in Le Jolis, *Enteromorpha intestinalis* (Linnaeus) Nees, and a minor species, *Cladophora albida* (Huds.) Kutz, grew on the interval surface of the well and served as food for *T. riqueti*. Because of the increase in size, after 3 mo the snails were moved to the larger wells of a 6-well cell culture cluster (cell diameter 3.5-cm) containing rearing solution. The mobility and fecundity were recorded weekly until the death of all individuals, except for the 10°C life table study, where mobility and fecundity were recorded daily. The death of a snail was judged according to the isolation of operculum and the decomposition of the body. If a snail was judged as dead, then the date of death was counted backwards to either the first week of the consecutively immobile period or the last reproduction week. The life history is divided into two stages; the pre-reproductive stage (the period prior to the first reproduction), and the adult stage (the period following the initiation of reproduction). Snail lengths were measured monthly. All experiments were carried out in growth chambers set at the above temperatures and a L:D=12:12 h photoperiod.

Life Table Analysis

The raw life history data for each individual, i.e., the length of the pre-reproductive stage and the adult stage, and the weekly fecundity of the adult stage, were pooled and analyzed according to the method described in Chi and Liu [13] and Chi [14]. In order to avoid the tedious efforts involved in raw data analysis, a computer program TWOSEX-MSChart (Chi, 2015) designed in Visual BASIC version 6 for the Windows operating system is available at http://140.120.197.173/Ecology/ and http://nhsbig.inhs.uiuc. edu/wes/chi.html (Illinois Natural History Survey). TWOSEX-MSChart analyzes the raw data and calculates all life table statistics; e.g, the age-stage specific survival rate (s_{xj}; where x = age and j = stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x). The population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase, $\lambda = e^r$; R_0, the net reproductive rate; T, the mean generation time) are calculated accordingly. The net reproductive rate is calculated as: $R_0 = \sum \sum s_{xj} f_{xj} = \sum l_x m_x$ [13]. Intrinsic rate of increase was estimated by using the iterative bisection method from the Euler-Lotka formula: $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$ with age indexed from 0 (Goodman, 1982). The life expectancy (e_{xj}) was calculated according to Chi and Su [16]. The mean generation time (T) is defined as the length of time that a population needs to increase to R_0-fold of its size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) as the stable increase rate (the intrinsic rate r and the finite increase rate λ) is reached. The mean generation time is calculated as $T = \ln R_0 / r$. The variances and standard errors of the population parameters were estimated by using the bootstrap procedure [18,19] during the life table analysis by using the TWOSEX-MSChart program [20].

RESULTS

The means and standard errors of the duration of the adult stage, the total longevity and fecundity are given in **Table 1.** Because *T. riqueti* survived less than one week and did not reproduce at 5% salinity, the data for 5% salinity are not listed in **Table 1** and are excluded from the following discussion. At 10°C, the total longevity of *T. riqueti* was only about 10 days and it failed to reproduce at all salinities. At 18°C, the total longevity ranged from 4.1 to 19.8 weeks, and only a few offspring (4) were produced at only one salinity (1%). At 25°C, *T. riqueti* reproduced at most salinities except 0.2% salinity **(Table 1).** An extraordinarily high fecundity (167 offspring) and long adult duration (58 wk) were recorded for the single female that emerged at 25°C and 1.0% salinity. At 30°C, *T. riqueti* reproduced successfully at all salinities. The maximum mean fecundity (79.1 offspring) and the longest mean longevity (39.0 wk) were obtained at 30°C and 2.0% salinity.

Table 1. Duration of the adult stage (the reproductive stage), the total longevity (d: day, w: week) and the fecundity (offspring) of *T. riqueti* at different temperatures and salinities.

1: n_0: total number of individuals used at the beginning of life table study.
2: Standard error cannot be calculated when only one individual survived this stage.
3: Fecundity is calculated by using those individuals that developed to the adult stage.

| Temperature/ Salinity	n_0[1]	Adult stage (d = day, w = week)			Total longevity (d = day, w = week)			Fecundity[3] (offspring)		
		n	Mean	SE[2]	*n*	Mean	SE	*n*	Mean	SE
10°C/0.2%	36	0	-	-	36	10.1 d	0.5	0	-	-
10°C/1.0%	36	0	-	-	36	11.0 d	0.3	0	-	-
10°C/2.0%	36	0	-	-	36	10.9 d	0.2	0	-	-
10°C/2.5%	36	0	-	-	36	10.8 d	0.2	0	-	-
10°C/3.0%	36	0	-	-	36	11.0 d	0.3	0	-	-
10°C/4.0%	36	0	-	-	36	10.8 d	0.3	0	-	-
18°C/0.2%	48	0	-	-	48	4.9 w	0.4	0	-	-
18°C/1.0%	48	1	44 w	-	48	19.8 w	3.3	1	4	-
18°C/2.0%	48	0	-	-	48	14.2 w	2.3	0	-	-
18°C/2.5%	48	0	-	-	48	9.3 w	0.5	0	-	-
18°C/3.0%	48	0	-	-	48	9.1 w	0.7	0	-	-
18°C/4.0%	48	0	-	-	48	4.1 w	0.3	0	-	-
25°C/0.2%	48	0	-	-	48	10.0 w	1.1	0	-	-
25°C/1.0%	48	1	58 w	-	48	14.0 w	2.3	1	167	-
25°C/2.0%	48	10	30.4 w	4.9	48	22.3 w	3.0	10	9.9	2.7
25°C/2.5%	48	5	25.0 w	4.5	48	16.3 w	2.2	5	9.8	3.1
25°C/3.0%	48	7	13.0 w	2.0	48	16.8 w	1.2	7	1.6	0.2
25°C/4.0%	48	3	10.3 w	2.6	48	14.0 w	1.8	3	1.7	0.7
30°C/0.2%	48	9	44.6 w	10.6	48	18.6 w	3.9	9	16.2	4.3
30°C/1.0%	48	29	36.1 w	6.3	48	37.8 w	5.2	29	49.6	11.9
30°C/2.0%	48	47	40.2 w	4.7	48	39.0 w	4.1	47	79.1	13.8
30°C/2.5%	72	31	20.6 w	5.7	72	15.8 w	2.8	31	29.0	10.8
30°C/3.0%	71	25	19.4 w	4.3	71	15.1 w	2.0	25	23.6	8.2
30°C/4.0%	48	7	8.1 w	1.9	48	13.3 w	0.9	7	6.3	1.4
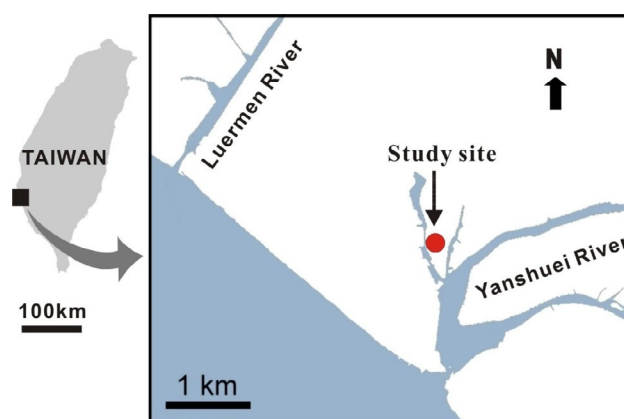
Figure 1. Study site located at the north side of Yanshuei River near the estuary.

The age-stage-specific survival rate (s_{xj}) for the pre-reproductive stage (P) and the female adult (A), and the age-specific fecundity (m_x) of adult *T. riqueti* at 25°C and 30°C are shown in **Figures 2 to 7** for different salinities. The age-stage-specific survival rate (s_{xj}) gives the probability that a newborn will survive to age x and stage j. At 25°C, the first reproduction began within 20 wk for salinities 2.0%, 2.5% and 3.0%. However, at low salinity (1.0%) it was recorded after 50 wk **(Figure 3)** and at high salinity (4.0%) after about 26 wk **(Figure 7)**. At 30°C, reproduction began about 10 weeks after birth and lasted as long as 60 to 120 wk for salinity ranging from 0.2% to 3.0%.

Population parameters at different temperatures and salinities are listed in Table 2. Because *T. riqueti* did not produce offspring at 10°C and 18°C (except 18°C and 1% salinity), no intrinsic rate can be estimated for these temperatures. At 18°C and 1% salinity, the net reproductive rate (R_0) is 0.083 offspring; the intrinsic rate of increase is -0.0218 wk^{-1}. At 25°C and 30°C, *T. riqueti* has a positive intrinsic rate of increase for all salinities, except 25°C/3.0% salinity and 25°C/4% salinity. In comparison to 25°C, life tables at 30°C were characterized by faster individual development, higher intrinsic rate of increase (r) and higher net reproductive rate (R_0). Higher intrinsic rates are found at 30°C with the value 0.1236, 0.1502, 0.1081 and 0.0946 for salinity 1.0%, 2.0%, 2.5% and 3.0%, respectively. The intrinsic rates of increase at 30°C fit a quadratic equation ($R^2 = 0.9552$) **(Figure 8).**
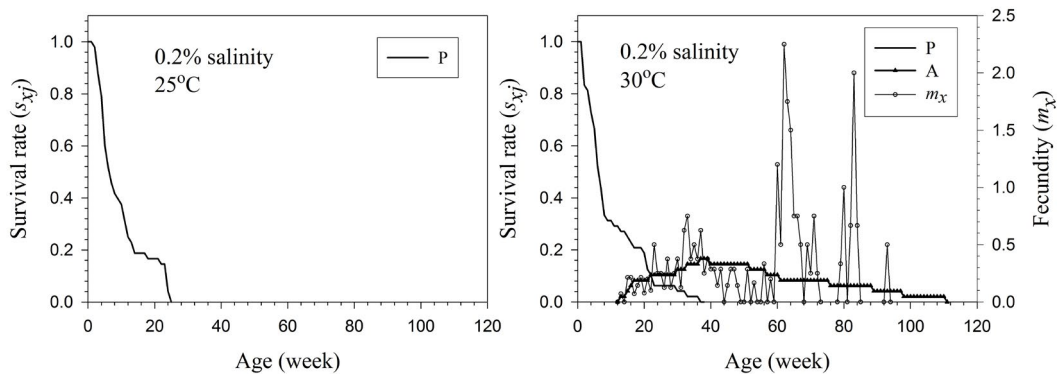

Figure 2. The age-stage survival rate (s_{xj}) of the pre-reproductive stage (P) and the adult stage (A), and the age-specific fecundity (m_x) of *T. riqueti* at 0.2% salinity.
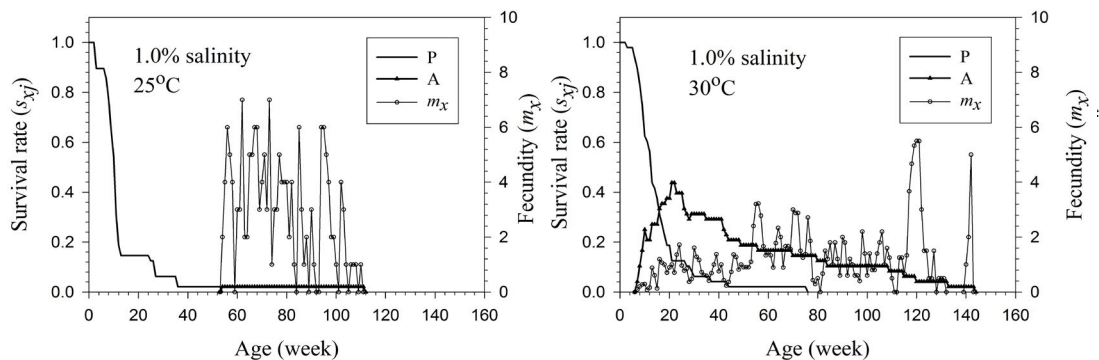

Figure 3. The age-stage survival rate (s_{xj}) of the pre-reproductive stage (P), the adult stage (A), and the age specific fecundity (m_x) of *T. riqueti* at 1.0% salinity.
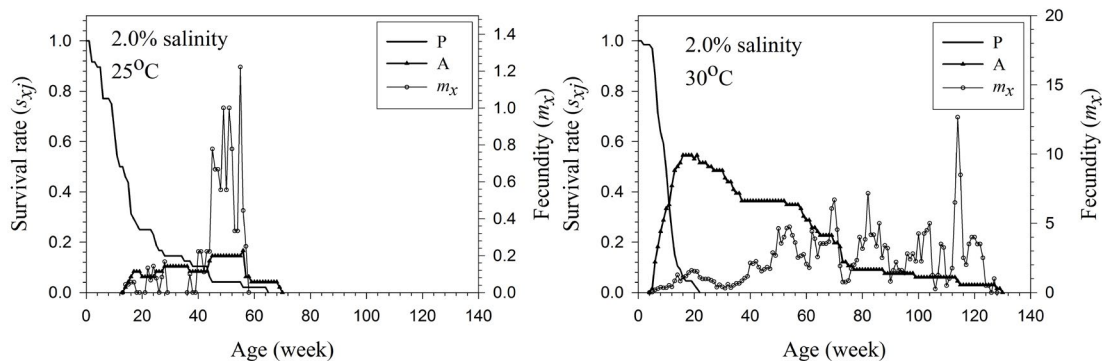

Figure 4. The age-stage survival rate (s_{xj}) of the pre-reproductive stage (P) and the adult stage (A), and the age-specific fecundity (m_x) of *T. riqueti* at 2.0% salinity.

Figure 5. The age-stage survival rate (s_{xj}) of the pre-reproductive stage (P) and the adult stage (A), and the age-specific fecundity (m_x) of *T. riqueti* at 2.5% salinity.
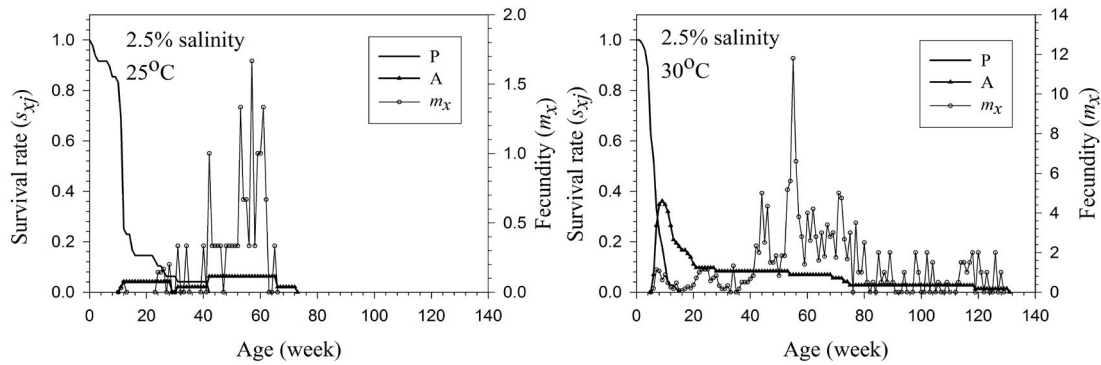

Figure 6. The age-stage survival rate (s_{xj}) of the pre-reproductive stage (P) and the adult stage (A), and the age-specific fecundity (m_x) of *T. riqueti* at 3.0% salinity.

Figure 7. The age-stage survival rate (s_{xj}) of the pre-reproductive stage (P) and the adult stage (A), and the age-specific fecundity (m_x) of *T. riqueti* at 4.0% salinity.
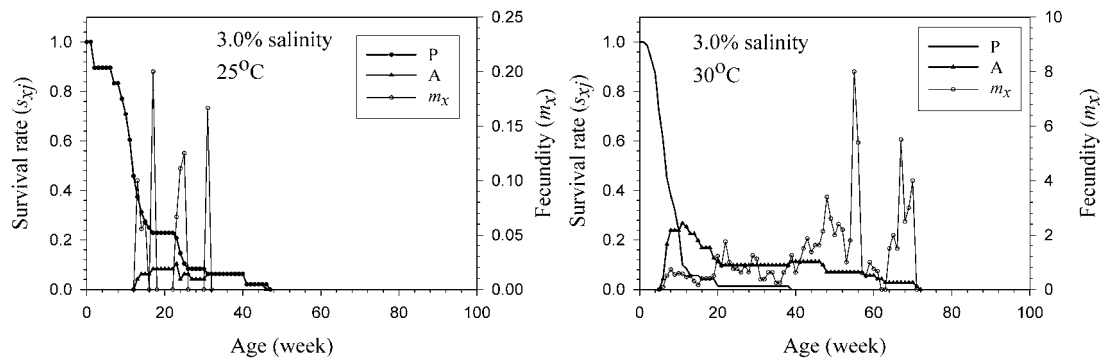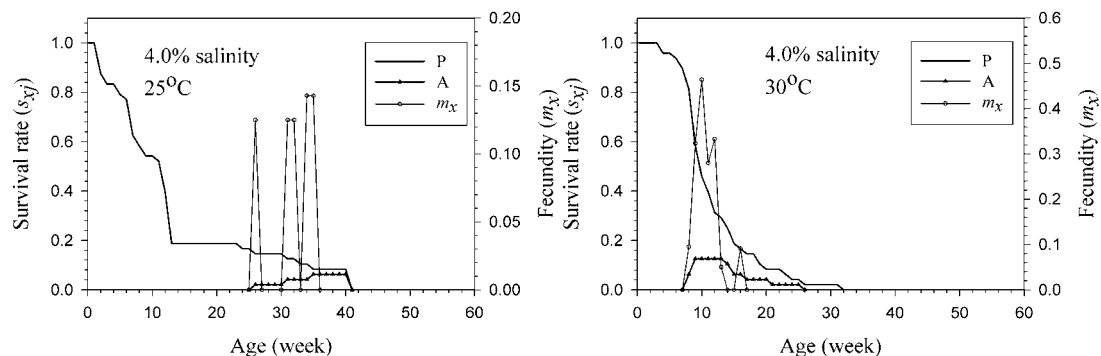

$$y = 0.009 + 0.136x - 0.0353x^2$$
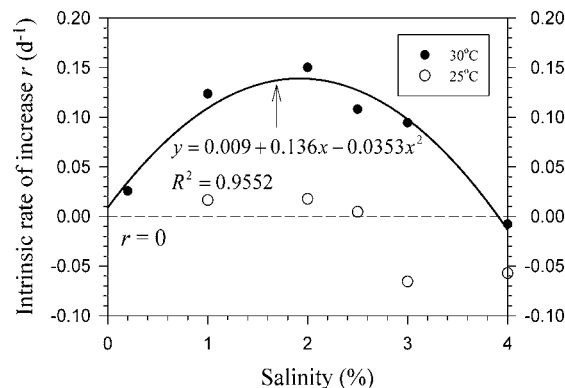$$R^2 = 0.9552$$

Figure 8. The intrinsic rate of increase of *T. riqueti* at 25°C and 30°C and different salinities. Data at 30°C were fitted to a quadratic equation.

DISCUSSION

Life Table

At 10°C and 18°C, the total longevity of *T. riqueti* was short and they did not produce offspring (with a minor exception

occurring at 18ºC /1% salinity), explaining the low density found for this species in winter. However, the longevity at 10ºC and 18ºC was adequate for it to survive the short, mild winter period in Taiwan. At 25ºC and 30ºC, *T. riqueti* survived and produced offspring at most salinity **(Table 1).** These results indicate that *T. riqueti* is euryhaline, and explains why *T. riqueti* is found in estuarine areas. This is consistent with the literature report by Abbott [21] classifying *T. riqueti* as a brackish water species.

Population parameters calculated from life table studies reveal the life-long effect of a variety of factors on the population. They summarize the joint effect of age-specific survival rate and fecundity on population growth. However, the tedious calculation inherent in life table analysis may result in errors in population parameters, and, consequently, affect interpretation. Ferrando et al. [22] studied the effect of the toxicant 3,4-dichloroaniline (DCA) on the freshwater rotifer *Brachionus calyciflorus* and their results showed that $R_0 > 1$ and $r < 0$ for the treatment of 10 ppm DCA (**Figure 3** in Ferrando et al. [22]). According to life table theory, $R_0 > 1$ must always be accompanied with $r > 0$. Thus, it was an obvious error in their results. Nandini and Sarma [23] studied the life table of four cladoceran species in relation to algal food density. In their report, the gross reproductive rate (*GRR*) for *Ceriodaphnia cornuta* is 25.8 eggs/female at food density of 0.5×10^6 cells/ml (**Table 1** in Nandini and Sarma, [23]). Because the *GRR* is the simple summation of the age-specific fecundity (m_x) over all ages, it can be easily estimated from the fecundity curve. According to the fecundity curve (**Figure 1** in Nandini and Sarma [23]), the *GRR* at food density of 0.5×10^6 cells/ml should be obviously much greater than the reported 25.8 eggs/female, indicating that their data may be in error. In our study, negative values of intrinsic rate were obtained at 18ºC/2.0% salinity, 25ºC/3.0% salinity, 25ºC/4.0% salinity, and 30ºC/4.0% salinity **(Table 2).** The respective net reproductive rates (R_0) were all less than one. These results are consistent with the theoretical relationship, i.e., if $R_0 < 1$ then $r <$ 0. Because life table studies are extremely time-consuming, eg, the life table of *T. riqueti* at 30ºC and 2.0% salinity took more than two years, the jackknife method and bootstrap technique have been used to estimate the mean and standard error of population parameters. Huang and Chi [24] proved, however, that the jackknife method should not be used for the estimation of population parameters. A few problems were also noticed in our application of the jackknife method in this study. At 30ºC and 4.0% salinity, the estimated mean of intrinsic rate is 0.0016 d⁻¹, and the mean of the net reproductive rate is 0.92 offspring. Because, according to life table theory that when $R_0 < 1$ r should always be < 0, the results obtained by using the jackknife method for these values are inconsistent with the life table theory. However, when the bootstrap method is used, it yields an intrinsic rate of -0.0077 d⁻¹ and a net reproductive rate of 0.92. The results are then consistent with the life table theory.

Table 2. Population parameters of *T. riqueti* at temperature (25ºC and 30ºC) and salinity (0.2, 1.0, 2.0, 3.0, 4.0%) based on age-stage, two sex life table in the laboratory

Temperature/ Salinity	Intrinsic rate of increase (*r*) (week⁻¹) (jackknife)		Intrinsic rate of increase (*r*) (week⁻¹) (bootstrap)		Net reproductive rate (R_0) (offspring)		Mean generation time (*T*) (week)	
	Mean	**SE***	**Mean**	**SE****	**Mean**	**SE****	**Mean**	**SE****
18ºC/1.0%	-0.0218	-	-0.0218	0.0039	0.083	0.067	114.23	0.04
25ºC/1.0%	0.0164	-	0.0164	0.0060	3.48	2.79	76.14	0.59
25ºC/2.0%	0.0176	0.0090	0.0158	0.0100	2.06	0.78	45.9	4.08
25ºC/2.5%	0.0046	0.0127	0.0004	0.0331	1.02	0.52	50.03	9.62
25ºC/3.0%	-0.0656	0.0184	-0.0695	0.0205	0.23	0.08	21.19	2.42
25ºC/4.0%	-0.0572	0.0299	-0.0687	0.0244	0.10	0.06	32.92	2.18
30ºC/0.2%	0.0275	0.0102	0.0257	0.0108	3.04	1.19	43.25	3.56
30ºC/1.0%	0.1244	0.0107	0.1236	0.0107	29.94	7.91	27.50	2.88
30ºC/2.0%	0.1504	0.0074	0.1502	0.0074	56.30	10.67	26.84	1.41
30ºC/2.5%	0.1091	0.0164	0.1081	0.0164	12.50	4.89	23.36	3.79
30ºC/3.0%	0.0963	0.0178	0.0946	0.0179	8.31	3.14	22.39	2.75
30ºC/4.0%	0.0016	0.0412	-0.0077	0.0434	0.92	0.37	11.26	1.61

*The means and standard errors were estimated by using the jackknife method. When only one female reproduced, standard error cannot be estimated.
** The standard errors were estimated by using the bootstrap technique.

Dudgeon [25] studied the population dynamics of the thiarid *Melanoides tuberculata* (Muller, 1774) and found there was a single peak in juvenile recruitment coinciding with the warmer months in Hong Kong. Dudgeon (1989) reported *T. scabra* is semelparous, parthenogenetic and viviparous. Haynes [27] reported that the thiarid *Fijidoma maculata* (Mousson) reproduced offspring parthenogenetically throughout the year in Fiji. Our results show that *T. riqueti* is iteroparous. Apparently there is abundant variation in reproduction strategy among different species of Thiaridae.

Life tables collected under different environmental conditions are useful for the explanation of field population dynamics. In most ecology textbooks, the intrinsic rate of increase (*r*) is used to describe the characteristics of a population as *r*-selected or *K*-selected. Dudgeon (1982) reported that there were two peaks of recruitment per annum for *Brotia hainanensis* (Brot, 1872). He pointed out that the preadult mortality is high due to severe seasonal spates, and the life cycle of this snail is typical of an *r*-selected species adapted to conditions of high density-independent mortality. Our results show that *T. riqueti* is an *r*-selected species.

Liang [29] built a structured equation model for physiochemical variables of water, benthic invertebrates, and feeding activity

of waterbirds in Sitsao (now named Su-Tsao) wetlands in Taiwan. Because their model is based only on statistical analysis without quantitative equations, its practical application is limited. Incorporation of life tables of benthic invertebrates will certainly help in revealing their population dynamics and biomass production. Raut [30] simulated the population growth of *Achatina fulica* (Gastropoda: Achatinidae) based on a life table and found 100 individuals may potentially give rise to 1.26×10^{12} individuals through successive generation within 2700 days. Such long-term projection of population growth will give meaningful results only when the variability of the life table at different conditions is taken into consideration.

Life tables give the most comprehensive description of the survival, development and reproduction of a population. Without life tables of different environments we cannot properly interpret population dynamics in the wild. However, life table traits vary with many different factors, and it is a very tedious and time-consuming process to collect life table data under all different environmental conditions. Maranhão and Marques [8] found both the duration of embryonic development and the number of juveniles produced per female of *Echinogammarus marinus* Leach (Gammaridae) were significantly affected by temperature. Marques [5] also observed that the fecundity of *Cyathura carinata* (Krøyer) was correlated with female size. Life tables are also important for the study of predator-prey relationships. Weider and Pijanowska [31] conducted life table experiments to study the plasticity of *Daphnia* life histories in response to chemical cues from predators. Walls and Ventelä [32] studied the life history variability in response to temperature and *Chaoborus* exposure in three *Daphnia pulex* clones and found that predator exposure and temperature significantly affected age and size at first reproduction and the total number of offspring in *Daphnia*. For use in the aquaculture of shrimp and fishes, Wang [33] studied the life table of the prey water flea *Moina macrocopa* Straus at different salinity and food conditions. Ahmad [34] studied the optimum feeding rate of the rotifer *Brachionus plicatilis* on the marine alga *Nannochloropsis* sp. using life tables. Garton and Stickle [35] showed that the predation rate of *Thais haemastoma* on oyster spat is sensitive to temperature and salinity. Chi and Yang [36] studied the stage-specific predation rate of the predator ladybird beetle *Propylaea japonica* Thunberg using the life table. These reports show that life tables can be used not only to evaluate the potential of a population in response to different environmental factors, but also to study the predator-prey relationship for aquaculture and other applications. These reports also show, however, that the effects of many factors which play important roles in the life tables of many organisms remain unknown. This is true in *T. riqueti* as well as most other organisms.

Cheung and Lam [37] showed that temperature, salinity and their interactions were significant in affecting the respiration rate of *Nassarius festivus* (Powys, 1835) (Gastropoda: Nassariidae). Berry and Hunt [38] showed that adults and juveniles of *Littorina rudis* (Maton) showed different tolerance to salinity and temperature. The yearly water temperature at Su-Tsao estuary ranged from about 15 to 35 ℃ and the salinity from 0.5 to 4.5%. Our results demonstrate that both temperature and salinity have significant effects on the population dynamics of *T. riqueti*. However, in our study *T. riqueti* was kept at constant salinity and temperature. The effect of fluctuating salinity and temperature on *T. riqueti* deserves further study. Nevertheless, our results possibly explain why the snail population almost disappears during the winter in Su-Tsao estuary when the temperature is low and before the rainy period when the salinity is high. They also explain the high fecundity, pregnancy and population density of *T. riqueti* in summer and fall as well. The optimal temperature and salinity combination observed in the life table study in the laboratory confirms the increase of the snail population during the warm and rainy period in Su-Tsao estuary [4]. The intrinsic rates of increase at 30℃ showed that both low and high salinities have an adverse effect on the *T. riqueti* population.

CONCLUSION

For predicting fluctuations in snail population, not only the life table but also the dispersal, the predation, the competition and other factors are required. For example, Pointier [39] studied the invasion dynamics of the Oriental thiarid snail *Thiara granifera* in the Martinique island, French Antilles and found colonization was faster downstream than upstream. Dudgeon [25] studied the population dynamics and productivity of the thiarid *Melanoides tuberculata* (Muller, 1774) in Hong Kong and indicated that parthenogenicity may enhance the retention of favorable adaptations and ensure a rapid spread through an expanding population. Myers [40] reported that thiarids are parthenogenetic and viviparous, and immature snails released from the adult stay in close proximity to their mothers and rely on passive dispersal for colonization of new habitats. Sexual reproduction, however, has been reported for the thiarid *Melanoides tuberculata* in Israel [41]. Chaniotis et al. [42] reported the presence of males in Puerto Rican *Thiara* (*Tarebia*) *granifera* which was previously thought to be only parthenogenetic. In our study, we did not dissect the snails which did not reproduce to check their sexes. However, because we used the two-sex life table and all individuals were included for the analysis, the uncertainty of parthenogenesis will not affect the analytical results of population parameters. Nevertheless, both the biology and ecology of many thiarids deserve further study. In Hong Kong, Dudgeon [43] reported that mollusks dominated the reservoir benthos and the most encountered gastropods were *Thiara scabra*, *Melanoides tuberculata*, *Sinotaia quadrata* and *Radix plicatulus*. Lai [44] reported the succession of algae and gastropods in autumn of Su-Tsao wetlands and concluded the seasonal variation of dominant benthic algae was controlled not only by water salinity but also by the population of herbivorous gastropods. Macro-invertebrates may play an important role in energy transfer and constitute an important prey for upper trophic levels [39,45]. For successful conservation practices in the future, we strongly recommend the necessity of studying the population dynamics of component species at different trophic levels of a food chain based on the life tables of their member species.

ACKNOWLEDGEMENTS

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