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A DEMOGRAPHIC STUDY OF THE LIFE CYCLE OF *TISBE FURCATA* (BAIRD, 1837) (COPEPODA: HARPACTICOIDA)

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(Figs. 1–4)

The life-cycle of the harpacticoid copepod *Tisbe furcata* (Baird, 1837) at 18 °C was studied quantitatively. Stage durations were determined by two different methods, using synchronous cohorts. Combined nauplius stages last for 80·4 h; the successive copepodite stages take 23·0, 23·2, 28·0 (♀) to 23·2 (♂), 33·4 (♀) to 24·2 (♂) and 48·8 (♀) to 34·7 (♂) h, respectively. Females develop more slowly but more synchronously than males. Age-specific survival and fertility rates were used to calculate the stable stage distribution in an exponentially growing population. From life-table data the following demographic parameters were computed: intrinsic rate of natural increase $r_m = 0{\cdot}233$ day^{-1}; net reproductive rate $R_0 = 94$; minimum generation time $T_{\min} = 14{\cdot}9$ days; parameters related to 'generation time': $T = 19{\cdot}5$ days, $\bar{T} = 16{\cdot}4$ days, $T_c = 25{\cdot}4$ days.

INTRODUCTION

Littoral harpacticoid copepods of the genus *Tisbe* are the object of a fast-growing body of research. As pointed out by Volkmann-Rocco (1971) earlier studies on these organisms suffered from the fact that several different (and only distantly related) species were lumped under the single name of *Tisbe furcata*. Perhaps the commonest of these often misidentified species is *Tisbe holothuriae* Humes, 1957. The latter is now well delimited taxonomically (Humes, 1957; Volkmann-Rocco, 1969, 1972*b*; Volkmann, 1975) and a good deal is already known about its ecology (Fava & Volkmann, 1975), demography (Hoppenheit, 1975*a*, *b*, 1976, 1977, 1978) and ecological genetics (Lazzaretto-Colombera, Fava & Gradenigo-Denes, 1976; Fava, Lazzaretto-Colombera & Cervelli, 1976).

However, *Tisbe* nearly always occurs as multi-species guilds in the field (Fava & Volkmann, 1975, 1977; Bergmans, 1979). Western-European samples such as those of Sars (1911) nearly always contain true *T. furcata* in addition to other congeners (Volkmann, personal communication, 1979). This apparently common species has been recently redescribed (Bergmans, 1979) but no body of information comparable to that on *T. holothuriae* is at present available. So far only a qualitative life-cycle study exists (Johnson & Olson, 1948), and in fact, as will be shown below, it is now evident that this work does not relate to the species *T. furcata*. Although demographic theory is well developed, there are relatively few life-tables for organisms other than man. This is true for marine invertebrates in particular (D'Apolito & Stancyk, 1979). Yet life-tables are the prime source of information on age-specific characteristics and, ultimately, on reproductive strategies. I here report the age-specific mortality and fertility curves of *T. furcata* at 18 °C. They will serve as prolegomena for further research on the demography and reproductive ecology of this species.

MATERIAL AND METHODS

On 24 April 1978 *Ulva* was collected near the border of the Sluice Dock in Ostend and brought to the laboratory. Next day, 40 females obviously about to release their nauplii were isolated in a 100 ml dish for 5 h. Immediately afterwards, all spontaneously released nauplii (no. 115) were isolated in groups of 5 in small covered plastic dishes containing 9 ml of Sluice Dock water (filtered on Millipore 0·8 μm), 1 ml of *Dunaliella* culture and a small fragment of rinsed *Ulva* thallus. The same procedure was repeated the next day ($\geqslant$ 40 females yielding 151 nauplii). Culture conditions were based on standard methods for *Tisbe* (Battaglia, 1970). As previous experience had shown that in glass bowls, copepodites and adults often crept out of the water and died prematurely, I raised my animals in plastic petri dishes with vertical walls where this behaviour virtually did not occur. All dishes were left at 18 °C with natural day and night cycle, and received 1 ml of *Dunaliella* suspension (optical density = 0·1) every second day until adulthood; afterwards the O.D. was no longer controlled but food was always in excess. (An O.D. of 0·1 corresponds to about 16 μg carbon per ml. Vanden Berghe & Bergmans (1981) observed an average carbon requirement of 0·17 μg adult male^{-1} day^{-1} for several species of *Tisbe* feeding on *Dunaliella*, with values of 0·05–0·12 for *T. furcata*. Rieper (1978) estimated 0·07 μg C animal^{-1} day^{-1} assimilated by *T. holothuriae* feeding on bacteria in a similar short-term radioactive labelling experiment.)

For the study of life-cycle parameters the procedure of Parise & Lazzaretto (1966) was adopted Over about 10 days, i.e. the length of the juvenile period, all dishes were checked every sixth (subsequently every twelfth) hour to determine survival, stage transitions and sex. Stages could be distinguished using the criteria of Johnson & Olson (1948), Vilela (1969) and Chua (1975). To ensure timely fertilization, females in the fifth copepodite stage (first cohort only) were transferred singly or by two to other dishes which had received a treatment as similar as possible to their original ones, and containing three adult males derived from the original Sluice Dock sample. Once fertilized they were again transferred singly to new small dishes, and these were checked daily to determine fertility and mortality. Their male siblings were redistributed by two or three upon reaching adulthood, and were also observed until death.

Though originally the dishes were 'clean', in the course of the experiment – after the *Tisbe* had become adults – they all got contaminated by the heterotrophic dinoflagellate *Oxyrrhis marina* Dujard., which developed dense clouds and ended by quickly devouring the *Dunaliella* as soon as it was added to the dishes. That the copepods did not experience any harmful effect from this becomes intelligible in the light of their feeding habits. When offered the choice between bacteria and *Dunaliella*, *T. furcata* obtains its assimilated carbon preferentially from the bacteria (Vanden Berghe & Bergmans, 1981). By the time *Oxyrrhis* appeared a protist film had already developed on the bottom of the dishes. For that matter, George (1976) observed no apparent ill effects of *O. marina* on his cultures of *Microlaophonte* sp. and Huizinga (1971) even claims to have found it among the gut contents of his *Tigriopus californicus*.

RESULTS

Duration of the larval stages

Raw data consist of the number of individuals in each stage observed at a series of discrete points in time. An obvious approach is to plot the observed probability $P(x)$ that an individual of age x has reached or passed each particular stage. If development times are approximately normally distributed, the probability paper plot is a series of straight lines (namely the cumulative transition time distributions). The horizontal distances between successive lines at the level $P = 0{\cdot}5$ estimate the duration of the different stages; the standard deviation of the transition time distributions is inversely proportional to the degree of synchrony of the corresponding transitions. As shown by Fig. 1, the relationship between probit ($P(x)$) and time was indeed approximately linear when 3 resp. 5 lagger-behinds (3 % of each cohort) were excluded from the calculations.

Sharpe *et al.* (1977) have suggested that often developmental rates, rather than development times, would be normally distributed. Expressing transition probabilities as a function of these rates, $P(1/x)$, did not result in improved linearity; therefore the conceptually simpler $P(x)$ relationship was used.

Sexual dimorphism in *Tisbe* is apparent from the 4th copepodite stage on. Thus it was possible to calculate the sex-specific transition time distributions and stage durations for the latter part of the life-cycle (Fig. 2).

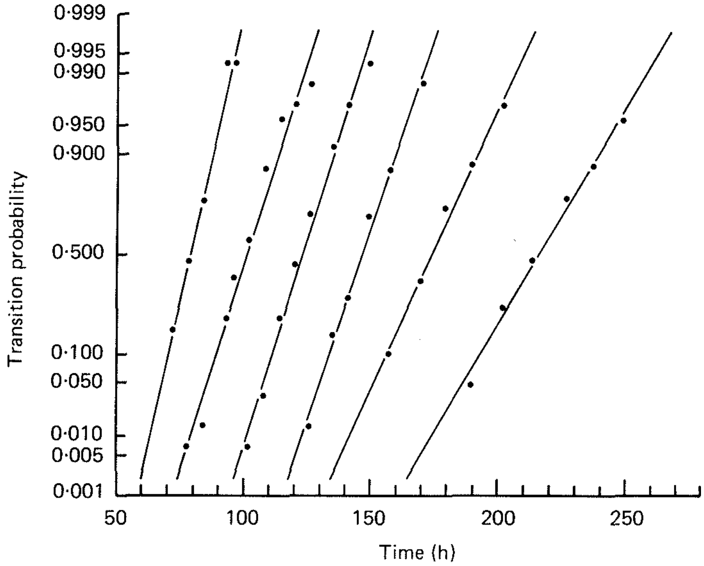

Fig. 1. *Tisbe furcata* (18 °C). Cumulative distributions of transition times between successive ontogenetic stages: nauplii (considered together), five copepodite stages and the adult. (Second cohort.)

Another technique to measure stage durations, which does not require the assumption of normality, was suggested by Nordby & Nordby (1976). They showed that, whatever the form of the transition time distribution,

$$\int_{x=0}^{\infty} \phi_s(x)\,\mathrm{d}x$$

equals the duration of stage s ($\phi_s(x)$ being the probability to be in stage s at age x). This technique was also applied to the data, using graphical integration and including the laggers-behind (Fig. 3). Values obtained by the second method differed from those of the first by only 3 % on the average. Table 1 lists durations and asynchrony values for both cohorts.

Cohort life-table, fecundity table and demographic parameters

Following standard practice, the life-table for female and male *T. furcata* at 18 °C was expressed in terms of l_x = survival probability to age x. As pointed out by Parise (1966), in most cohort studies the fundamental (directly observable) quantity relating

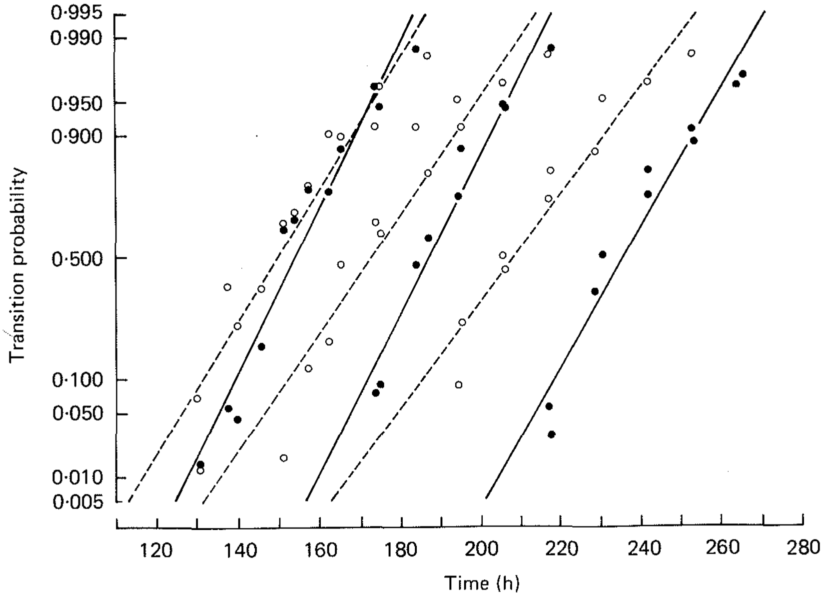

Fig. 2. *Tisbe furcata* (18 °C). Sex-specific cumulative transition time distributions. ○...○, Males; ●—●, females. (Data from first cohort moved forward and those from second cohort moved backward by 4·5 h for better coincidence.)

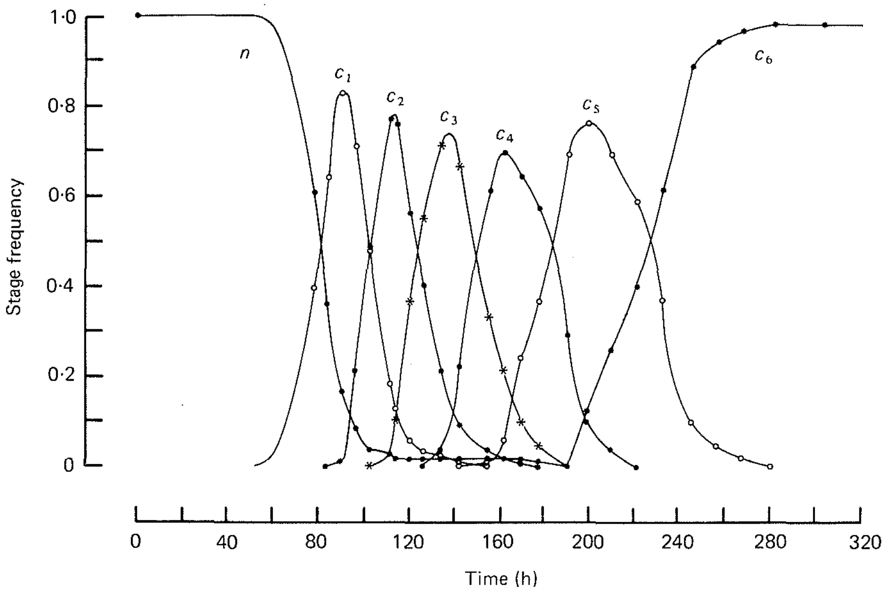

Fig. 3. *Tisbe furcata* (18 °C). Stage frequencies as a function of time (first cohort). For the sake of clarity the slowest individuals are not drawn here, though they were included in the calculations.

Table 1. *Duration (in hours) and asynchrony (s.d. of transition time distribution, in hours) of larval stages in* T. furcata *at* 18 °C

Each cohort was born within a 5 h time span. All values were calculated by the linear regression method, except the average durations for sexes pooled, which include the graphical integration method also.

	Cohort 1			Cohort 2			Grand average		
Stage	Sexes pooled	♀	♂	Sexes pooled	♀	♂	Sexes pooled	♀	♂
n	80·2	—	—	78·5	—	—	80·4	—	—
c_1	25·0	—	—	22·3	—	—	23·0	—	—
c_2	23·0	—	—	22·3	—	—	23·2	—	—
c_3	25·4	28·1	23·6	23·3	28·0	22·9	24·7	28·0	23·2
c_4	29·7	34·6	27·5	27·3	32·2	21·0	28·7	33·4	24·2
c_5	40·6	48·6	32·0	41·9	48·9	37·4	41·5	48·8	34·7
Transition									
$n \to c_1$	9·5	—	—	6·7	—	—	8·1	—	—
$c_1 \to c_2$	8·9	—	—	9·4	—	—	9·2	—	—
$c_2 \to c_3$	12·8	—	—	9·4	—	—	11·1	—	—
$c_3 \to c_4$	12·8	11·0	17·1	10·1	11·7	11·1	11·4	11·3	14·1
$c_4 \to c_5$	13·6	10·3	16·7	13·7	12·5	12·0	13·7	11·4	14·3
$c_5 \to$ ad.	20·3	13·7	20·3	17·8	13·4	12·0	19·1	13·6	16·2

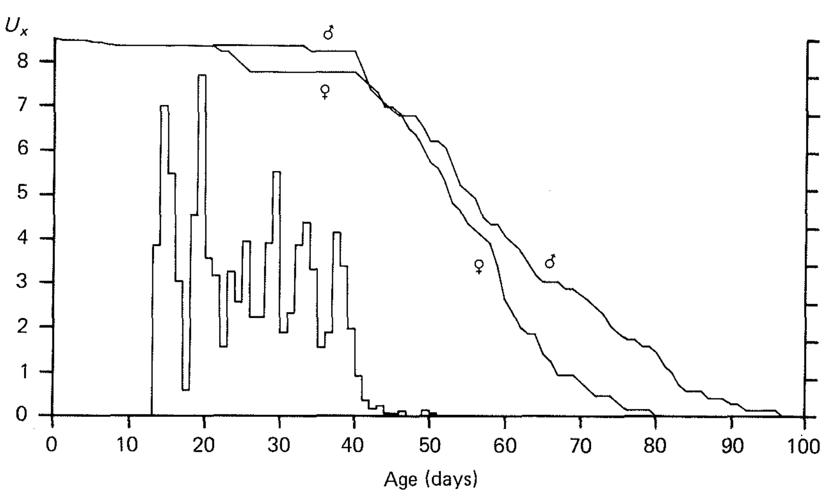

Fig. 4. *Tisbe furcata* (18° C). Age-specific survival (l_x) and fertility (U_x).

to reproduction is not age-specific fecundity m_x but U_x = the number of female newborns produced per female newborn of the preceding generation when that generation is in the age interval $[x, x+1]$. Therefore the use of U_x rather than $m_x = U_x/l_x$ was adopted here. U_x was obtained by taking the average number of nauplii harvested after $[x, x+1]$ per mother, correcting for sex ratio and survival to adulthood (assuming these to be constant across generations) and dividing by $l_1/2$ to allow for naupliar mortality prior to harvesting. U_x and l_x schedules are presented in Fig. 4.

The *intrinsic rate of natural increase*, r, is the solution of the well-known (discretized) Lotka equation

$$\sum_{x=0}^{\infty} U_x e^{-rx} = 1.$$

When solved by iteration, it was found that $r = 0{\cdot}233$ for *T. furcata* at 18 °C. The net reproductive rate is

$$R_0 = \sum_{x=0}^{\infty} U_x = 94{\cdot}0.$$

It is the factor by which the female population is multiplied from one generation to the next. *Minimum generation time*, i.e. the time elapsing between birth and the deposition of the first batch of offspring, was found to be 14·9 days. *Mean generation time* (in days) is defined by $T = \ln R_0/r = 19{\cdot}5$. The age of the mother of an average newborn in an exponentially growing population is

$$\bar{T} = \sum_{x=0}^{\infty} (x+0{\cdot}5)\, U_x e^{-rx} = 16{\cdot}4.$$

Finally, the average age of a mother at reproduction, or *cohort generation time*, equals

$$T_c = \frac{1}{R_0} \sum_{x=0}^{\infty} (x+0{\cdot}5)\, U_x = 25{\cdot}4.$$

(The 0·5 in the last two formulae is a correction for grouping by 1-day intervals.)

Stable stage age-distribution

The *stable age-distribution* is that age distribution towards which a population growing according to fixed mortality and fecundity schedules will tend, irrespective of its original composition. It is determined by the age-specific survival probabilities l_x and by the fact that the population is growing at the finite rate $\lambda = e^r$: hence, using a discrete approximation, the proportion of animals of age between a and b is

$$\sum_{x=a}^{b} L_x \lambda^{-x} \Big/ \sum_{x=0}^{\infty} L_x \lambda^{-x},$$

where $L_x = (l_x + l_{x+1})/2$, and a and b take discrete entire values (Pielou, 1977, p. 47).

Age is not a directly observable parameter in *Tisbe*, but the age distribution can be converted into a stage distribution by splitting some of the terms in the numerator of the above formula, using the average stage transition times as boundaries. Table 2 lists the *stable stage distributions* thus obtained.

Table 2. *Relative stage frequency in the stable age distribution of an exponentially growing population of* T. furcata *at* 18 °*C*

	n	c_1	c_2	c_3	c_4	c_5	c_6
Females	54·1	9·3	7·4	6·9	6·2	6·1	9·9
Males	54·1	9·3	7·4	5·9	4·9	5·2	13·1

DISCUSSION

Duration of the larval stages

Data on the duration of the larval stages in harpacticoids are scanty. The few relevant observations have often been derived from too small a number of animals, and as it is never stated how the reported values were actually calculated, they are probably best considered rough estimates (Feller, 1980, being a notable exception). To make matters worse, some authors have failed to distinguish between successive stages. In spite of (mostly old) reports to the contrary, all harpacticoids probably have six naupliar and six copepodite stages (including the adult) – see especially Sarvala (1977, Discussion). Nevertheless, Huizinga (1971) managed to find only four nauplii and four copepodites in *Tigriopus californicus*. Only five naupliar stages are mentioned for *Harpacticus littoralis* (Castel, 1976), *Tigriopus brevicornis* (Fraser, 1936; Harris, 1973 – but see Itô, 1970, on its congener *T. japonicus*) and even *Tisbe holothuriae* (Hoppenheit, 1975*a*, *b* – but see Johnson & Olson, 1948; Battaglia, 1957; Battaglia & Talamini, 1957; Vilela, 1969; Chua, 1975; Lopez, 1980, on six other species of the genus).

Table 3, then, lists the available stage-duration data. It appears that, but for the very first and very last larval stages, *Euterpina acutifrons* conforms quite well to the concept of *isochronal development* (equal duration for every stage) as defined by Miller, Johnson & Heinle (1977) for species of the calanoid genus *Acartia*. The other harpacticoids in Table 3, including *T. furcata*, tend to a progressively increasing duration of the later stages. Miller *et al.* (1977) interpreted the observed patterns of stage-duration as an evolutionary response to differential, stage-specific mortality. If their hypothesis is correct, isochronal development may be but one particular type among the various possibilities created by the interaction of mortality schedules and developmental constraints. In that case, copepods should not in general be expected to conform to 'regular' ontogenetic patterns (such as constant or, say, linearly increasing stage durations).

Coull & Dudley (1976) presented suggestive evidence that some harpacticoid species are able to extend the duration of the early naupliar stages. Though they claimed that delayed naupliar development has not been found in epiphytic and semi-pelagic forms, prolonged n_1 stages have been reported in *Euterpina acutifrons* (Haq, 1972), *Tigriopus brevicornis* (Fraser, 1936) and *T. californicus* (Shaw, 1938, quoted in Haq, 1972; both species were referred to as *T. fulvus*). On the other hand, they did quote a study by Smol & Heip (1974) who claimed that the relative duration of the naupliar stages increases with temperature in *Tachidius discipes*. The latter authors noted that *T. discipes* is subject to higher predation intensity at higher temperatures, and – like Miller *et al.* (1977) – explained the change in relative duration as an anti-predatory strategy protecting the most vulnerable stages, namely the copepodites. Unfortunately, this attractive hypothesis is belied by the data (table 3 in Smol & Heip, 1974), which demonstrate that ratios of naupliar to embryonic resp. to copepodite time-spans *decrease* with increasing temperature.

Thus it is clear that more detailed and more consistent knowledge must be acquired before the fascinating problem of relative stage duration will satisfactorily be settled. A point of major importance in assessing the strategic significance of delayed naupliar

Table 3. *Published data on larval stage duration (in days) in harpacticoid copepods*

	n_1	n_2	n_3	n_4	n_5	n_6	c_1	c_2	c_3	c_4	c_5
Euterpina acutifrons, 18 °C (Neunes & Pongolini, 1965)	1·8	1·4	1·3	1·5	1·5	1·0	1·6	1·7	1·9	1·6	2·2
E. acutifrons, 16 °C* (Haq, 1972)	2	1	1·1	1·1	1·1	1·0	1·1	1·0	1·0	1·7† 1·4 1·4	1·9† 1·8 1·3
Harpacticus littoralis, 15 °C (Castel, 1976)	1–2	1–2	2	2	2						
Tigriopus brevicornis‡§ (Fraser, 1936)	3–7	1	1–2	2–3	3		2–5	7	7–10	7–10	14
	← 15 →										
T. brevicornis, 15 °C (Harris, 1973)	1·5	1·5	1	1	2·5		2	2	2	3	7
Tisbe furcata, 18 °C (this paper)	← 3·4 →						1·0	1·0	1·2‖ 1·0	1·4‖ 1·0	2·0‖ 1·4
Arenopontia indica§ (Rao, 1967)	2	1–2	1–2	2	2–3	3–4	2	2	3	3–4	5‖ 7
Huntemannia jadensis, 8 °C (Feller, 1980)	← 37·6 →						9·6	7·6	8·4	8·4	11·9

* Approximate values read off fig. 2 in Haq (1972).
† Values referring to females, 'large males' and 'small males', respectively.
‡ Species called *T. fulvus* by Fraser (1936).
§ Temperature not controlled.
‖ Values referring to females and males, respectively.

development is the fitness of individuals displaying it. Neither Coull & Dudley, nor Smol & Heip comment on the fate of the slow developers. Haq (1972) states that 'individuals in which moulting was delayed for a considerable time failed to survive'. (In my present cohorts extreme delay of development did not occur. Only two individuals were still nauplii after 7 days; one of them died as a c_2 15 days after hatching, the other became an adult male after 21 days.)

In *Tisbe furcata*, males need less time to complete larval development than females (Table 1). Similar observations – or inferences – have been made on *Euterpina acutifrons* (Haq, 1972; Zurlini, Ferrari & Nassogne, 1978), *Harpacticus uniremis* (Jewett & Feder, 1977), *Tisbe reticulata* (Bocquet, 1951), *Platychelipus littoralis* and *P. laophontoides* (Barnett, 1970). There is a conflicting report on *Arenopontia indica* by Rao (1967). The greater speed of male development has been linked by some authors to the almost certainly erroneous suggestion that females are fertilized in the fifth copepodite stage (a suggestion stemming from the fact that in many genera, but not *Tisbe*, adult males 'ride' or 'mount' female copepodites). Rather, the shorter duration as well as the lesser synchrony of male development may be an evolutionary response to competition for mates. Other conceivable explanations include promotion of outbreeding and ensurance of timely fertilization. None of these are mutually exclusive, but the latter may require a colonizing situation (as perhaps exemplified by the findings of Hauspie & Polk, 1973).

Life tables and population structure

Graphical life-tables of the form of Fig. 4 have been published for the following *Tisbe* species, all under the same culture conditions: *T. holothuriae* (referred to as *T. furcata*: Parise & Lazzaretto, 1966; Parise, 1978), *T. reluctans* and *T. persimilis* (Volkmann-Rocco & Fava, 1969), *T. dobzhanskii* (Volkmann-Rocco & Battaglia, 1972), *T. clodiensis* (Volkmann-Rocco & Battaglia, 1972; Lazzaretto-Colombera & Polo, 1969).

Apart from these studies, the only copepod life-tables published are those of the freshwater calanoid *Diaptomus clavipes* (Gehrs & Robertson, 1975) and two marine harpacticoids: the pelagic species *Euterpina acutifrons* (D'Apolito & Stancyk, 1979) and the burrowing *Huntemannia jadensis* (Feller, 1980). The former two are stage- instead of age-related life-tables, and none includes age-specific fecundity measures. Survivorship curves are of the same general form in *Tisbe* and *Diaptomus*, namely a period of larval and one of senile mortality, separated by an adult phase suffering no mortality. The *Tisbe* curves are collectively distinguished from that of *Diaptomus* by the relative magnitude of the two mortality phases: in the laboratory only 22·5% of the *Diaptomus* reach the adult stage; this figure was about 60% for *T. reluctans* and *T. persimilis* (in conditions that may have been suboptimal) and 80–95% for the other *Tisbe* (see Table 4). The *Huntemannia* and *Euterpina* survival curves lack a 'shoulder' corresponding to the adult stage. In *Huntemannia*, survival to adulthood reached about 30% at 8 °C. For *Euterpina*, a survival rate of 61% can be re-calculated from gross fertility, R_0 and sex ratio data in Zurlini *et al.* (1978); however, all attempts to measure survival directly have yielded much lower values: 42% (Haq, 1972), 24% (Neunes & Pongolini, 1965), 4% (D'Apolito & Stancyk, 1979) were optima in the laboratory.

It must be borne in mind that, as a result of predation and competition, survival rates

Table 4. *Demographic parameters of* Tisbe *sp. and* Euterpina acutifrons

Species	R_0	r_m	r_c	T	T_c	$T_{\min}$	Survival of nauplii to adulthood	%♀♀	References
Tisbe furcata (Ostend)	94	0·233	0·179	19·5	25·4	14·9	0·98	47	Present work
T. clodiensis (Venice)*									
PP	92	0·215	0·188	21·0	24·1	15·6	0·81	51	Lazzaretto-Colombera & Polo (1969)
Pp	167	0·250	0·204	20·5	25·1	14·8	0·83	47	
pp	99	0·221	0·188	20·8	24·4	15·2	0·81	48	
(Anzio)	55	0·187	0·173	21·4	23·1	17·0	0·84	41	Volkmann-Rocco & Battaglia (1972)
T. dobzhanskii (Anzio)	124	0·291	0·233	16·6	20·7	13·0	0·89	41–43	Volkmann-Rocco & Battaglia (1972)
T. reluctans (Chioggia)	58	—	0·102	—	39·8	26·1	0·56	46	Volkmann-Rocco & Fava (1969)
T. persimilis (Malta)	32	—	0·088	—	39·0	26·1	0·60	41	Volkmann-Rocco & Fava (1969)
T. holothuriae									
(Various origins)	86–187, mean 140	0·270–0·319, mean 0·293	0·254–0·282, mean 0·268	15·9–18·0, mean 16·8	17·5–19·0, mean 18·4	11·2–11·9, mean 11·5	0·77–0·95, mean 0·87	32–63, mean 49	Parise & Lazzaretto (1966), Battaglia & Parise (1967), Lazzaretto & Parise (1967), Lazzaretto-Colombera (1970), Braioni & Parise (1971), Parise (personal communication, 1975), Gaudy & Guérin (1977)†
(Banyuls & Sigean)	231–340, mean 279	—		—	20·5–20·8, mean 20·7				Battaglia (1970), Lazzaretto-Colombera *et al.* (1976)
Euterpina acutifrons (Ligurian Sea)	71	0·161		26·5				40‡	Zurlini *et al.* 1978§

* Different genotypes of this polychromatic species.

† Much lower R_0 and r_c reported by Gaudy & Guérin (1978) were not included. Additional survival data from Fava *et al.* (1976) and Hoppenheit (1976); additional sex-ratio data from Battaglia (1962), Volkmann-Rocco (1972*a*) and Hoppenheit (1976). Values of time-related parameters obtained by Gaudy & Guérin (1977) and Rieper (1978) were not included because these authors worked at 19 °C and 38 ppm and 18 °C and 28–30 ppm, respectively – small differences from standard conditions which are nevertheless sufficient to cause deviations of the observed magnitude in time parameters (judging from studies by Parise & Lazzaretto, 1966; Battaglia & Parise, 1967; Parise, personal communication, 1975; and Lazzaretto-Colombera, 1970, respectively).

‡ Corrected value, personal communication, 1980.

§ Less successful breeding experiments yielded slightly longer development times (Neunes & Pongolini, 1965) and drastically lower survival rates (Neunes & Pongolini, 1965; Haq, 1972).

in the field are often much lower than those observed in the laboratory (Gehrs & Robertson, 1975; D'Apolito & Stancyk, 1979).

The present paper is the first to present a stable stage distribution for an exponentially growing copepod population, so that direct comparisons with other species cannot at present be made. Neither are there empirical data available on *T. furcata* population structure. Hoppenheit (1975*b*) observed how in *T. holothuriae*, the proportion of nauplii rose from 58% to 68% in populations exploited at increasing rates (10% to 90% of the population harvested weekly). Such a shift towards younger ages is a purely passive phenomenon accompanying increasing growth rates, as can easily be seen from the method to compute the stable age distribution. There remains the possibility of a synergistic direct effect of density on naupliar mortality, less-intense exploitation leading to higher population densities and nauplii being more sensitive than adults to crowding (some evidence for this in Hoppenheit, 1977). Neither of these explanations justifies the use of increased naupliar frequency as evidence for an *r*-strategy, as by Hoppenheit (1978, pp. 295, 296).

Demographic parameters

The existing literature on harpacticoid demography suffers from terminological confusion as well as biased estimates of certain parameters. This matter will be considered elsewhere (Bergmans, in preparation). It is a fortunate circumstance that papers such as Parise & Lazzaretto (1966) and Parise (1978) are among the very few where calculations have a sound demographic basis.

Table 4 lists the values obtained under standard conditions: 18 °C and salinities of 33–36 ppm. (Gaudy & Guérin (1977) presented a similar if less-complete literature review into which, unfortunately, some errors have slipped: some 'longevity' values quoted were determined starting from birth, others from the beginning of adulthood; some 'numbers of eggs per sac' are actually numbers of nauplii per sac; some r_m are actually $r_c = \ln R_0/T_c$; and sex-ratio was incorrectly inferred from Parise & Lazzaretto's (1966) data.)

Survival rates from nauplius to adult and sex ratios among newly adults (Table 4) were obtained from batches of newborns at somewhat different densities. These values are to be interpreted with some caution, e.g. survival rates are sensitive to differences in the age at which the nauplii are isolated (cf. Neunes & Pongolini, 1965; Lazzaretto-Colombera, 1970). Also, the exceptionally high survival probability in *T. furcata* may stem from the fact that my animals grew up in groups of five in small vessels; other authors used batches of up to 100 in larger vessels. Concerning sex ratio, it must be remembered that sex determination in harpacticoids is not yet completely understood. Ginsburger-Vogel (1975) has reviewed relevant research on the genus *Tigriopus*. In *Tisbe*, sex determination is known to be genetic (Battaglia, 1961; Battaglia & Malesani, 1962; Scudo, 1967) and sensitive both to degree of inbreeding (Battaglia, 1958; Lazzaretto-Colombera *et al.* 1976) and time of fertilization (Volkmann-Rocco, 1972*a*).

All data in Table 4 other than survival and sex ratio are derived from females isolated singly. For *T. holothuriae*, which is a popular experimental animal, the values reported are the extremes and mean of published estimates, not weighted for sample size. The data on the Banyuls and Sigean populations have been separated from the remaining ones because, like my own *T. furcata* data, they were determined using the F_1 offspring of wild-caught animals. This may reflect itself in a much higher R_0 and correspondingly longer T_c. (All other data in Table 4 refer to laboratory-adapted populations.)

Of particular interest are the older reports where the life-cycle data quoted may assist in a re-identification (see Introduction) of the *Tisbe* material used. Lwoff (1927) published a thorough and important study on pigmentary physiology in '*T. furcata*'. His statement that 'la durée totale du cycle' ($= T_{\text{min}}$) 'dure environ 10 jours à 17°' seems to confirm my earlier surmise (Bergmans, 1979) that he was dealing with a species of the *holothuriae* group – this surmise being based on the commonness of *T. holothuriae* as a contaminant of sea-water aquaria and on the fact that Lwoff studying pigment metabolism could hardly have overlooked the real *furcata*'s striking colour pattern.

Johnson & Olson's (1948) paper on the life-cycle of '*T. furcata*' has become a standard reference; their observation that T_{min} is 19–24 days at 17–18 °C, however, all but rules out the possibility that their material was true *T. furcata*. The evidence from my present life-cycle study thus supports the view (Monk, 1941; Volkmann-Rocco, 1971) that '*T. furcata* var. *johnsoni*' and *T. furcata* are distinct species.

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REFERENCES

Barnett, P. R. O., 1970. The life cycles of two species of *Platychelipus* Brady (Harpacticoida) on an intertidal mudflat. *Internationale Revue der gesamten Hydrobiologie*, **55**, 169–195.

Battaglia, B., 1957. Ricerche sul ciclo biologico di *Tisbe gracilis* (T. Scott), (Copepoda, Harpacticoida), studiato in condizioni di laboratorio. *Archivio di Oceanografia e Limnologia*, **11**, 29–46.

Battaglia, B., 1958. Selezione e rapporto dei sessi nel Copepode Harpacticoide *Tisbe gracilis* (T. Scott). *Atti della Accademia nazionale dei Lincei, Rendiconti*, **24**, 327–335.

Battaglia, B., 1961. Rapporti tra geni per la pigmentazione e la sessualità in *Tisbe reticulata*. *Atti della Associazione genetica italiana*, **6**, 439–447.

Battaglia, B., 1962. Controllo genetico della velocità di sviluppo in popolazioni geografiche del copepode marino *Tisbe furcata* (Baird). Nota preliminare. *Atti dell' Istituto veneto di scienze, lettere ed arti*, **120**, 83–91.

Battaglia, B., 1970. Cultivation of marine copepods for genetic and evolutionary research. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **20**, 385–392.

Battaglia, B. & Malesani, L., 1962. Gli effetti della selezione operata in assenza di inincrocio sugli spostamenti del rapporto-sessi in *Tisbe gracilis* (Copepoda, Harpacticoida). *Atti della Accademia nazionale dei Lincei, Rendiconti*, **32**, 251–257.

Battaglia, B. & Parise, A., 1967. Ricerche sulla 'fitness' in razze geografiche del Copepode *Tisbe furcata* (Baird) (Harpacticoida). *Bollettino di zoologia*, **34**, 88–89.

Battaglia, B. & Talamini, P., 1957. Osservazioni sullo sviluppo larvale di *Tisbe reticulata* Bocquet (Copepoda, Harpacticoida). *Archivio di Oceanografia e Limnologia*, **11**, 63–68.

Bergmans, M., 1979. Taxonomic notes on species of *Tisbe* (Copepoda, Harpacticoida) from a Belgian sluice dock. *Zoologica Scripta*, **8**, 211–220.

Bocquet, C., 1951. Recherches sur *Tisbe* (= *Idyaea*) *reticulata*, n.sp. Essai d'analyse génétique du polychromatisme d'un Copépode Harpacticoïde. *Archives de zoologie expérimentale et générale*, **87**, 335–416.

BRAIONI, G. M. & PARISE, A., 1971. Affollamento e dinamica di popolazioni di *Tisbe* (Copepoda, Harpacticoida). *Bollettino di zoologia*, **38**, 500–501.

CASTEL, J., 1976. Développement larvaire et biologie de *Harpacticus littoralis* Sars 1910 (Copépode, Harpacticoïde) dans les étangs saumâtres de la région d'Arcachon. *Cahiers de biologie marine*, **17**, 195–212.

CHUA, T.-E., 1975. The developmental stages of *Tisbe longisetosa* Gurney, 1927 (Copepoda, Harpacticoida). *Crustaceana*, **28**, 158–167.

COULL, B. C. & DUDLEY, B. W., 1976. Delayed naupliar development of meiobenthic copepods. *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass.*, **150**, 38–46.

D'APOLITO, L. M. & STANCYK, S. E., 1979. Population dynamics of *Euterpina acutifrons* (Copepoda: Harpacticoida) from North Inlet, South Carolina, with reference to dimorphic males. *Marine Biology*, **54**, 251–260.

FAVA, G., LAZZARETTO-COLOMBERA, I. & CERVELLI, M. (1976). Carico genetico in *Tisbe* (Copepoda, Harpacticoida). II. *T. holothuriae* e *T. bulbisetosa* della laguna di Venezia. *Atti dell' Accademia nazionale dei Lincei. Rendiconti*, **60**, 699–708.

FAVA, G. & VOLKMANN, B., 1975. *Tisbe* (Copepoda: Harpacticoida) species from the lagoon of Venice. I. Seasonal fluctuations and ecology. *Marine Biology*, **30**, 151–165.

FAVA, G. & VOLKMANN, B., 1977. *Tisbe* (Copepoda, Harpacticoida) species from the estuarine embayment of Scardovari. *Archivio di Oceanografia e Limnologia*, **19**, 55–64.

FELLER, R. J., 1980. Development of the sand-dwelling meiobenthic harpacticoid copepod *Huntemannia jadensis* Poppe in the laboratory. *Journal of Experimental Marine Biology and Ecology*, **46**, 1–15.

FRASER, J. H., 1936. The occurrence, ecology and life history of *Tigriopus fulvus* (Fischer.) *Journal of the Marine Biological Association of the United Kingdom*, **20**, 523–536.

GAUDY, R. & GUÉRIN, J.-P., 1977. Dynamique des populations de *Tisbe holothuriae* (Crustacea: Copepoda) en élevage sur trois régimes artificiels différents. *Marine Biology*, **39**, 137–145.

GAUDY, R. & GUÉRIN, J.-P. 1978. Étude expérimentale de la respiration, de la croissance et de la fécondité de *Tisbe holothuriae* (Copépode: Harpacticoïde) élevé à des températures différentes. In *Physiology and Behaviour of Marine Organisms*. Proceedings of the 12th European Symposium on Marine Biology, Stirling, Scotland, 1977 (ed. D. S. McLusky and A. J. Berry), pp. 31–38. Pergamon Press.

GEHRS, C. W. & ROBERTSON, A., 1975. Use of life tables in analyzing the dynamics of copepod populations. *Ecology*, **56**, 665–672.

GEORGE, J. D., 1976. The culture of benthic polychaetes and harpacticoid copepods on agar. In *Research in Mariculture at Laboratory and Pilot Scale*, vol. 1. Proceedings of the 10th European Symposium on Marine Biology, Ostend, Belgium, 1975 (ed. G. Persoone and E. Jaspers), pp. 143–159. Wetteren, Belgium: Universa Press.

GINSBURGER-VOGEL, T., 1975. Température et différenciation sexuelle chez les crustacés. *Bulletin de la Société zoologique de France*, **100**, 95–115.

HAQ, S. M., 1972. Breeding of *Euterpina acutifrons*, a harpacticid copepod, with special reference to dimorphic males. *Marine Biology*, **15**, 221–235.

HARRIS, R. P., 1973. Feeding, growth, reproduction and nitrogen utilization by the harpacticoid copepod, *Tigriopus brevicornis*. *Journal of the Marine Biological Association of the United Kingdom*, **53**, 785–800.

HAUSPIE, R. & POLK, P., 1973. Swimming behaviour patterns in certain benthic harpacticoids (Copepoda). *Crustaceana*, **25**, 95–103.

HOPPENHEIT, M., 1975*a*. Zur Dynamik exploitierter Populationen von *Tisbe holothuriae* (Copepoda, Harpacticoida). I. Methoden, Verlauf der Populationsentwicklung und Einfluss der Wassererneuerung. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **27**, 235–253.

HOPPENHEIT, M., 1975*b*. Zur Dynamik exploitierter Populationen von *Tisbe holothuriae* (Copepoda, Harpacticoida). II. Populationsdichte, Alterszusammensetzung, Wachstum und Ausbeute. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **27**, 377–395.

HOPPENHEIT, M., 1976. Zur Dynamik exploitierter Populationen von *Tisbe holothuriae* (Copepoda, Harpacticoida). III. Reproduktion, Geschlechtsverhältnis, Entwicklungsdauer und Überlebenszeit. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **28**, 109–137.

HOPPENHEIT, M., 1977. On the dynamics of exploited populations of *Tisbe holothuriae* (Copepoda, Harpacticoida). V. The toxicity of cadmium: Response to sub-lethal exposure. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **29**, 503–523.

HOPPENHEIT, M., 1978. On the dynamics of exploited populations of *Tisbe holothuriae* (Copepoda, Harpacticoida). VI. Response to perturbation by temporarily elevated mortality. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **31**, 285–297.

HUIZINGA, H. W., 1971. Cultivation, life history and salinity tolerance of the tidepool copepod, *Tigriopus californicus* Baker 1912, in artificial sea water. *Transactions of the Illinois State Academy of Science*, **64**, 230–236.

HUMES, A. G., 1957. Deux copépodes harpacticoïdes nouveaux du genre *Tisbe*, parasites des holothuries de la Méditerranée. *Vie et milieu*, **8**, 9–22.

ITÔ, T., 1970. The biology of a harpacticoid copepod, *Tigriopus japonicus* Mori. *Journal of the Faculty of Science, Hokkaido University* (Zoology), **17**, 474–500.

JEWETT, S. C. & FEDER, H. M., 1977. Biology of the harpacticoid copepod, *Harpacticus uniremis* Kröyer on Dayville Flats, Port Valdez, Alaska. *Ophelia*, **16**, 111–129.

JOHNSON, M. W. & OLSON, J. B., 1948. The life history and biology of a marine harpacticoid copepod, *Tisbe furcata* (Baird). *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass.*, **95**, 320–332.

LAZZARETTO, I. & PARISE, A., 1967. Effetto dell' inincrocio protratto su alcuni parametri di popolazione in *Tisbe furcata* (Baird) (Copepoda Harpacticoida). *Bollettino di zoologia*, **34**, 128–129.

LAZZARETTO-COLOMBERA, I., 1970. Effetti della diluizione su alcuni parametri di popolazione in razze geografiche del copepode *Tisbe holothuriae* Humes (Harpacticoida). *Archivio di Oceanografia e Limnologia*, **16**, 263–274.

LAZZARETTO-COLOMBERA, I., FAVA, G. & GRADENIGO-DENES, M., 1976. Carico genetico in *Tisbe* (Copepoda, Harpacticoida). I. *Tisbe holothuriae* di due popolazioni del Mediterraneo occidentale. *Atti dell' Accademia nazionale dei Lincei. Rendiconti*, **60**, 691–698.

LAZZARETTO-COLOMBERA, I. & POLO, G., 1969. Polimorfismo e superiorità degli eterozigoti nel copepode harpacticoide *Tisbe clodiensis*. *Atti dell' Istituto veneto di scienze, lettere ed arti*, **127**, 383–392.

LOPEZ, G. W., 1980. Description of the larval stages of *Tisbe cucumariae* (Copepoda: Harpacticoida) and comparative development within the genus *Tisbe*. *Marine Biology*, **57**, 61–71.

LWOFF, A., 1927. Le cycle du pigment carotinoïde chez *Idya furcata* (Baird) (Copépode harpacticide). Nature, origine, évolution du pigment et des réserves ovulaires au cours de la segmentation. Structure de l'oeil chez les Copépodes. *Bulletin biologique de la France et de la Belgique*, **61**, 193–240.

MILLER, C. B., JOHNSON, J. K. & HEINLE, D. R., 1977. Growth rules in the marine copepod genus *Acartia*. *Limnology and Oceanography*, **22**, 326–335.

MONK, C. R., 1941. Marine harpacticoid copepods from California. *Transactions of the American Microscopical Society*, **60**, 75–99.

NEUNES, H. W. & PONGOLINI, G.-F., 1965. Breeding a pelagic copepod, *Euterpina acutifrons* (Dana), in the laboratory. *Nature, London*, **208**, 571–573.

NORDBY, Ø. & NORDBY, G., 1976. Measurement of division stage durations and degree of synchrony during meiosis. *Experimental Cell Research*, **103**, 31–38.

PARISE, A., 1966. Ciclo sessuale e dinamica di popolazioni di *Euchlanis* (Rotatoria) in condizioni sperimentali. *Archivio di Oceanografia e Limnologia*, **14**, 387–411.

PARISE, A., 1978. Population dynamics and food supply in a copepod of the genus *Tisbe*. *Bollettino di zoologia*, **45**, 375–381.

PARISE, A. & LAZZARETTO, I., 1966. Misure di popolazione sul copepode *Tisbe furcata* (Baird) (Harpacticoida). *Memorie della Accademia Patavina di Scienze, Lettere ed Arti*, **79**, 3–11.

PIELOU, E. C., 1977. *Mathematical Ecology*. 385 pp. New York: Wiley-Interscience.

RAO, G. C., 1967. On the life-history of a new sand dwelling harpacticoid copepod. *Crustaceana*, **13**, 129–136.

RIEPER, M., 1978. Bacteria as food for marine harpacticoid copepods. *Marine Biology*, **45**, 337–345.

SARS, G. O., 1911. *An Account of the Crustacea of Norway with short Descriptions and Figures of all the Species*. Vol. V. *Copepoda Harpacticoida*. 449 pp. Bergen: The Bergen Museum.

SARVALA, J., 1977. The naupliar development of six species of freshwater harpacticoid Copepoda. *Annales zoologici fennici*, **14**, 135–161.

SCUDO, F. M., 1967. Criteria for the analysis of multifactorial sex determination. *Monitore zoologico italiano*, **1**, 1–21.

SHARPE, P. J. H., CURRY, G. L., DEMICHELE, D. W. & COLE, C. L., 1977. Distribution model of organism development times. *Journal of Theoretical Biology*, **66**, 21–38.

SMOL, N. & HEIP, C., 1974. The culturing of some harpacticoid copepods from brackish water. *Biologisch jaarboek Dodonaea*, **42**, 159–169.

VANDEN BERGHE, W. & BERGMANS, M., 1981. Differential food preferences in three co-occurring species of *Tisbe* (Copepoda, Harpacticoida). *Marine Ecology-Progress Series*, **4**, 213–219.

VILELA, M. H., 1969. The life cycle of *Tisbe* sp. (Copepoda, Harpacticoida) under laboratory conditions. *Notas e estudos do Instituto de biologia marítima*, **36**, 1–16.

VOLKMANN, B., 1975. *Tisbe remanei* (Copepoda, Harpacticoida) a new sibling species of the *holothuriae* group. *Archivio di Oceanografia e Limnologia*, **18**, 147–157.

VOLKMANN-ROCCO, B., 1969. *Tisbe pontina* n.sp., a harpacticoid copepod from the island Ponza. *Archivio di Oceanografia e Limnologia*, **16**, 117–128.

VOLKMANN-ROCCO, B., 1971. Some critical remarks on the taxonomy of *Tisbe* (Copepoda, Harpacticoida). *Crustaceana*, **21**, 127–132.

VOLKMANN-ROCCO, B., 1972*a*. The effect of delayed fertilization in some species of the genus *Tisbe* (Copepoda, Harpacticoida). *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass.*, **142**, 520–529.

VOLKMANN-ROCCO, B., 1972*b*. *Tisbe battagliai* n.sp., a sibling species of *Tisbe holothuriae* Humes (Copepoda, Harpacticoida). *Archivio di Oceanografia e Limnologia*, **17**, 259–273.

VOLKMANN-ROCCO, B. & BATTAGLIA, B., 1972. A new case of sibling species in the genus *Tisbe* (Copepoda, Harpacticoida). In *Proceedings of the Fifth European Marine Biology Symposium*, Venice, 1970 (ed. B. Battaglia), pp. 67–80. Padova: Piccin Editore.

VOLKMANN-ROCCO, B. & FAVA, G., 1969. Two sibling species of *Tisbe* (Copepoda, Harpacticoida): *Tisbe reluctans* and *T. persimilis* n.sp. Research on their morphology and population dynamics. *Marine Biology*, **3**, 159–164.

ZURLINI, G., FERRARI, I. & NASSOGNE, A., 1978. Reproduction and growth of *Euterpina acutifrons* (Copepoda: Harpacticoida) under experimental conditions. *Marine Biology*, **46**, 59–64.