Vrije Universiteit Brussel
Faculteit Wetenschappen
Laboratorium voor Ecologie en Systematiek

Population Biology of the Harpacticoid Copepod *Tisbe furcata* (Baird, 1837)

Promotor : Prof. Dr. Ph. Polk
Co-Promotor : Prof. Dr. D.R. Roggen

Proefschrift voorgelegd tot het behalen
van de wettelijke graad van
Doctor in de Wetenschappen

Marc BERGMANS 1983

1760s.

STELLING

(bij het proefschrift 'Population Biology of the Harpacticoid Copepod Tisbe furcata (Baird, 1837)' ingediend door Marc Bergmans)

Istock (Amer. Natur. 111, 279-287) verklaart de coëxistentie van 2 soorten corixiden door competitie van het Lotka-Volterra-type, en sluit daarbij differentiële seizoeninvloeden als causale factor uit. De gegevens waarop deze interpretatie gebaseerd is wijzen, bij correcte analyse, precies in tegenovergestelde richting.

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Acknowledgments
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Upon completion of this work, it is my pleasant duty to acknowledge the contributions made by many people towards its realization.

To my supervisor, Professor Ph. POLK, credit is due for bringing Tisbe into my life. For his continued interest and support I feel very grateful.

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In the agitation of the finishing spurt, proof-reading by my mother and brother has been tremendously helpful.

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This is the place to pay tribute to some people very dear to me : my wife Joke and my parents. If they had not, each in their turn, relieved me of the burden of material cares, this work might never have come into existence. To self-effacing Joke I also owe thanks for invaluable help, from the heroic early Sluice Dock samplings to the splendid job she did typing this MS. This work, I hope, will not be unworthy of my parental milieu, which was one of wide-ranging interests and, indeed, 'academic freedom'. My father did not live to see it in finished form; I dedicate it to his memory.

M.B.

Samenvatting

Hoofdstuk I. Taxonomisch overzicht van het genus Tisbe in de Spuikom.

Tisbe furcata, T.gracilis, T.bulbisetosa, T.holothuriae, T.battagliai en een vooralsnog niet geïdentificeerde 6de soort werden in de Spuikom van Oostende aangetroffen. Laatstgenoemde 3 spp. zijn nieuw voor België. T.holothuriae uit Oostende werd gekruist met een Venetiaanse stam, waarbij interfertiliteit en zelfs de karakteristieke 'hybrid vigor' werden aangetoond. T.furcata, het struikelblok van het genus en tevens voorwerp van het hierna gerapporteerd onderzoek, wordt opnieuw beschreven met inbegrip van het kleurpatroon bij juvenielen en adulten.

Hoofdstuk 2. Fenologie der soorten, met analyse van de populatiedynamiek van T.furcata.

Gedurende de jaren I975-I977 werd door veertiendaagse staalname een overzicht bekomen van de fenologie der Tisbe spp. in de Spuikom, en dit enerzijds in een fytaal microhabitat nabij de oever, anderzijds op oesterpannen in het centrum van de kom. De patronen zijn gelijklopend voor beide substraten en vrij reproduceerbaar van jaar tot jaar. T.bulbisetosa (in de herfst) en T.gracilis (het hele jaar door) zijn vermoedelijk dwaalgasten uit de haven. T.sp.A en T.furcata zijn het talrijkst in de lente, T.battagliai en T.holothuriae daarbuiten. De timing van beide laatste spp. lijkt overigens onvoorspelbaar, wat ook in andere biotopen is waargenomen. Beide spp. coëxisteren nabij de oever van de kom, terwijl de populatie in het centrum uit louter T.battagliai bestaat; dit verschil ligt vermoedelijk aan de geringere buffering

van de ondiepe waterkant t.o.v. temperatuur- en saliniteitsfluctuaties.

T.furcata gedraagt zich zeer voorspelbaar, met een jaarlijks terugkerende lentebloei waarbij exponentiële groeisnelheden ('instantaneous rate of increase') van .10 - .14 worden gehaald - waarden die vermoedelijk dicht bij het fysiologisch maximum liggen. Verschuivingen in de leeftijdsstructuur wijzen op het bestaan van 2 opeenvolgende generaties. Populatiedensiteiten worden niet door 'resources' bepaald; toch is in de fytale populatie een densiteitsafhankelijke remming van de netto voortplanting aantoonbaar. De empirische relatie die deze beschrijft geeft, in combinatie met de voorspelde leeftijdssamenstelling van een evenwichtspopulatie, aanleiding tot een schatting van de draagkracht van het Ulva-milieu. Gerealiseerde populatiegroottes bedragen minder dan 1/20 van K.

Hoofdstuk 3. Demografie van Harpacticoida : Kritische beschouwingen bij de status questionis.

Hier wordt betoogd dat demografische studies over Harpacticoida in tweeërlei zin mank lopen. De gewoonte om r_m te schatten als $\ln R_o/T_c$ leidt tot onderschattingen met 10 - 30% voor soorten met snelle levenscycli (zoals Tisbe). Ook van enkele andere, min of meer geïmproviseerde, berekeningswijzen worden de gevaren gesignaleerd. Wat het conceptuele aspect betreft wordt de noodzaak van meer respect voor begripsinhouden bepleit. Al te vlug worden louter passieve verschijnselen als adaptaties geïnterpreteerd, en al te vlug wordt aan al dan niet vermeende adaptaties een diagnostische waarde t.o.v. voortplantingsstrategieën toegeschreven.

Hoofdstuk 4. Ontogenie en levenscyclus van T.furcata in een demografisch perspectief.

De levenscyclus van T.furcata bij 18°C werd gekwantificeerd door observatie van synchrone cohorten. Twee onafhankelijke methodes leveren gelijkaardige schattingen voor de duur der opeenvolgende larvale stadia : 80.4 h voor de gecombineerde naupliusstadia; 23.0 h, 23.2 h, 23.2 (♂) tot 28.0 h (♀), 24.2 (♂) tot 33.4 h (♀) en 34.7 (♂) tot 48.8 h (♀) voor de 5 opeenvolgende copepodietstadia. De ontwikkeling der wijfjes verloopt trager maar meer synchroon dan die der mannetjes. Leeftijdsspecifieke overleving en fecunditeit laten toe de stabiele leeftijdsverdeling van een exponentiëel groeiende populatie te voorspellen. Dezelfde overlevings- en fecunditeitstabel levert waarden voor de volgende klassieke parameters : intrinsieke groeisnelheid r_m = .236 d^{-1}; netto groeifactor R_o = 94; minimum generatietijd T_{min} = 14.9 d; "generatietijd" s.s. T = 19.2 d; gewogen gemiddelde generatietijd T_c = 25.4 d. Deze waarnemingen blijken dienstig bij het herzien van de taxonomische identiteit van het Tisbe-materiaal in enkele belangrijke oudere studies.

Hoofdstuk 5. Korte-termijn evolutie van de levenscyclus tijdens een bloei ?

De mogelijkheid werd onderzocht dat de jaarlijkse bloei van T.furcata (interpreteerbaar als een bijzondere vorm van seizoen-invloed) een waarneembaar r-selectieproces met zich brengt. Ter toetsing werden 2 cohorten vergeleken, waarvan de moedertjes 'vroeg' c.q. 'laat' in de bloei van 1979 werden verzameld. Toegenomen snelheid van de levenscyclus, grotere r en fecunditeit, gereduceerde levensverwachting en juveniele leefbaarheid,

en een afgenomen variantie van alle voornoemde kenmerken zijn met de hypothese van r-selectie in overeenstemming. Toch bestaan aanwijzingen dat de reële grootte van de selectieve respons werd overschat; onderlinge verwantschap van de experimentele individuen is hiervan de vermoedelijke oorzaak.

Hoofdstuk 6. Adaptatie van de levenscyclus aan een quasi-stationair demografisch regime.

Een laboratoriumpopulatie die gedurende 35 generaties een constante voedselinput kreeg, en geacht mag worden een quasi-stationair regime te hebben gekend, werd onderzocht op adaptatie van de levenscyclus. De respons van T.furcata op densiteitsregulatie bestond uit een verhoogde (potentiële) netto reproductiefactor R_o. Dit bevestigt theoretische voorspellingen over fitness in populaties met leeftijdsstructuur (maar is in tegenspraak met intuïties gebaseerd op de r-K-dichotomie). De fysiologische mechanismen die tot een toename van R_o bijdragen zijn: toegenomen leeftijdsspecifieke fecunditeit, uitgestelde senescentie, en - vooral - verhoogde frequentie van eizak-productie. De "prijs" van voortplanting op jonge leeftijd biedt een verklaring voor de verschillende distributie van T_{min} bij de 4 in dit werk onderzochte cohorten : indirecte selectie van het 'truncation'-type (bij de stationaire cultuur) staat daarbij tegenover directe symmetrische selectie (in exponentiele regimes). Tot op heden is meestal naar adaptatie gezocht in r-geselecteerde populaties; dit is één van de eerste studies die op een populatie bij evenwicht werd toegespitst.

Introduction and overview

According to Cole (1957), some of the earliest demographic observations worthy of that name -and not pertaining to the human species - have been made on marine copepods. Of the venerable tradition that was thus initiated, the present work is a recent offshoot. It was born out of a dual fascination with a taxonomically 'difficult' group, and with the evolution of life histories as perhaps the most 'beautiful' challenge to ecology, demography and genetics combined. It is hoped that the present study of Tisbe furcata adds a contribution, however modest, to meeting that challenge; yet, after perusing it, many a reader will share my view that it is only a stepping stone on the way to more sophisticated analyses than have been carried out here.

The material has been organized as follows. Chapters 1-3 are, each in their own way, introductory. Chapter 1 contains taxonomic specifications which, in a genus like Tisbe, are hardly superfluous; it may however be skipped without loss of essential information by readers with exclusive ecological interests. Chapter 2 describes the in situ dynamics of the Tisbe guild whence the T. furcata cohorts studied later were obtained. Review chapter 3 sets the computational and conceptual stage for the life history analyses that follow. In chapter 4, basic demographic methodology is introduced and applied to T. furcata. The final part of this thesis is devoted to a search for life history variation in situations where classical r-selection (chapter 5) and selection for high net reproductive rate (chapter 6) were held to operate.

Chapter 1

Taxonomic notes on the species of *Tisbe* occurring in the Sluice Dock

Abstract

Tisbe furcata, *T. gracilis*, *T. bulbisetosa*, *T. holothuriae*, *T. battagliai* and an unidentified species are reported from the Sluice Dock near Ostend. The three last-named species are new to the Belgian fauna. A cross-breeding experiment between strains of *T.holothuriae* from Ostend and Venice (Italy) confirms perfect interfertility and hybrid F_1 heterosis. *T. furcata*, the "stumbling block" of the genus, is redescribed and an account is presented of the characteristics and ontogeny of its colour pattern.

Introduction

Identification of Tisbe species is notoriously difficult, and Volkmann-Rocco (1971) has stressed the necessity of extremely detailed observation, and sometimes even of cross-breeding experiments, to arrive at reliable identifications. Even the recent literature is teeming with misidentifications made by authors, some of them professional copepodologists, who were not thoroughly acquainted with the genus; and the number of times that different species have been lumped together under a single name can only be conjectured.

All Tisbe material for the present thesis was obtained from the Sluice Dock ('Spuikom') of Ostend, a man-made lagunar habitat on the Flemish coast. In the course of a three-year sampling programme (1975-77) aimed at providing insight into the dynamics of the Tisbe populations in situ, no less than 6 sympatric species were discovered there. The research carried out on one of these, and to be reported in the chapters that follow, has life history and demography as its central theme; yet in view of the taxonomic difficulties referred to above, and in view of the correspondingly fragmentary biogeographical knowledge of the genus a prefatory chapter devoted to these aspects is appropriate.

Good descriptions are already available of Tisbe holothuriae, T. battagliai, T. gracilis and T. bulbisetosa. Of these, only T. bulbisetosa will here be examined from a purely morphological point of view, as some of its sibling species may yet remain to be described. Attention will mainly be focused on T. furcata, the object of chapters 4-6, which also happens to be the 'stumbling block' of the genus.

Methods

The animals were obtained either by wringing out fragments of Ulva which had drifted to the border, or by scraping earthenware tiles after a fortnightly submersion in the center of the Dock (see Chapter 2). The Tisbe were sorted live in order to take advantage of differing colour patterns, and monospecific laboratory cultures were set up.

The cross-breeding technique adopted was essentially the same as the one described by Battaglia & Volkmann-Rocco (1973).

In the holothuriae crosses, five synchronous ovigerous females were individually isolated from both the Venice and Ostend mass cultures until they had released their nauplii. When these had grown up, experimental and control pairs were set up between an adult male and an subadult, and therefore virgin, female (4th or 5th copepodite) of a different "family". After fertilization the male was discarded and the female transferred to a new vial for each successive egg batch produced. The nauplii from the first egg batch of each female were subdivided in groups of five per dish to determine their survival under minimal crowding. All the offspring produced within the female's lifetime were counted and sexed upon reaching adulthood.

In the case of the holothuriae x battagliai crosses, mass culture males were used to fertilize the experimental and control females; reproductive success was evaluated qualitatively only (after 6 and 11 days). Further details were as in the T. holothuriae-experiment.

Throughout both experiments plastic petri-dishes (Ø 5.5 cm) containing 10 ml of seawater were used. Temperature and salinity were approximately constant at 18°C and 35 ppm. Each dish received 1 ml of full-grown Dunaliella culture every 5th day (every 3rd day for the most numerous F_1 batches).

For morphological examination, specimens were dissected in glycerine and drawn with the help of a camera lucida. Abbreviations used in the text and figures are as follows:

A_1	antennule
A_2	antenna
Md	mandible
Mxl	maxillula
Mx	maxilla
Mxp	maxilliped
P_1-P_6	legs 1-6
enp	endopod
exp	exopod

Remarks on the species

Tisbe holothuriae Humes, 1957

This is one of a group of sibling species (Volkmann-Rocco 1972b, 1975) the females of which are qualitatively indistinguishable (but for T. remanei). The males however can be discriminated fairly easily by combined observation of their A_1, P_2 and P_5. The proximal endopod segment of the male P_2 bears a characteristically modified seta which is species-specific in the case of T. holothuriae. Fig. 1.1 is a camera lucida drawing of this spine, featuring the biserial lamellar system and the point of attachment suggesting a mobile joint.

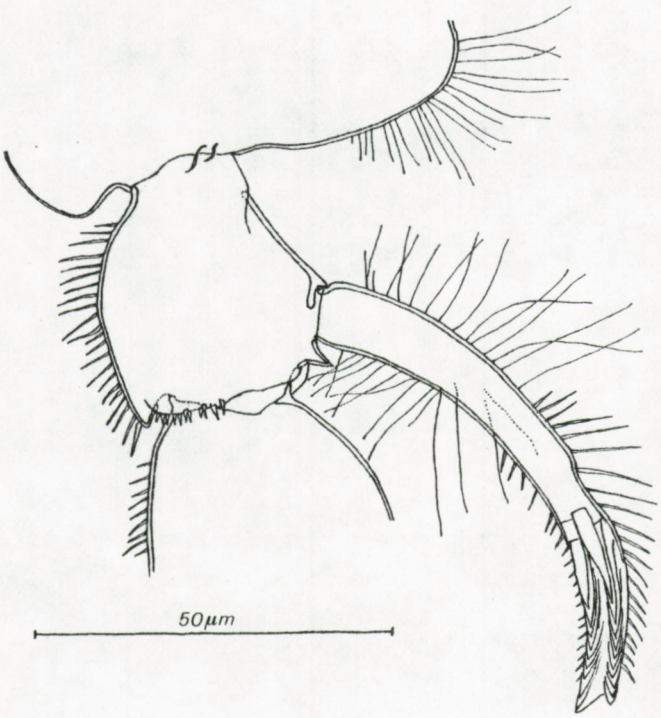


Fig. 1.1. Tisbe holothuriae male. Transformed spine on P_2 enp segment 1.

Table 1.1. Summary of a cross-breeding experiment between *T. holothuriae* from Ostend and Venice
The values in column 4-7 are averages over all fertile crosses

Type of cross	Number of crosses attempted	Number of sterile crosses	F_1 percentage survival (minimal crowding)	Total F_1 reaching adulthood per female	Percentage of females in F_1	R_o (number of daughters per mother)
♀V x ♂O	11	4	95.2	410	51.3	212
♀O x ♂V	9	2	93.2	400	42.0	191
♀V x ♂V	9	3	87.3	296	39.9	129
♀O x ♂O	8	2	87.6	332	25.8	82

The identification on morphological grounds was checked by a cross-breeding experiment using a Venetian laboratory strain of T. holothuriae kindly put at my disposal by Dr. Volkmann. In view of the small number of crosses, the results presented must be considered indicative rather than quantitative.

The proportion of unsuccessful crosses, though rather high (cf. Table 1.1), is similar for experimental and control matings and, in fact, similar to the figure of 35 % reported by Battaglia (1957a) for intrapopulation controls in T. reticulata.

From the parameter values obtained in this experiment (Table 1.1), two clear trends are apparent. First, for R_o and F_1 sex ratio there is a definite influence of the female's geographic origin on the parameter value. Battaglia & Volkmann-Rocco (1973) have observed a strong correlation between the female's geographic origin and the number of nauplii of its first egg sac. The same effect is also substantiated in my data (♀V x ♂O : 36.4, ♀V x ♂V : 37.3; ♀O x ♂V : 41.4, ♀O x ♂O : 41.0).

Second and more important, the experimental crosses are consistently superior to the controls in all parameters considered. In spite of the low number of replicas, the net reproduction rate R_o, i.e. the number of F_1 females produced per P female, is significantly higher in "hybrid" crosses (cf. Table 1.2). Also, it is interesting to note the heterotic effect of crossing distant populations on F_1 viability; it closely parallels the findings of Battaglia & Volkmann-Rocco (1973) even from a quantitative point of view (cf. Table 1.3).

Table 1.2. Anovar of R_o values for pooled experimental ($\bar{R}_o$= 202, s.d.= 121) and pooled control crosses ($\bar{R}_o$= 106, s.d.= 79) of T. holothuriae

Source of variation	Sum of squares	Degrees of freedom	Mean square	F
Between levels	59 905	1	59 905	5.535
Residual	259 719	24	10 822	$P < 0.05$
Total	319 624	25		

Table 1.3. Survival to adulthood of "hybrid" F_1 relative to intrapopulation controls in T. holothuriae
V= Venice, O= Ostend, H= Helgoland, B= Beaufort, USA

Crosses considered	Relative viability of "hybrids"	Source
♀V x ♂O / ♀V x ♂V	1.09	Present work
♀O x ♂V / ♀O x ♂O	1.06	Present work
♀H x ♂B / ♀H x ♂H	1.03	Battaglia & Volkmann-Rocco (1973)
♀B x ♂H / ♀B x ♂B	1.10	Battaglia & Volkmann-Rocco (1973)

Table 1.4. Summary of a cross-breeding experiment between T.holothuriae and T. battagliai from the Sluice Dock

Type of cross	Number of crosses attempted	Females retaining the eggs in the oviducts	Females extruding a sterile egg-sac	Females producing nauplii and copepodites
♀ hol x ♂ bat	10	9	1	-
♀ hol x ♂ hol	10	-	-	10
♀ bat x ♂ hol	9	7	2	-
♀ bat x ♂ bat	7	-	-	7

From the foregoing it may be concluded that the Sluice Dock population under consideration freely interbreeds with Venetian T. holothuriae and, moreover, that it shows the characteristic behaviour of this species in crosses between widely spaced populations.

T. holothuriae has often been confused with T. furcata (Volkmann-Rocco, 1971); it has also been described under four junior synonyms (see Volkmann-Rocco, 1971, 1972b; Volkmann, 1979b). Its known geographical distribution is summarized in Volkmann-Rocco (1972b). The species is new for the Belgian fauna but its presence is hardly surprising, as it has been recorded from Wimereux (France) and Helgoland (Germany).

Tisbe battagliai Volkmann-Rocco, 1972

This is a sibling species of the former. The modified spine of the males is nearly indistinguishable from that of T. remanei, but their A_1 and P_5 both allow easy identification (Volkmann, 1975).

The reproductive distinctness of the holothuriae and battagliai populations from the Sluice Dock was confirmed by a cross-breeding experiment involving both strains. The results (Table 1.4) are clearly conclusive.

T. battagliai is new for the Belgian fauna. Other localities where it is known to occur are given by Volkmann-Rocco (1972b). To these must be added the brackish ditches in the salt-marsh "Zwin" (Knokke, Flemish coast). A casual sample of superficial detritic mud taken there on 14-11- 1976 yielded 6 adult Tisbe and 2 copepodites, all of which proved to be T. battagliai.

Tisbe gracilis (T. Scott, 1895)

This species belongs to another group with a sexually dimorphic P_2 which is, in this case, sufficient for unequivocal identification of the male. The females can be discriminated on the basis of the genital field (Volkmann-Rocco, 1973b). The Sluice Dock specimens show a general agreement in morphology with Scott's (1895) and Volkmann-Rocco's (1973b) descriptions.

The suggestion made by Volkmann, that the whole animal length of 1.4 mm quoted by Scott includes the caudal setae, is not borne out by the latter's original paper (cf. the magnification mentioned in Scott, 1895, p. 173). It has been found, though, that his size indications do not always agree with his material (Volkmann, pers. comm.). My own culture specimens average about 0.87 mm (5 ♀♀) and 0.65 mm (5 ♂♂), respectively, from the tip of the rostrum to the end of the furcal rami. These figures are in close agreement with those of Volkmann (0.85 - 1.05 mm resp. 0.56 - 0.70 mm). With regard to Scott's data, it must of course be remembered that size in copepods is strongly influenced by environmental factors, and also that an animal's length varies with its degree of contraction.

Living adults of both sexes as well as the later copepodid stages contain red droplets. These are distributed symmetrically on the ventral side of the body, a small group of them being situated in front of the attachment of swimming legs P_2-P_4. At least in my culture animals there appears to be a sexual dimorphism, the droplets of

the females occurring in front of the P_1 as well and being rather more orange and definitely less opaque. In addition to the droplets and the bright red eye, there may also be a faint pinkish tinge in the cuticula of adult animals, especially in the abdomen.

T. gracilis does not seem to be a true resident of the Sluice Dock; it has however been recorded (Persoone, 1967) from artificial substrates in the harbour of Ostend to which the Dock is connected by a sluice. The species appears to be limited to 'cold' seas,e.g. the North Atlantic (Volkmann-Rocco, 1973b; Volkmann, 1979b).

Tisbe sp. A

This species has so far remained refractory to identification, and may well be new to science. The fact that juveniles (and, rarely, adults) contain orange lipid droplets is a characteristic shared with the gracilis group but also with other totally unrelated microcrustaceans. The internal seta on P_2 enp 1 is not obviously sexually dimorphic. As speculations based upon superficial similarities stand a good chance to be misleading, this species will, pending a complete description, henceforth be designated as Tisbe sp.A.

Tisbe bulbisetosa Volkmann-Rocco, 1972

The species under consideration belongs to a group, members of which have been described by Klie (1949), Vilela (1969), and Volkmann-Rocco (1972a; Volkmann, 1979b). According to Volkmann (1979b), T. dilatata Klie, 1949 should be considered incertae sedis (!) because its colour pattern, which is essential for reliable identification, is unknown. Its membership of the present group of sibling species is, however, unquestionable, and the name might even

retain priority if it were shown, e.g., that only T. bulbisetosa occurs in Klie's type locality. Therefore it appears justified to consider T. dilatata here, on the understanding that Klie's description differs from his type material on essential points (Volkmann, 1979b). In the Mediterranean, several populations of unclear taxonomic status have been subsumed under the name of T. dilatata (e.g. Marcus, quoted in Volkmann-Rocco, 1972a; Renzoni, 1974).

My Sluice Dock specimens (3 ♀♀ and 4 ♂♂ dissected) differ from Klie's (1949) description of T. dilatata in a number of ways, the two most important of these concerning (1) the female genital field, which bears three setae on each side, and (2) the Mxp, which is strongly sexually dimorphic. Both observations are in contrast with explicit statements by Klie -but see Volkmann (1979b)! Also, there are a number of minor differences involving the two lateral accessory furcal setae (of about equal length, 1/10 of the longest terminal seta); the spinulosity of all six furcal setae (not sparse as stated by Klie); the 2nd and 3rd A_1 segment of the female (length ratio 1.2 instead of 1); the 2nd enp segment of P_1 (length / width ratio 0.25 instead of 0.36); the P_5 of the female (the single seta on the basipodite and the marginal one on the exp not swollen at their base, as loosely stated, but not drawn, by Klie); the relative lengths of the marginal exopod seta and the adjacent subterminal one (reversed with respect to Klie's values). Instead of describing the female's mouthparts Klie refers to Sars's (1911) drawings of T. furcata, which are acceptable as to general shape but obscure as to details of the setation. It is clear, however, that small differences of setation do exist between species, and in particular between T. furcata and the population under consideration. Lastly,

differences between Klie's description and my specimens which concern the proportions of abdominal and P_1 segments may at least in part be attributed to the difficulty of obtaining well defined and objective measurements of them.

Vilela's (1969) description of a Tisbe sp. may now beyond doubt be referred to T. bulbisetosa (Volkmann, pers. comm.). If one assumes that the setation of her specimens is not rendered in all completeness in her drawings, and further that the spines on the P_5 exp surface of females are not distributed irregularly (text) but in rows (drawing!), there is a close agreement between her material and mine. (The statement that the male A_1 is 8-segmented obviously results from overlooking the very small 4th segment.)

There also exist some differences between Volkmann-Rocco's (1972a) description and my material. The second A_1 segment of females bears 15 setae instead of 14 as in her drawing, the difference involving a rather short seta in the middle of the segment and usually closely appressed to it. Two setae are found on A_1 segment 5, exactly as in the reticulata group (Volkmann-Rocco, 1973a) and T. furcata (see below). The most external apical seta of Md exp is ciliated. The Mx endite bears a long and a short seta; the terminal (spiniform) Mx segment has a row of small hairs near its tip. The basis of P_1 has an anterior surface row. There exists a row of fine hairs along the upper part of the interior margin of P_1 enp segment 2, viz. above the insertion of the marginal seta. The row of hairs on the surface of P_1 exp segment 2 and the submarginal row of bristles on enp segment 1 occur on the opposite

(posterior) side with respect to the rest of the surface adornment ot the appendage drawn by Volkmann. In addition to this, exp. segment 1 has a somewhat less conspicuous row of small hairs (oriented like that on exp segment 2) on its posterior surface. Similarly, the surface adornment of P_2-P_4 coxa and basis (as drawn by Volkmann) on one hand, and that of the rami on the other, occur on different sides of the appendages. As the ornamentation is nearly identical to that in T. furcata, the reader is referred to the relevant paragraph and to Figs. 1.8 to 1.10 for comparison. My material differs from T. furcata in the following P_2-P_4 details only:

-absence of the innermost surface comb of longer spinules on the coxa of P_2-P_4
-absence of the surface comb above the rami on the basis of P_2
-the posterior distal fringe of small hairs does not seem to be present on exp segment 1 of P_2-P_4
-spinules of the distal rim of the terminal enp segment apparently more numerous than in T. furcata, especially on P_2 where there are 6 or more of them
-posterior surface adornment of the P_4 coxa altogether different from that of T. furcata; it is shown in Fig.1.2 and consists of a subhorizontal spinule field, a skew row and three subvertical ones, the external two staggered and made up of minute spinules.

Finally, as observed by Klie, the 2nd and 3rd abdominal segments carry two long hairs posteriorly on either side.

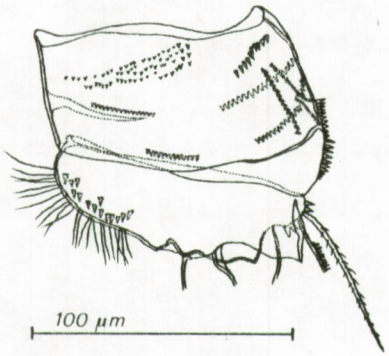


Fig. 1.2. Tisbe bulbisetosa female. Coxa and basis of P_4, posterior view.

For morphological comparison, I dissected a female T. bulbisetosa which I had collected on October 7, 1975 on the Arsenale canal wall, Venice (Station 5 of Fava & Volkmann, 1975). This animal agrees with my Sluice Dock material in each of the details listed above, and hence I suspect the discrepancies between my material and Volkmann-Rocco's description to be due to slight inaccuracies of the latter. The only genuine difference which I observed concerns the posterior margin of the fourth abdominal segment. In the Venetian specimen the latter is ventrally provided with a central and two lateral rows of spinules separated by broad gaps, agreeing with Volkmann's statement. The Sluice Dock animals have a continuous row instead, but there is an abrupt transition to much finer spinules in the zones corresponding to the gaps referred to above.

There exist some slight differences concerning the male also. But for the sexually dimorphic A_1, Mxp, P_5 and P_6 its appendages agree with the female's in every detail. Segment 2 of A_1 bears 15 setae, though this is rather difficult to observe. Relative lengths of the second, third and fifth segment (posterior margin of sclerified parts) 2.50:1:2.05 (average of 4 specimens). P_5 exp surface with five rows of spinules, the additional one somewhat oblique and distal with respect to those drawn by Volkmann. The length of the terminal spine may be slightly shorter or slightly longer than the exp. Though I could not dissect a Venetian bulbisetosa male for reference, none of these differences appears to necessitate or warrant distinction at the species level.

Taken together, my specimens do not differ significantly from either Vilela's or Volkmann-Rocco's specimens of T. bulbisetosa. T. inflatiseta Volkmann, 1979 may only be distinguished from T. bulbisetosa on the basis of colour pattern, as even the female genital field and P_5 are too variable to allow a reliable identification (Volkmann-Rocco, 1972a; Volkmann, 1979b). My material closely agrees with the T. bulbisetosa description even in these respects. It may therefore safely be assigned to T. bulbisetosa, even if more cross-breeding experiments must be awaited before the taxonomy of the dilatata group of sibling species will definitely be settled. In her recent paper, Dr. Volkmann (1979b) supports the present identification.

T. bulbisetosa is new for the Belgian fauna. Like T. gracilis, it may not be a regular inhabitant of the Sluice Dock. Its presence in Ostend (relatively close to the type locality of T. dilatata) adds another Atlantic record to a distribution including the Tagus estuary, Portugal (Vilela, 1969), Concarneau and Roscoff France (Volkmann, 1979b and pers.comm.), Beaufort, N.C. (Volkmann-Rocco, 1972a) and Bermuda (Volkmann, 1979a).

Tisbe furcata (Baird, 1837)

Principally owing to the fact that many Tisbe species conform to a common "furcata" habitus, this species has given rise to considerable confusion in the literature (Volkmann-Rocco, 1971). In fact, it may be asked to what extent its being recorded as cosmopolitic, eurythermic, nearly euryhaline, perennial and eurytopic (Lang, 1948) is, at least in part, due to the lumping together of superficially similar but ecologically differentiated species. Sars's (1911) redescription of Baird's species does not adequately bring out the details characterizing it. My identification is based on a comparison with Venetian culture specimens, which

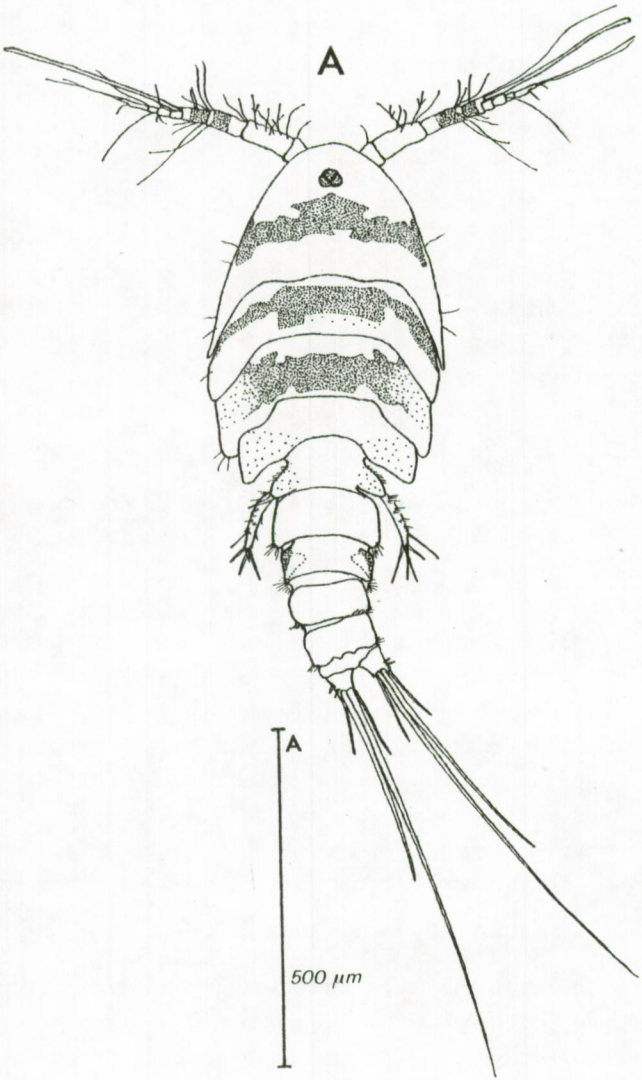
have themselves been determined by Dr Volkmann on the basis of close comparative examination of Sars's material. The present record confirms the observation by Polk (1963) who first found T. furcata in the Sluice Dock.

A redescription of T. furcata

The insufficiency of the accounts published so far calls for a redescription of this species. Measurements in this section are based upon wild-caught specimens unless stated otherwise.

Description of the female

Habitus (Fig. 1.3A) cyclopoid, as is the rule in the genus. The bright red eye consists of 3 ocelli. The total length, from tip of rostrum to end of furca, amounts to 0.99 mm (1.06-0.92 mm, 10 specimens); this value is given with the same reserve as mentioned for T. gracilis. Maximum width of the cephalothorax 0.40 mm (0.38-0.44 mm, 10 specimens). Genital double segment (Fig. 1.5A) dorsally and laterally with a suture, which contains some prominent spinules laterally only. Ventrally are two interlocking chitinous ridges surrounding the aperture of the oviducts, and a seminal receptacle of a characteristic though somewhat variable shape (Fig. 1.5B). Lang's (1948) drawing of the genital area of T. furcata, in my opinion, certainly refers to this very species. Second and third abdominal segment with a long and isolated seta inserted posteriorly on either side. Posterior rim of the genital double segment and the next two abdominal segments ventrally and laterally with spinules. The ventral ones are flat and triangular and much coarser than in T. bulbisetosa or, a fortiori,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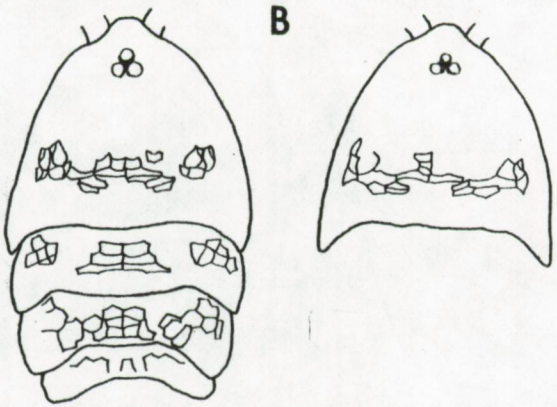


Fig. 1.3. Tisbe furcata female. - A, habitus. - B, aspect of parts of the hypodermal cellular reticulum, as seen in two partly discoloured individuals.

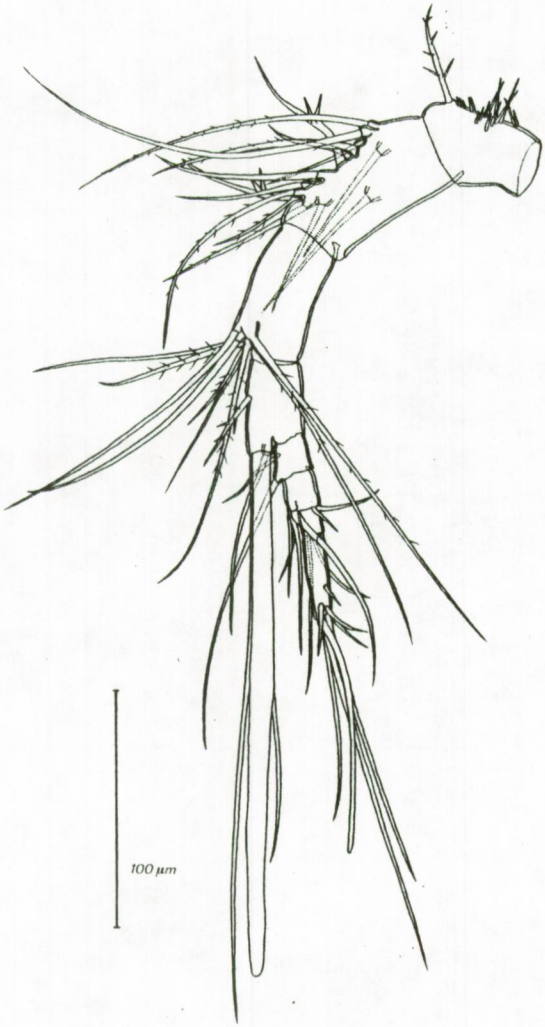
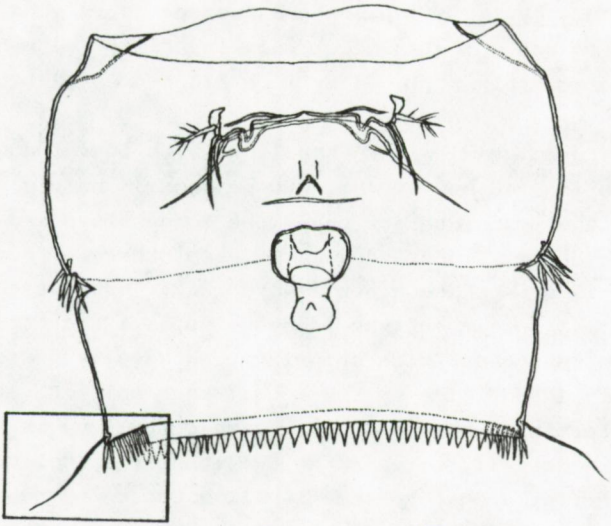


Fig. 1.4. Tisbe furcata female. A_1.



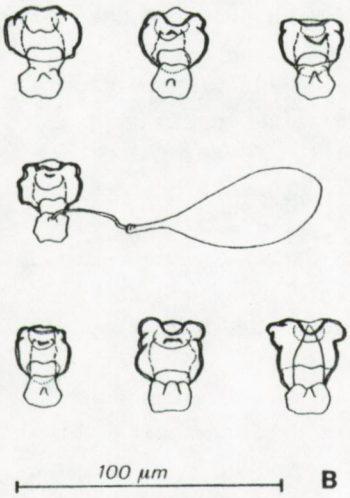


Fig. 1.5. Tisbe furcata female. - A, genital double-segment (main drawing: ventral view; insert: dorsal view). - B, variability of the seminal receptacle (laboratory culture specimens).

the holothuriae group; on the last-named (= 4th) segment, such coarse spinules occur only laterally and centrally, being abruptly replaced by much finer ones in between.

Furca: rami wider than long, with four long setae measuring 140 µm, 600 µm, 400 µm and 135 µm beginning with the most interior one. The longest two are often 'telescoped' (independently of each other). The interior seta is often though not always bent. But for the proximal portion of the longest two, all four are provided throughout with spinules of gradually decreasing size. In addition to the four larger ones, three shorter setae of about equal size occur; one is inserted dorsally between the two longest apical ones, another at about the same level as these on the exterior side of the ramus, and the third one ventral and more rostrad. The latter two have a comb of spinules above their point of attachment.

Antennule (A_1) eight-segmented, stouter than drawn by Sars (1911). E.g., the length-width ratio or segment 2 is usually much closer to 1.5 than to 2.0. Form and setation otherwise as in Fig. 1.4. Relative lengths of the sclerified parts of segments 2, 3 and 4 measured along the posterior (unarmed) margin 1.79: 1.59: 1 (1.71: 1.62: 1 - 1.89: 1.57: 1, 5 specimens). Number of setae on the successive segments 1/15/9/4+aesthetask/2/6/2/7+aesthetask. On the second segment, two of these setae are more robust and provided with 2 to 4 lateral tips giving them a characteristic 'forked' appearance (which can be observed even on living animals at low magnification). These two setae are implanted somewhat 'against the grain', a character shared with T. bulbisetosa and

the T. reticulata-species group (cf. the drawings in Volkmann-Rocco, 1973a). The central seta on segment 4 and the single one on segment 1 are intermediate in appearance between these two peculiar setae and the normal plumose type.

The basis of the antenna (A_2) has a surface comb of about seven hairs near the implantation of the internal large seta. Enp segment 1 with one seta on the internal margin. The terminal enp segment has an external row of long thin hairs; it bears 9 large setae (5 of them bent and naked, 1 spiniform with a row of short hairs, 3 curved and plumose) and an additional internal one, which is smaller and thinner and has 2 to 3 short spinules of unlike length implanted near its base. In addition to the large distal seta of exp segment 1, there is a very short one in the middle of the interior margin. Subsequently exp segments with 1, 1 and 3 setae. All A_2 setae except those on the terminal enp segment are ciliated, although both Sars (1911, plate LI) and Lang (1948, figs. 12 and 164) picture one of the apical setae on exp segment 4 naked (which is true in the holothuriae group).

Mandible (Md) setation as follows. Inside of masticatory part with a strong regularly plumose seta, basal lobe with a much shorter, irregularly plumose one. Enp surface with two parallel oblique (sublongitudinal) rows of hairs (along with an apical one and one along each margin), exp surface with long bristles more or less distinctly organized into four transverse rows, including the apical one. Exp with 3 and enp with 3+6 setae, as usual; the most external exp seta is ciliated.

I have been unable to observe the precise setation of the maxillula (Mx1).

External rim of the basal segment of the maxilla (Mx) provided with a central row and a distal tuft of hairs, the latter being more dense than the former. The single endite bears a long and a short seta; claw-like enp with short hairs, its spiniform seta with long hairs. (The appendage under consideration is consistently, but erroneously, termed 'first maxilla' by Volkmann-Rocco (1972a, b, 1973a, b). Though 'maxilla' seems to be its most appropriate denomination, it has also been called 'second maxilla' or 'first maxilliped' by various authors: cf. Lang 1948, pp. 56 - 57.)

Maxilliped (Mxp) as shown in Fig. 1.6A.

First leg (P_1) (Fig. 1.7) with spines and setae distributed as typical for Tisbe. The external seta of exp segment 2, the four proximal ones of exp segment 3 and the longest of the two claws on enp segment 3 have a terminal tuft of hairs. Second claw with a row of short hairs on its concave side. (Again, it is drawn naked by Sars and Lang, as it should have been in the holothuriae group.) Setation of lateral segment margins as shown in Fig. 1.7. The coxa has an exterior-posterior flap bearing a row of long bristles. Surface adornment anterior on coxa and basis. Exp segment 1 with an anterior comb of spinules and a posterior row of short hairs. Surface adornment of exp segment 2 and enp segment 1 posterior. There is a fringe of hairs near the posterior distal borders of exp segments 1 and 2 (difference with T. bulbisetosa,

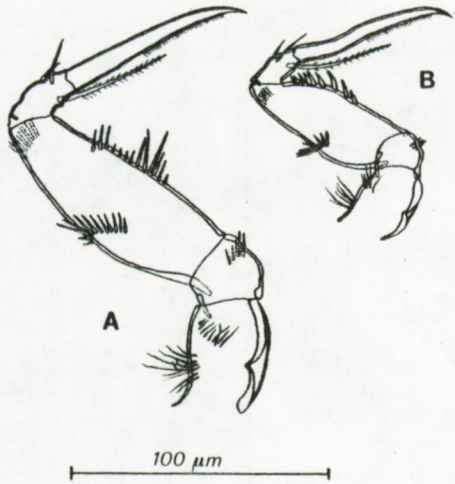
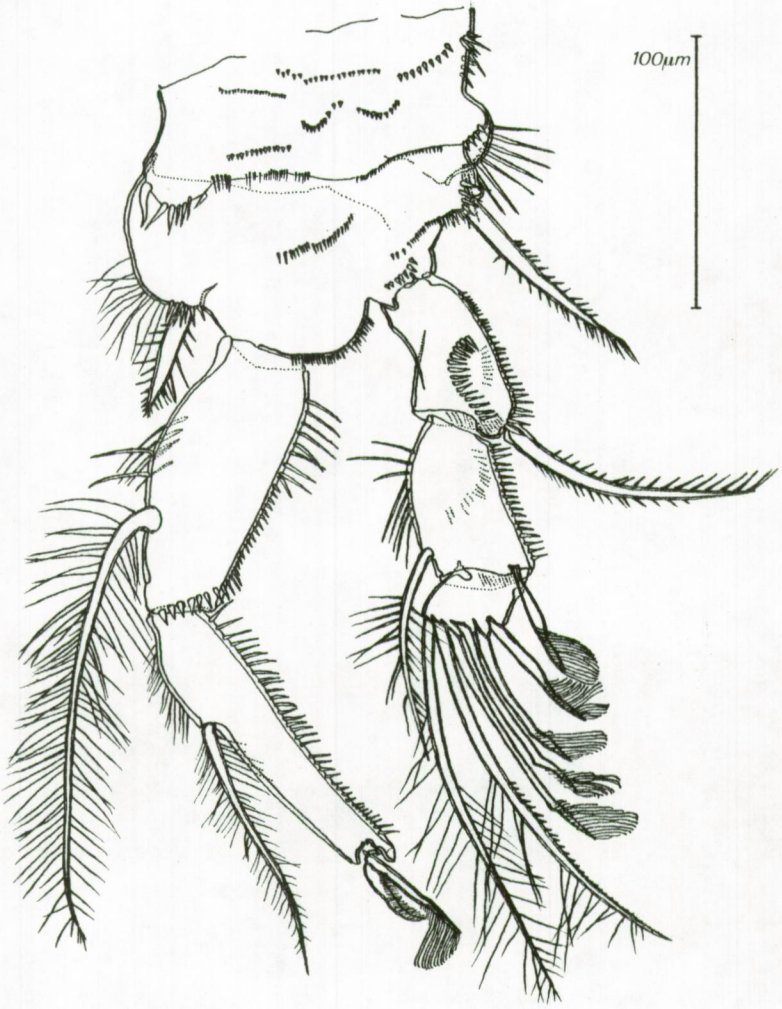


Fig. 1.6. Tisbe furcata. - A, Mxp of female.
- B, Mxp of male.

Fig. 1.7. (opposite page) Tisbe furcata female.
P_1, anterior view.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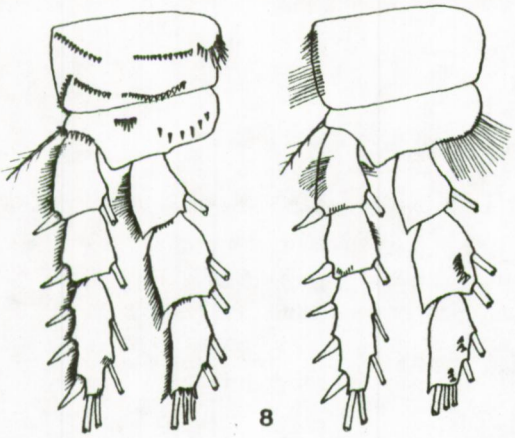
which has no such fringe on exp segment 1 and an anterior one on exp segment 2 !). There is a row of spinules near the anterior distal border of enp segment 1. Length-width ratio of enp segment 1 2.40 (2.21-2.71, 5 specimens); of enp segment 2 4.80 (4.38-5.24, 5 specimens). Enp segment 2 about 1.15 times as long as segment 1 (1.10-1.22, 5 specimens) and with its internal seta inserted proximally at 1/3 of the segment length.

Second to fourth leg (P_2-P_4) (Figs. 1.8 to 1.10) of the chaetotaxy typical for the genus (Lang, 1948). Anterior surface adornment of the coxa in each case consisting of two subhorizontal sets of spinule rows and a subvertical one, the latter more marginal and prominent on P_4. On P_2 and P_3 there occurs a posterior row of hairs near to the external coxa rim; it consists of two series of hairs of dissimilar length and inclination. On P_3 only, this row is parallelled by one situated external (anterior) to it and consisting of short stiff hairs. P_4 posterior coxa adornment as indicated in Fig.1.10. The bases of P_2-P_4 adorned as shown in the Figs. and bearing an external plumose seta; their distal rim with an anterior row of spinules along the seta implantation and exp attachment. Basis of P_2 only with an additional surface comb above the rami. Large bristle-like hairs are present along the external side of all exp and enp segments, whereas tiny spinules surround the base of the spiniform setae of the exps. Spinules of progressively smaller size can be found anteriorly on P_2 through P_4:

- on the distal rim of exp segment 2 (external part)
- dispersed among the apical setae and spines of the terminal enp segments (2-3, rarely more)



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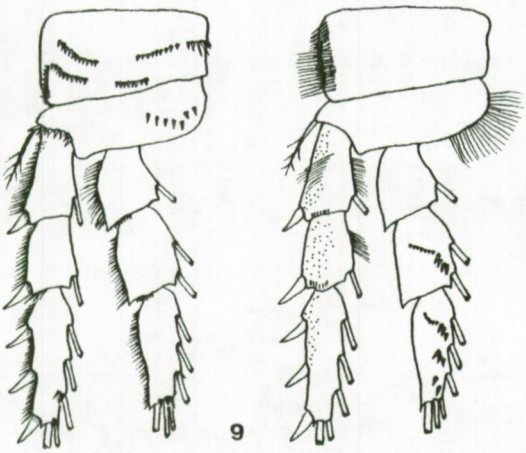

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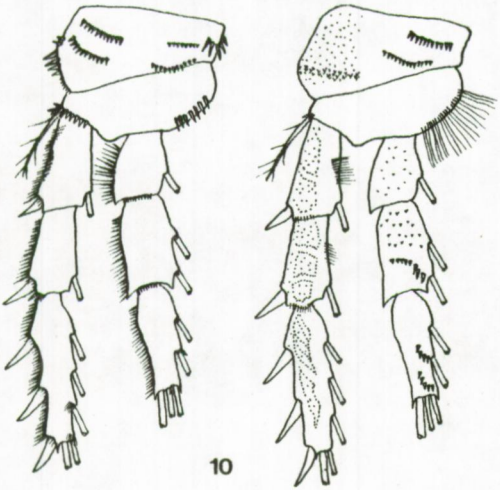

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Figs. 1.8 to 1.10.
Tisbe furcata ♀.
Diagrams of P_2 - P_4.
Left : external marginal and anterior adornment.
Right : internal marginal and posterior adornment.

- on the distal rim of enp segments 1 and 2 (second quarter starting from the outside on P_2 and P_3, somewhat more extensive on P_4).

The attachment of the marginal setae of P_2-P_4 enp segments 2 and 3 is anteriorly surrounded by a few tiny spinules, which are especially prominent at the most distal seta. An anterior comb of fine hairs occurs above the insertion of the ultimate and penultimate interior setae of each exp segment 3 (the one above the ultimate seta of P_2 being inconspicuous).

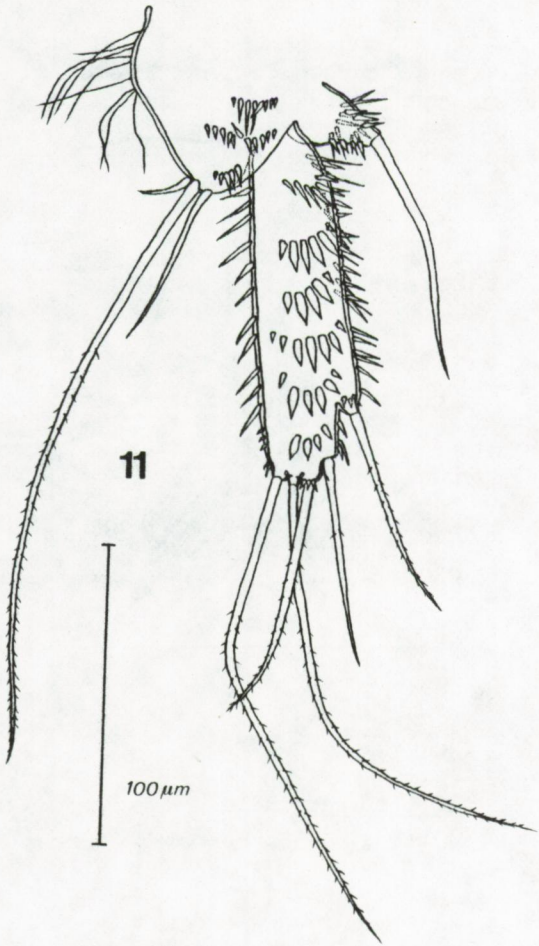
Posterior surface adornment of the rami as follows. Exp segment 1 with a row of fine rather long hairs on its surface (P_2-P_3) and on its internal margin (P_2-P_4); exp segment 2 also with a marginal row (P_2-P_4); both segments with a fringe of short hairs extending near their distal border (P_2-P_4). Enp segment 2 of P_2-P_4 with one oblique row of spinules; enp segment 3 with 2, 3 and 2 such rows on the successive pereiopods, respectively. P_4 enp segments 1 and 2 with scattered spinules; likewise, all P_3 and P_4 exp segments with numerous minute hairs. On P_4 exp segment 3 these occur in somewhat oblique, anastomosing rows. On segment 2, they are organised into three distinct, more or less square fields with well-marked limits; on segment 1 and 3 they are indistinctly divided into two groups. As I have observed the same striking P_4 pattern in my four other species, and as moreover it is pictured in the description of T. bocqueti (Volkmann-Rocco, 1972a), one can be certain that it is much more widespread - perhaps even general - in the genus than is apparent from published descriptions.

Fifth leg (P_5) as pictured in Fig. 1.11. Baseoendopodite with three rows of spines on its surface. Its inner lobe bears three setae of widely different length. Length-width ratio of the exopodite 3.71 (3.52-4.00, 5 specimens). Its surface bears well-defined rows of rather flat and triangular spines. Six rows appear on intact specimens, though often a worn-like patch was found instead of the distal ones.

Description of the male

Habitus cyclopoid but more slender than the female (as usual in Tisbe). Total length averaging 0.66 mm (0.62-0.74 mm, 5 specimens); width of cephalothorax 0.27 mm (0.25-0.29 mm, 5 specimens). Distal border of the 2nd, 3rd and 4th abdominal segments ventrally and laterally fringed with spinules, exactly as in the female. On the first abdominal segment such spinules are present only laterally, above the P_6.

Appendages, but for their size, as in the female unless stated otherwise. The A_1 (Fig. 1.12A) is prehensile, 9-segmented, the 5th and 9th bearing an aesthetask. The peculiar forked setae are present here as well, with those on segment 2 especially prominent. The Mxp (Fig. 1.6B) exhibits a clear sex-dimorphism: the terminal hook is sinuous, the internal margin of the basal segment more arched distally and its bristles stronger, more procumbent and more regularly inserted than in the female. The dimorphism is however less pronounced than, e.g., in T. bulbisetosa (Volkmann-Rocco, 1972a) and the gracilis species group (Volkmann-Rocco, 1973b).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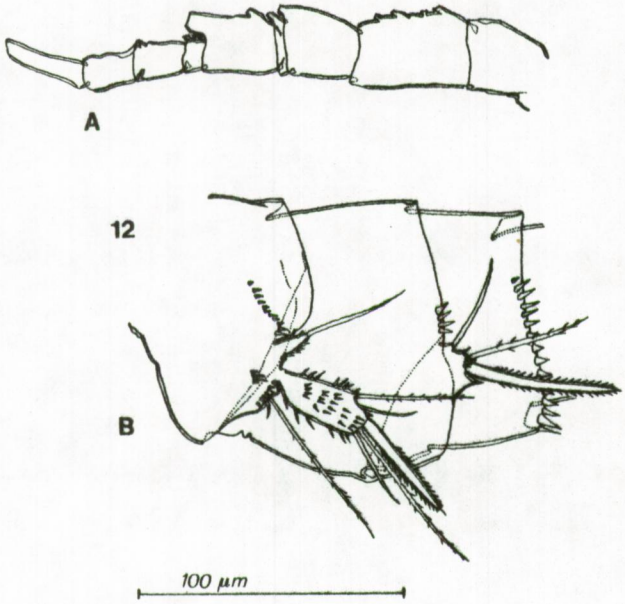


Fig. 1.12. Tisbe furcata male. - A, A_1 (setation omitted). - B, P_5 and P_6.

Fig. 1.11. (opposite page) Tisbe furcata female. P_5.

Male P_5 and P_6 as in Fig. 1.12B (size indications on these appendages refer to laboratory-raised individuals). Baseoendopodite of P_5 with an external spinulose projection carrying a seta of 42 µm (38-49 µm, 4 specimens); internal lobe, corresponding to the endopodite, with a seta of 66 µm (58-83 µm, 5 specimens) flanked by a very short internal one (6 µm, 4-7 µm, 6 specimens) and a few spinules more or less exterior to it. P_5 exp with five short transverse rows of spinules; it is 37 µm long (35-40 um, 8 specimens) and 16 µm wide (14-18 µm, 7 specimens), with ratio 2.34 (2.16-2.50, 7 specimens). The rim of this segment bears (from inside to outside) a subterminal seta (30 µm; 25-38 µm, 5 specimens), a terminal seta (56 µm; 52-60 µm, 5 specimens), a stout terminal spine (43 µm; 36-48 µm, 9 specimens) carrying a short apical setule (4 µm; 2-5 um, 7 specimens), a subterminal seta (22 µm; 18-28 µm, 4 specimens) and a final lateral one (44 µm, 41-46 µm, 4 specimens). P_6 represented by a lobe bearing a stout ciliated spine (59 µm; 55-67 µm, 6 specimens) and two setae, one of 48 µm (44-54 µm, 4 specimens) inserted near the base of the spine and one of 36 µm (29-41 µm, 3 specimens) at some distance anterior to it.

Description and ontogeny of the colour pattern

Tisbe furcata exhibit a distinctive colour pattern. Adult females (Fig. 1.3A) have a pigmented band of varying width across the cephalothorax and each of the three free thoracic segments, the last one however being extremely faint and indistinct. These thorax bands may be interrupted by unpigmented gaps between the lateral and central parts (sometimes on one side only). Central or lateral parts may be missing altogether. The first

and third free thoracic segment also have some pigment concentrated ventrally along their exterior margin. The distal half of the 3rd and the proximal half of the 4th A_1 segment are also coloured; so are the margins of the labrum. The swimming legs appear increasingly pigmented towards their distal ends, but mainly at the joints and the external exopod spines. The P_5 (baseoendopodite + exp) and the large furcal setae may be slightly tinged pinkish. Finally, there is a streak of colour running along the lateral sutures of the genital double-segment and bending rostrad on the ventral side.

The pattern is somewhat different in adult males. They do have a band across the cephalothorax, but instead of those in the middle of each thorax tergite there is a thin stripe bordering its posterior margin (as in the holothuriae group). The margins of the abdominal segments are likewise coloured (hardly so in the female). There is an intense spot of pigment, ventrally on either side, in the turned-over edge of the cephalothorax - about on a level with the mouth. There are no streaks of colour in the genital area. A_1 pigmentation is present in the distal half of segment 3, segment 4 and the proximal half of segment 5.

As will be evident from the foregoing description, the localisation of pigment in this species is extremely similar to that in T. bulbisetosa (Volkmann-Rocco, 1972a), in T. pentataenia (Volkmann-Rocco, 1973a) and in the trifasciata morph of T. reticulata (Bocquet, 1951; Volkmann-Rocco, 1973a).

The shade of the pigment may appear anything from brick-red in intensely coloured individuals, to pink, sometimes even with a faint orange tinge, in animals containing hardly any pigment at all. The intensity of the colouring is influenced by the molting cycle (see below) but there remains considerable variation even when it is finally stabilized in adults. Also the relative intensities of different parts of the body may vary, the genital area of the female usually being stained more intensely than the cephalosome though it may hardly be marked on some occasions. The dorsal banding pattern often exhibits an antero-posterior gradient of intensity (and shade), just as can be observed in the trifasciata morph of T. reticulata (Bocquet, 1951).

Serial observations on isolated individuals have shown that each newly molted copepodite stage is initially colourless. As pointed out by Bocquet (1951) on T. reticulata, stage III seems to be the first to show traces of the banding pattern. The latter is gradually acquired anew after each subsequent molt, the pigmentation of metasome and appendages being limited to the adult. Exuviae are normally colourless (cf. also Bocquet, 1951). This is probably not due to a rapid loss of pigment, as exceptional banded exuviae remain so very long. It seems therefore that pigment is rapidly resorbed before each ecdysis and slowly reconcentrated afterwards. Mobilisation of carotenoids (dissolved in lipo-protein droplets) into the hemolymph has actually been observed by Lwoff (1927) in adult female Tisbe transferring pigment to the eggs during ovogenesis. (He was probably dealing with a species of the holothuriae-group rather than with T. furcata: see chapter 4.)

Sexual dimorphism of the pigment distribution is expressed in the adults only. Casual observations on another species, T. clodiensis, revealed that in this species copepodites are banded while adults are not. Bocquet (1951) remarks how in T. reticulata the last molt is accompanied by "une véritable métamorphose pigmentaire" from the single copepodite pattern to the various colour morphs of that species.

In partly discoloured specimens of T. furcata, two of which have been drawn in Fig.1.3B, the pattern of relict pigmentation points to the existence of a cellular reticulum which is very similar, though not identical, to that found in two species of the reticulata-group, viz. T. reticulata (Bocquet, 1951) and T. aragoi (Volkmann-Rocco, 1973a). The diversity of band contours which I have observed also suggests that the pigmentation of single cells may be controlled by a 'minor polychromatism' as in T. reticulata (Bocquet, 1951), though the bilateral symmetry of pigment presence is often imperfect in T.furcata. To someone acquainted with the papers quoted, the beautiful drawings by Itô (1976) of several species and colour morphs of Scutellidium (a genus closely allied to Tisbe) are also clear evidence of the presence of a reticulum. It may be assumed that both the general banding pattern and its expression on a cellular reticulum are widespread and presumably monophyletic characteristics shared by Scutellidium spp., T. furcata and the members of the reticulata, clodiensis and dilatata groups.

Chapter 2

In situ phenology of *Tisbe* spp., with special regard to the dynamics of *T. furcata*

Abstract

The *Tisbe* guild of the Sluice Dock was surveyed from 1975 to 1977. Seasonal samples of a phytal population near-shore and a level-bottom population in the Dock's centre are in general agreement, and certain patterns recur from year to year. *T.bulbisetosa* (fall) and *T. gracilis* (year-round) are considered stray elements from the harbour. *T.*sp.A and *T.furcata* have their main development in spring, *T.battagliai* and *T. holothuriae* outside this season. Timing of the latter two spp. appears rather unpredictable, in agreement with observations in other localities. A mixed population inhabits the nearshore substrates, but pure *T.battagliai* is found centrally; differences in the level of temperature/salinity fluctuations are held responsible for this. *T.furcata* has a highly predictable spring bloom during which rates of increase of .10 - .14 are realized - probably fairly close to the intrinsic maximum. Stage structure shifts in the copepodite population (and a temperature accumulation argument) suggest a sequence of two generations. Densities attained are not controlled by resource limitation either on the tiles or the *Ulva*, but density-dependent inhibition of population growth is detected in the phytal samples. In combination with the predicted composition of an equilibrium population, this yields an estimate of the carrying capacity of the *Ulva* environment. The low standing stock (less than 1/20th of K) and the form of density dependence are in accordance with theoretical expectations.

Introduction

Members of the genus Tisbe are a ubiquitous component of the benthic copepod fauna in shallow marine and brackish-water environments. They have been considered opportunistic, a characteristic explicitly demonstrated for T. cucumariae - of the carrion-exploiting gracilis group - (Lopez, 1982) and which may hold for other species as well (Hicks, 1980). Characteristically 5 or more species coexist in the same habitat (e.g. chapter 1; Volkmann-Rocco, 1972a; Volkmann, 1979a), which poses interesting and largely unsolved problems with regard to the distinctness of their niches. To date, few studies of the seasonal phenology of these 'guilds' have been published, all of which were carried out in the Northern Adriatic (Fava & Volkmann, 1975, 1977; Fava, 1980). In this chapter, seasonal dynamics in the Sluice Dock are described with a dual purpose. The first seasonal data for a region outside the Mediterranean present some interest of their own. More important, knowledge of the demographic background of T. furcata will be essential to the interpretation of the cohort studies that follow. With this goal in mind, censuses were not limited to adult females (as in the N. Adriatic studies), but the structure of the entire copepodite population (species, sex and stage) was estimated in an effort to provide insight into population processes and interactions.

Material & Methods

The habitat chosen for the present study is the Sluice Dock in Ostend (Flemish coast), a large (86 ha)

shallow (1.5 m on the average) polyhaline man-made basin connected by sluices to the Ostend harbour. It has been the object of much research: see, in particular Leloup & Polk (1967) for a faunistic inventory and Podamo (1976a, b, c, d, e) for ecosystem characteristics.

During the spring of 1975 and throughout the years 1976 and 1977, fortnightly samples of two kinds were taken. The phytal Tisbe population living on drift Ulva which accumulates near the eastern border of the Dock was sampled semi-quantitatively by collecting half a bucket of thalli (loosely stacked); the fauna was extracted by stirring and squeezing the thalli three times consecutively and filtering the 'supernatant' over a sieve (mesh width 38 µm until september 28, 1976, and 88 µm thereafter). Extraction by this procedure was nearly complete, even for first-stage copepodites (cf. their very high proportions occasionally observed: up to 47 %, well in excess of predicted equilibrium frequency).

For the second type of sample use was made of earthenware oyster tiles suspended from a wooden pile construction in the centre of the dock (site 3 in Podamo, 1976a, Fig. 1), in such a way that they either 1° rested upon the sediment but could not sink into it, or 2° hung .5 m below surface without contact with either sediment or wooden pilings. The surface area of the convex (upper) and concave sides is equal to 570 cm^2 (each); it is not known whether space on both sides was equally exploited by the copepods. After fortnightly submersion, the tiles were gently hauled up and slipped into individual buckets (below surface). In the laboratory

they were cleaned by means of a soft brush; 'supernatant' was twice poured over 100 µm filtering cloth while coarse material (sediment, detritus, diatoms, and macrofauna) was collected in its entirety. (Smaller copepodites that might not be retained on the cloth are in fact highly thigmotactic and were probably collected along with the detritus.) Controls showed that extraction was virtually complete in this way:

- on May 26, 1976, animals collected from 1st and 2nd sievings were counted separately; they numbered 511 and 4, respectively.
- on June 12, 1975, the '2x100 µm ' filtrate was sieved once more over 31 µm; no Tisbe were found for 2 samples having yielded 66 and 42 individuals on 100 µm. Therefore, extraction efficiency was better than 98 %.

Samples were stored in a refrigerator until they were counted 1-3 days after collection. For very dense populations, subsampling by pipette after thorough homogenizing was performed and proved highly replicable. It was decided to count all samples live to allow 1° easy detection of smaller stages among debris, 2° straightforward identification of the older copepodites and adults through their characteristic colour patterns, and 3° the possibility to raise and/or cross-breed as yet unidentified individuals. No attempt was made to include nauplii in the counts. All Tisbe copepodites were staged, sexed (from C_4 onwards) and identified to species - if necessary by raising them. (Individuals dying before becoming identifiable were allotted to the most probable species. When only 1 species was present in the C_4 - adult population of a sample, the conspecificity of C_1 - C_3 was taken for granted.)

In the case of the sibling species T. holothuriae and T. battagliai, cursory identification was to species group only; 20 ♂♂ or the male offspring of 20 ♀♀ (or less, depending on availability) were dissected to estimate the relative frequencies of these spp.

Results

The physical environment

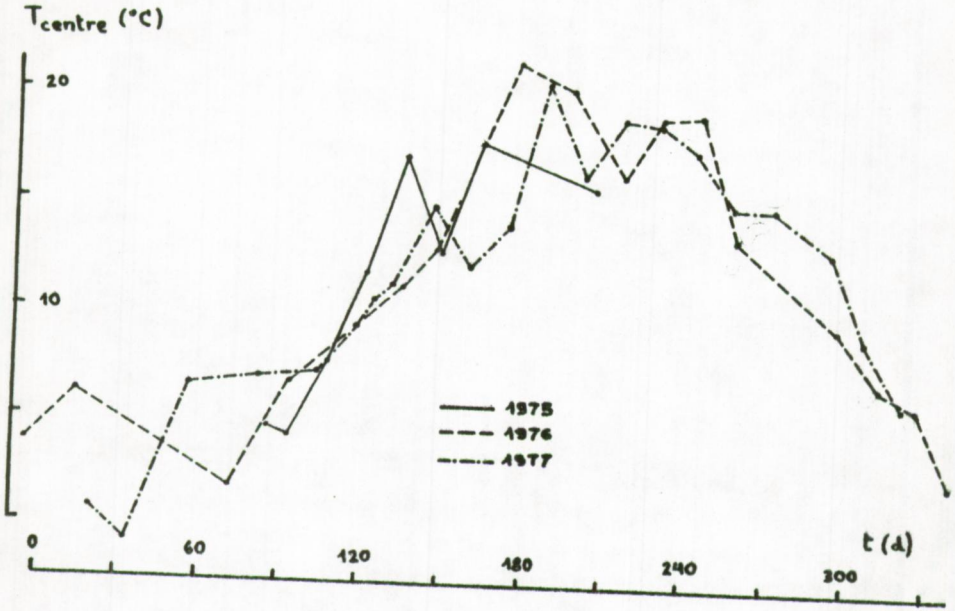
Fig. 2.1 depicts the water temperature regime during the three observation years as determined at the central site (10 cm below surface). Temperatures observed at time h were standardized to daily average according to the empirical formula

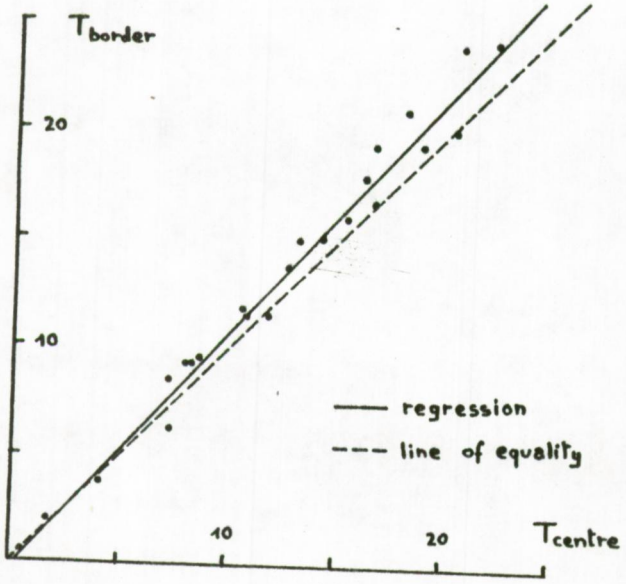
$$\bar{T} = T_h - 1.5 \sin (2\pi(h-9)/ 24)$$

(Mommaerts, 1978). Seasonal fluctuations are larger at the shore site, temperatures being lower than at the central site when below 3°C and vice versa (linear regression: $T_{shore} = 1.097\ T_{centre} - .288$, n= 24, r= .99 - see Fig. 2.2). Presumably, also daily fluctuations near-shore exceed those in the centre of the Dock.

Salinity variations for 1976 and 1977 are given in Fig. 2.3 (data after April 2, 1976 kindly provided by Luc Thielemans, State University of Ghent).

A notable feature of the Sluice Dock as a habitat is that it may be partially or completely emptied and refilled with harbour water at unpredictable dates, depending on the needs of oyster farming


T centre (°C)
20
10
1975
1976
1977
0
60
120
180
240
300
t (d)


T border
20
10
regression
line of equality
10
20
T centre

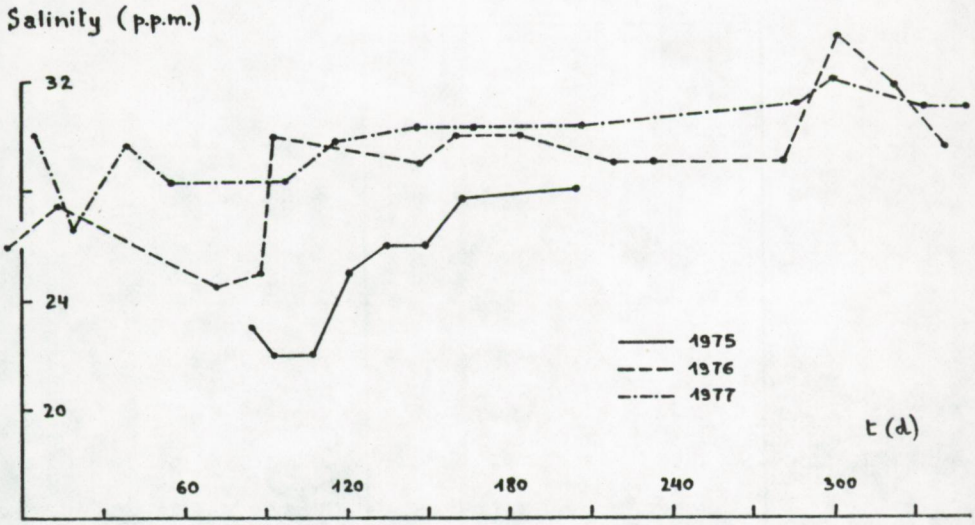
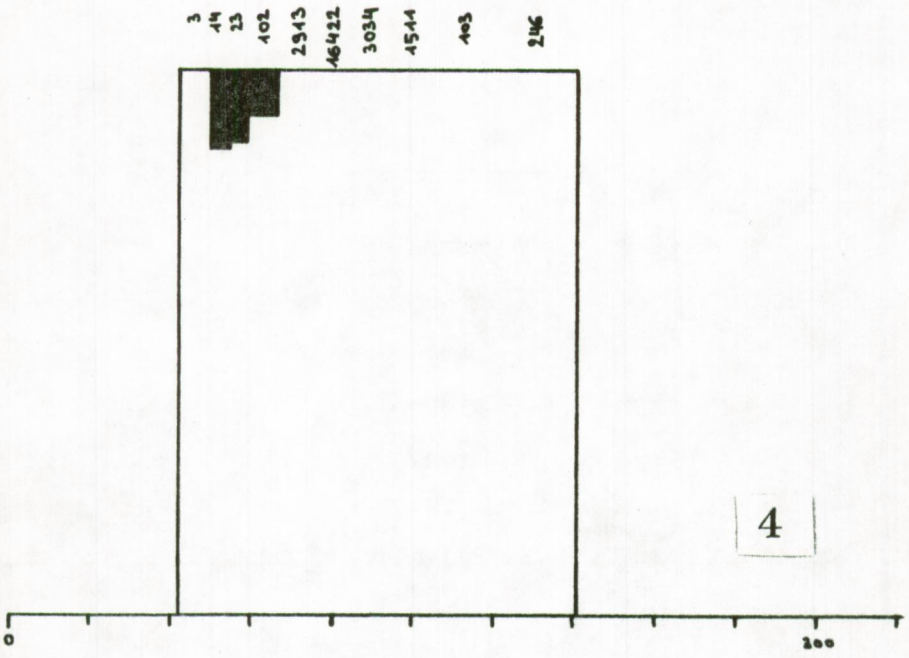


Fig. 2.1. Subsurface water temperatures recorded at the central site in 1975-1977.

Fig. 2.2. Relationship between water temperatures at the border and central sites.

Fig. 2.3. Salinity changes of Sluice Dock water recorded in 1975-1977.



Phenology of Tisbe species in the Sluice Dock.

Fig. 2.4. Bottom tiles, 1975.
Fig. 2.5. Bottom tiles, 1976.
Fig. 2.6. Bottom tiles, 1977.
Fig. 2.7. Subsurface tiles, 1975.
Fig. 2.8. Subsurface tiles, 1977.
Fig. 2.9. Ulva, 1976.
Fig. 2. 10. Ulva 1977.

Legend: T. furcata T. bulbisetosa T. sp.A

T. battagliai T. holothuriae T. gracilis

The figures above the histograms are total sample sizes.

3
31
3
8
233
545
200
2089
346
445
397
no obs.
no Tisbe
0
300

5

83
137
130
32
23
224
637
1596
192
162
1514
6049
158
119
47
32
180
82
190
0
300

6

7
0
300
64
32
4865
22344
1024
357
92
35
8
0
300
52
473
178
105
1260
145
95
42
167
844
14
79
70
3
57
145
346
246

9
no obs.
no Tisbe
0
300
1
2
30
1
1
4
34
960
941
2648
1067
40
20

10
0
300
18
17
3
4
2
13
134
234
53
58
442
1435
179
22
105
122
715
82
699
281
188
1939
4622
5
215

carried out in it. When the entire water mass is changed, the Ulva on the border becomes exposed to the air for about half a day; this need not destroy its fauna, as evidenced by the fact that live Tisbe (as well as other organisms) have been recovered from thalli collected under these circumstances. At the central site, by contrast, the 'sub-surface' tiles become completely defaunated, whereas those on the sediment remain submerged in a shallow pool of water, and would thus appear to receive least stress of all. A second effect of water changes may be the introduction of faunal elements foreign to the Sluice Dock proper (see below!). The available records of **sluicings**, which may not be complete, are indicated in Fig. 2.**11**. Double asterisks stand for known dates of complete water change, single asterisks for known dates of partial change, and daggers for the presence of Noctiluca in the samples; as this inhabitant of the harbour cannot survive in the Sluice Dock for more than a few days, at least partial refilling must have immediately preceded these dates.

Phenology of the holothuriae group and the minor species

Six species of Tisbe have been observed in the Sluice Dock: T. holothuriae, T. battagliai, T.gracilis, T. bulbisetosa, T. furcata and one as yet unidentified (and possibly new) species, referred to as T. sp.A (see chapter 1). Except for T. holothuriae and T. battagliai none of the other spp. appear particularly closely related within the genus. Fig. 2.4 to 2.10 depict their relative frequencies in different habitats for different years. In spite of occasional low numbers of individuals for a given date, there are patterns which recur from one year to another. The

clearest example is the spring bloom of T. furcata, on which fairly detailed information could be obtained. First, however, the phenology of the other species must briefly be considered.

T. bulbisetosa and T. gracilis are infrequently observed, the former apparently being a fall species and the latter occurring sporadically year-round. Their presence in the Sluice Dock is evidently associated with a fresh import of harbour water: Two out of three finds of T. bulbisetosa and eight out of twelve of T. gracilis follow 0.5 - 4 days after a known introduction of harbour water. T. gracilis has indeed previously been recorded from artificial substrates in the harbour (see chapter 1).

T. sp.A is a low-density vernal species, the presence of which seems to parallel that of T. furcata (see below). Because of this, and due to the fact that its adult colour pattern - although distinctive - is superficially reminiscent of that of T. furcata, its presence actually went undetected in 1975. During that year, however, records were kept of all observed colour patterns; this allows a posteriori estimates of T. sp.A frequencies to be made with reasonable confidence. It is conceivable that this species is also a stray immigrant from the harbour, yet its continuous population development between April 27 and July 11, 1977, when the sluices most likely remained closed, suggests it to be a regular resident in the Dock.

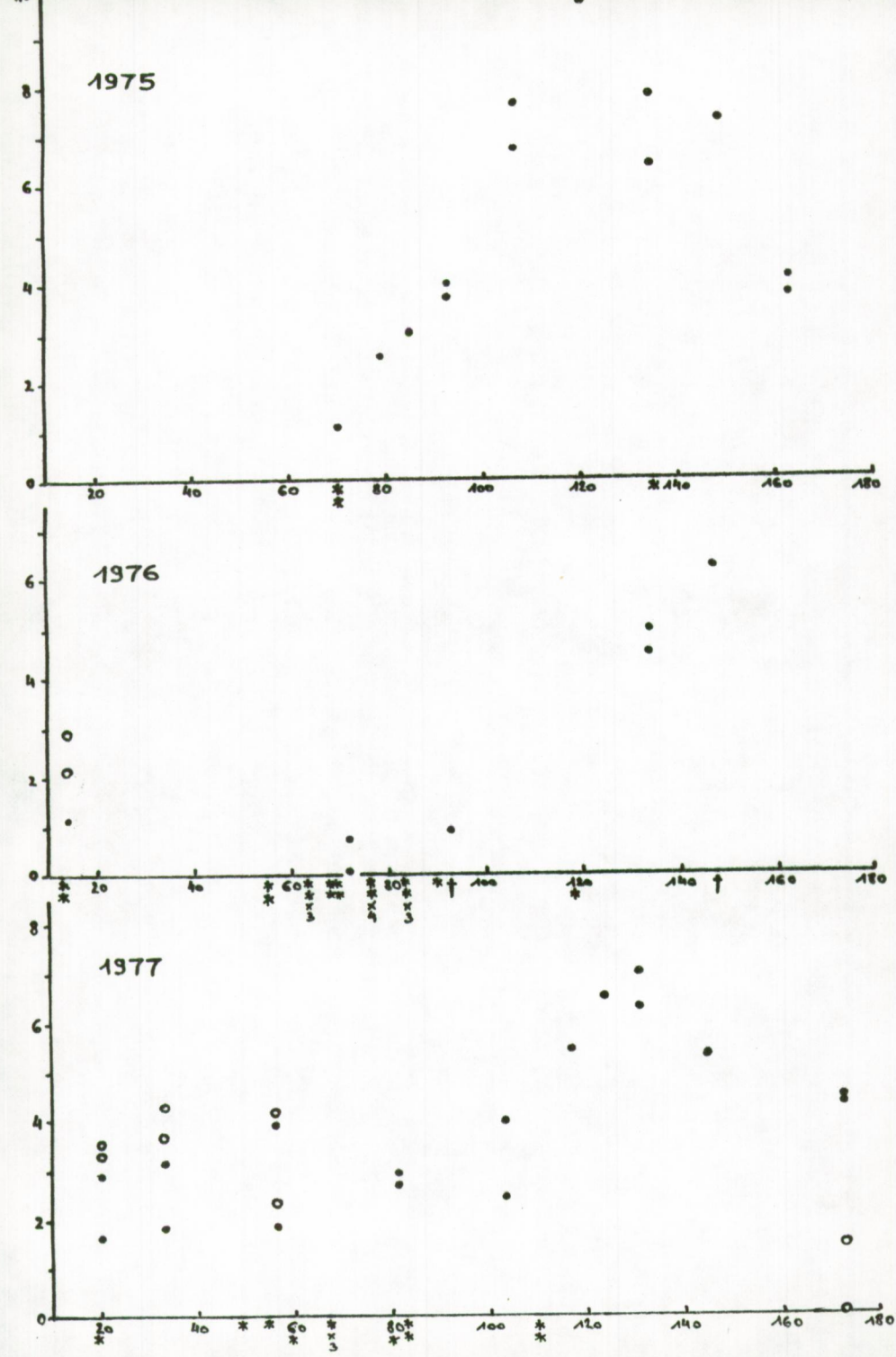
Individuals belonging to the holothuriae group were collected in large numbers both from the tiles and the Ulva. Though they were never observed

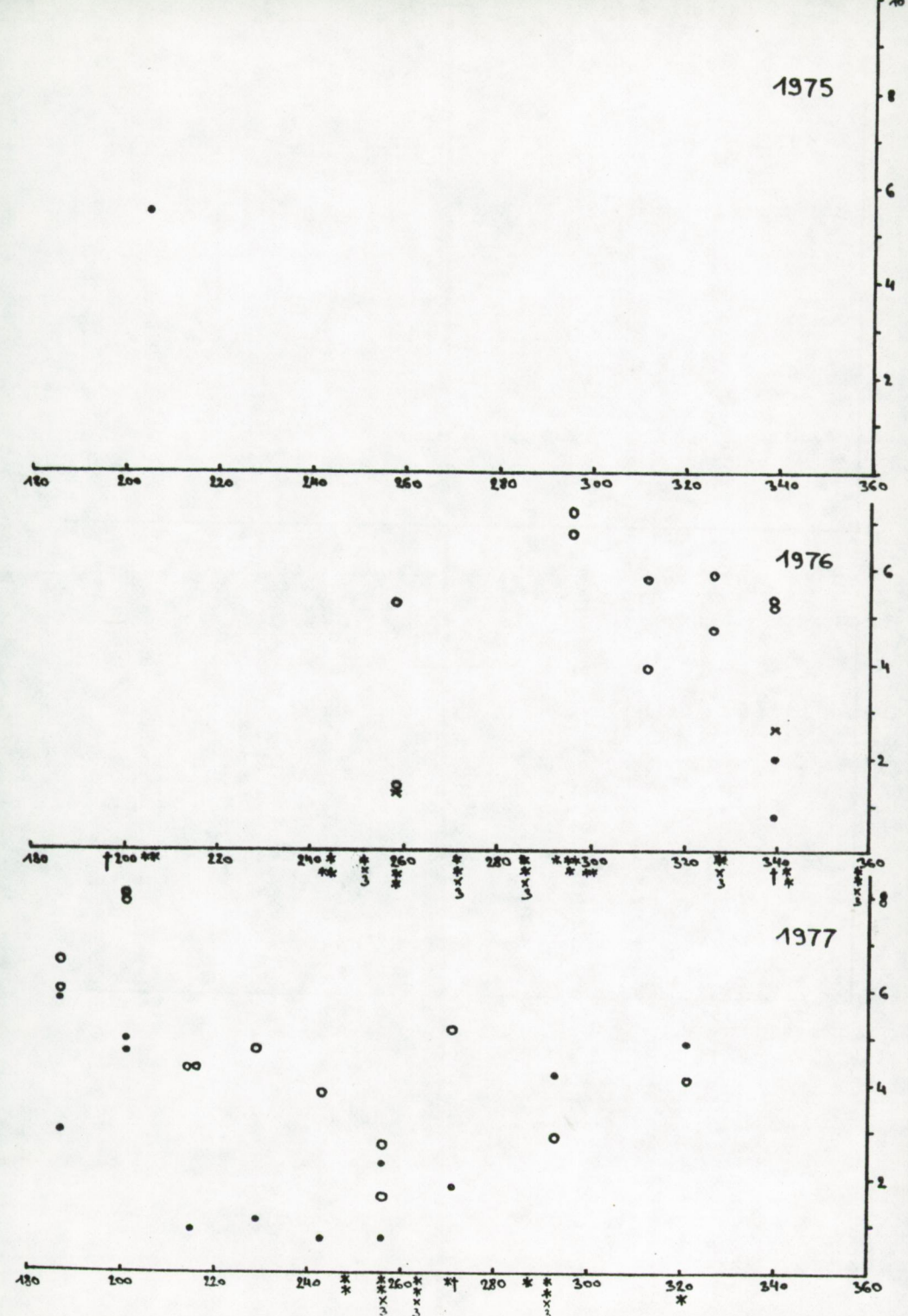
during the March-May bloom of T. furcata, their populations probably continued to exist in low numbers during these months (they may even have done so during the aftermath of the very hot summer of 1976, when for some time no Tisbe were observed at all). Apart from the spring gap, no obvious year-to-year similarities of timing emerge from Fig. 2.11 to 2.13. There are, however, differences between sites which merit consideration.

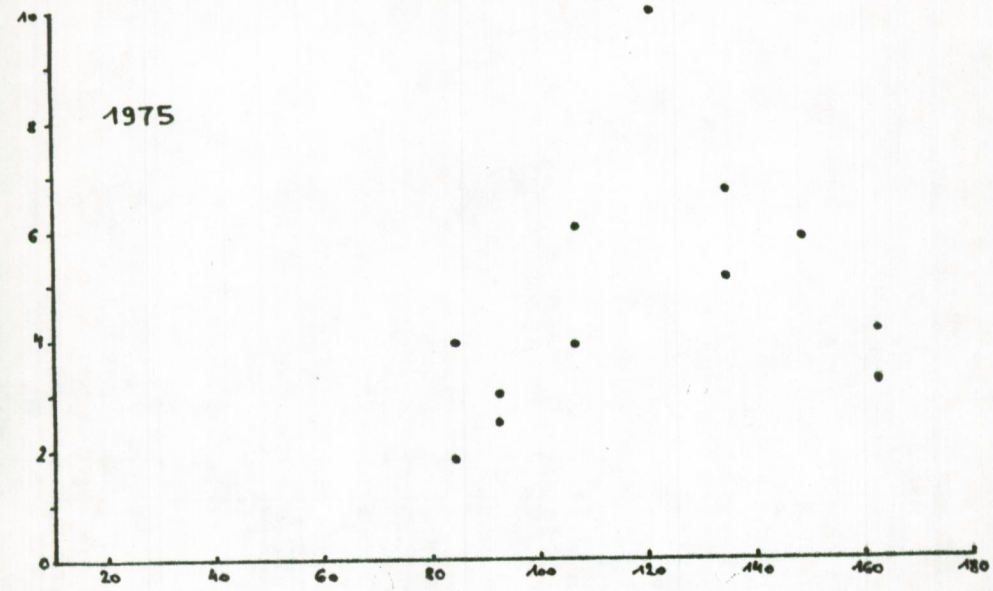
T. holothuriae and T. battagliai have often been found to occur together in small-surface samples (Volkmann-Rocco, 1972b; Volkmann, 1975; Fava & Volkmann, 1975, 1977). They are for all practical purposes indistinguishable as to those aspects of morphology usually considered of ecological relevance, such as general size, shape of mouthparts ... (Recently Volkmann (1979a) reported T. battagliai to be smaller than T. holothuriae in Bermuda, but in this case the two species did not co-occur in the same samples.) Vanden Berghe & Bergmans (1981) found the same indiscriminate feeding behaviour for both species in a simple food choice experiment. In view of this puzzling accumulation of similarities, one of the most rewarding results of the sampling programme was that some autecological differentiation between them was detected. Out of 247 individuals collected from the tiles in the centre of the dock and identified to species, only 3 were holothuriae (1.2%)! In the Ulva near the border, during the same time, a mixed population is maintained with both species reasonably abundant (Fig. 2.12).

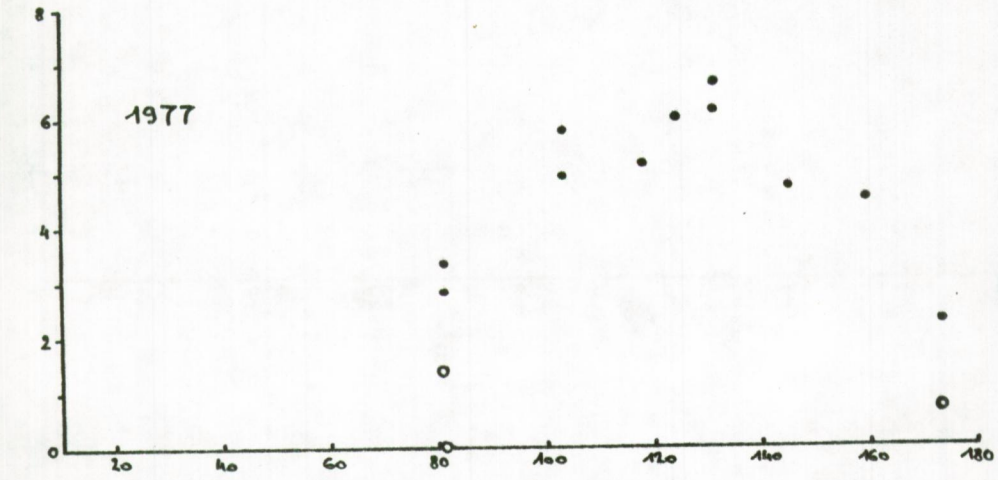
Next pages :

Fig. 2.11. Total-population densities of *T. furcata* (black dots), *T. battagliai* (white dots), and *T. holothuriae* (crosses) on the bottom tiles.


1975
1976
1977


1975
1976
1977
180
200
220
240
260
280
300
320
340
360
2
4
6
8


1975
10
8
6
4
2
0
20
40
60
80
100
120
140
160
180


1977
8
6
4
2
0
20
40
60
80
100
120
140
160
180

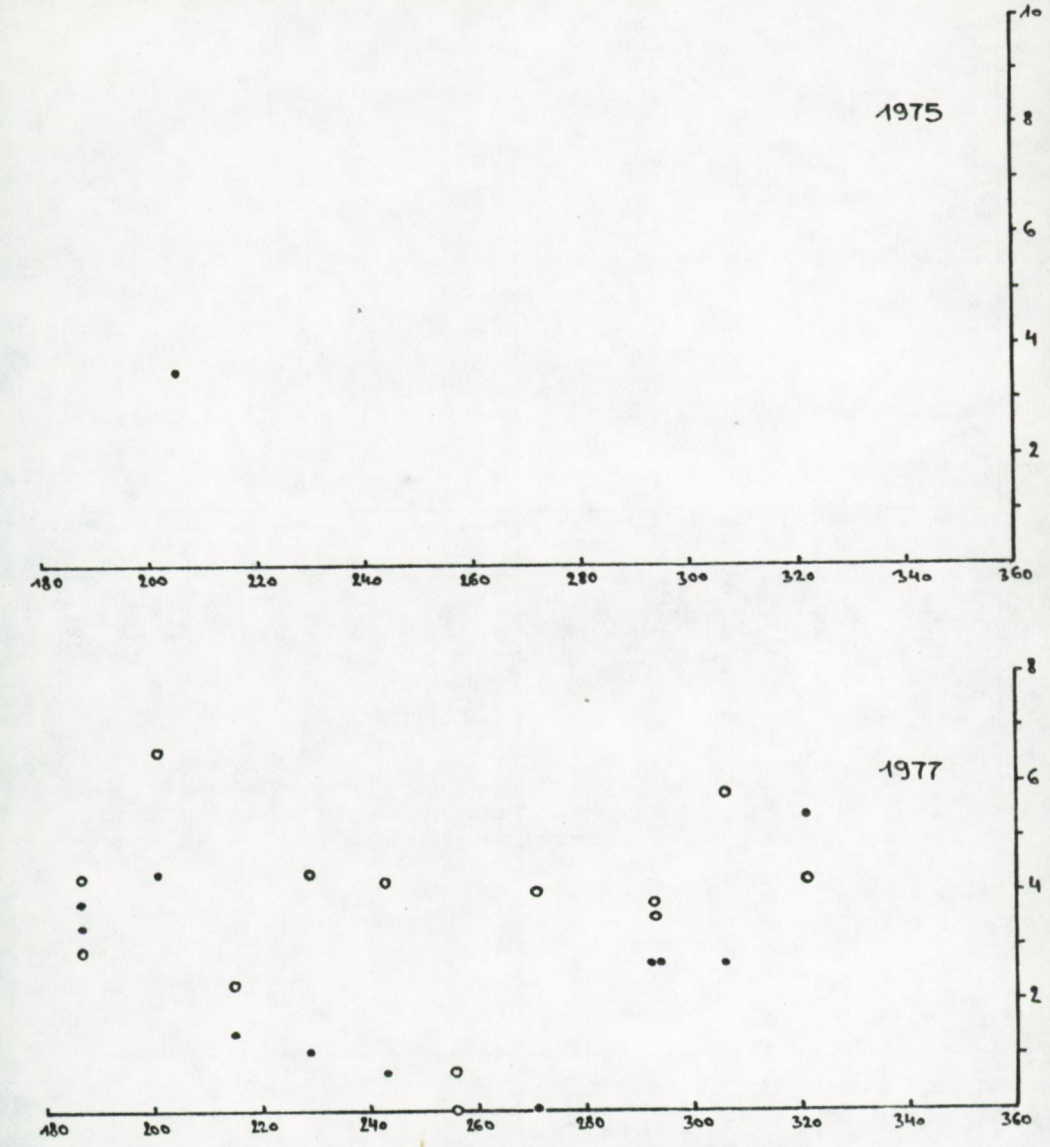
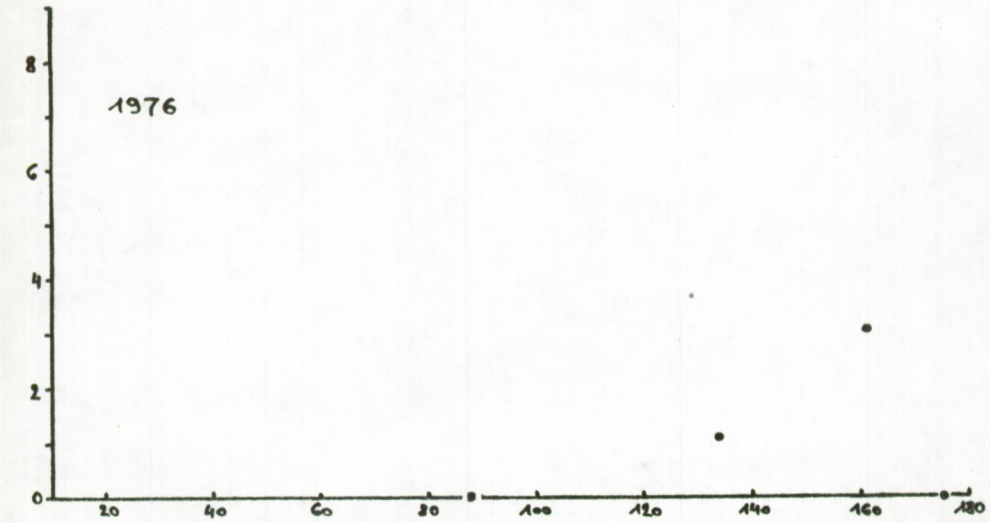
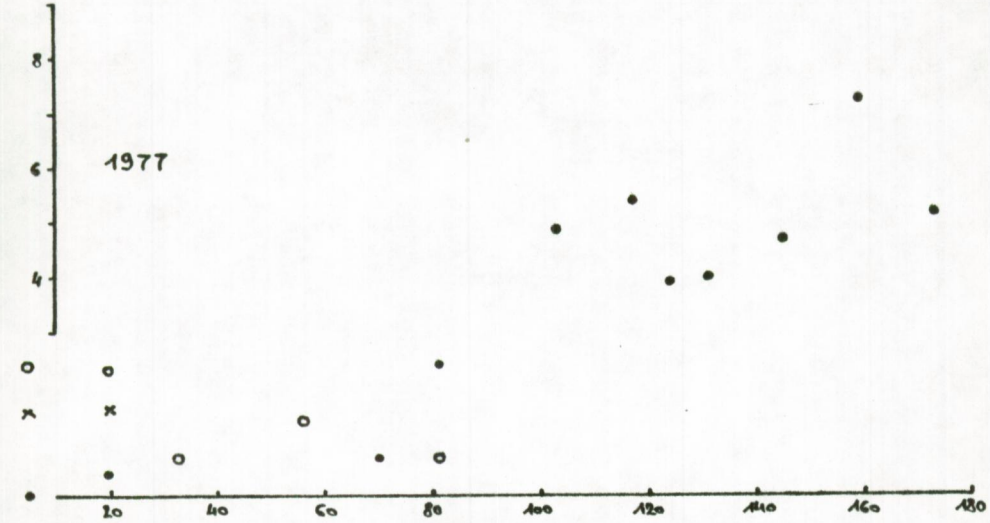


Fig. 2.12. Total-population densities of T. furcata and T. battagliai on the subsurface tiles. Symbols as in Fig. 2.11.


1976
8
6
4
2
0
20
40
60
80
100
120
140
160
180


1977
8
6
4
20
40
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80
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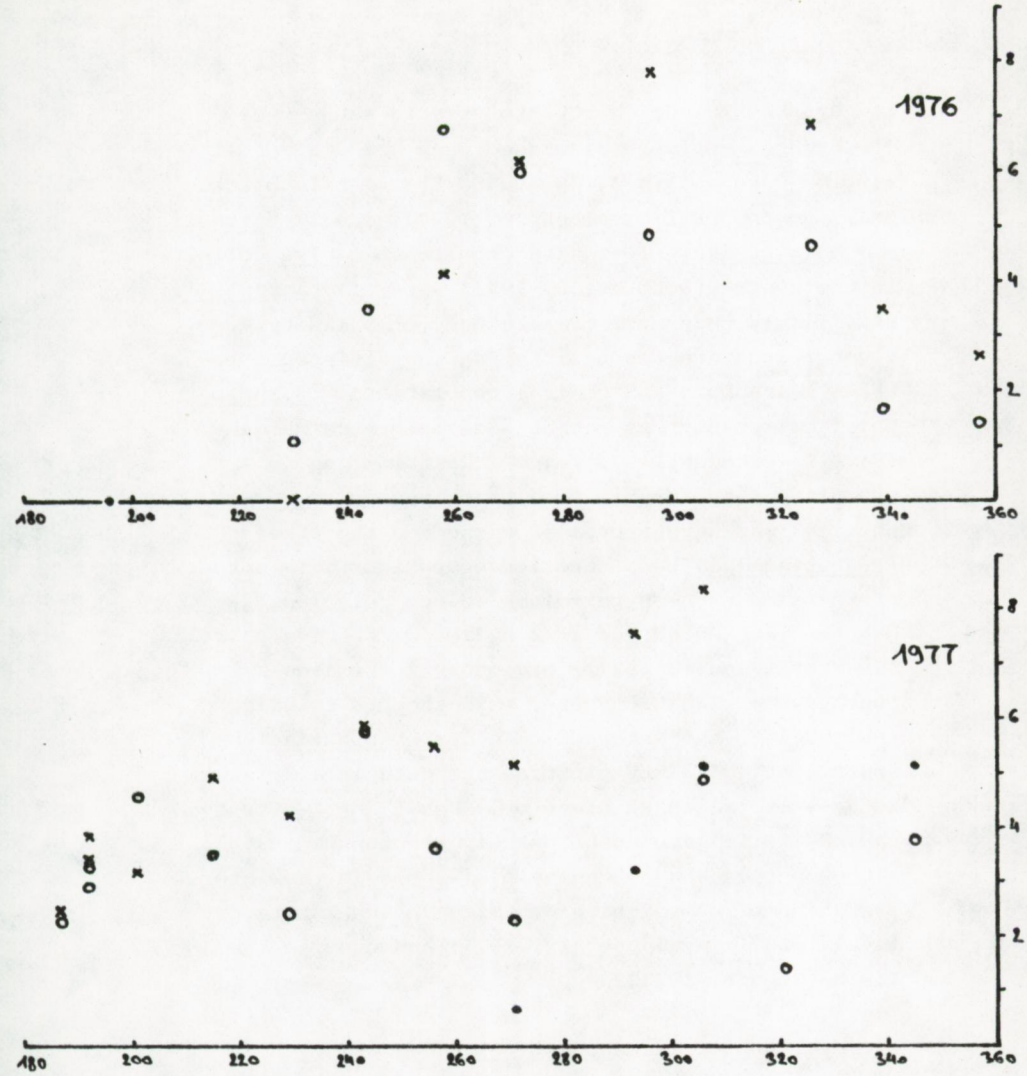


Fig. 2.13. Total-population densities of T. furcata, T. battagliai and T. holothuriae on the Ulva. Symbols as in Fig. 2.11.

The hypothesis that substrate effects cause these differences could be dismissed when some "atypical" samples were analysed: 20 adults from a tile placed near the border (September 28, 1977) were 17 battagliai + 3 holothuriae; 10 adults from benthic Ulva collected in the centre (October 20, 1977) were all battagliai. More likely than not, temperature (or salinity?) fluctuations are responsible for the difference between near-shore and central populations. T. holothuriae probably has rather wide tolerance margins (Fava & Volkmann, 1975), and it is tempting to speculate that in this species pair, one (T. holothuriae) may have a broader niche and the other (T. battagliai) be a superior competitor in a subset of the same niche hypervolume. Such relationship has been suggested for an Enhydrosoma species pair (Ivester & Coull, 1977); obviously it remains a tentative explanation here. My attempts to gain insight into the interaction of T. holothuriae and T. battagliai by plotting the data in a Lotka-Volterra phase plane or a Dewit input-output-ratio diagram have unfortunately been unsuccessful, although these have been helpful tools in the interpretation of competitive dynamics in the laboratory (Ayala, 1971; Ayala et al., 1973) and even in the field (Dhondt, 1977).

A comparison of Tisbe phenologies

Seasonality data on the Sluice Dock species may be compared with what limited findings have been published for other habitats. Seasonal censuses have been made in the lagoons of Venice (Fava & Volkmann, 1975), Scardovari (Fava & Volkmann, 1977) and Marano (Fava, 1980). Hicks' (1977) work in Cook Strait, New Zealand seems to contain the only

diachronic Tisbe data worthy of that name outside the Northern Adriatic.

As may be expected from biogeographical considerations, data for comparison are not available for T. gracilis. T. furcata was also absent in the above-mentioned localities except for the lagoon of Venice, where it was nevertheless exceedingly rare. The fact that 8 out of 11 specimens were collected in May (Fava & Volkmann, 1975) does, however, suggest a Venice phenology similar to the March-May bloom in Ostend. The T. bulbisetosa population behaved predictably both in Venice and Scardovari (the Marano data being fragmentary), but here the patterns differed greatly: a recurrent fall-winter bloom in Scardovari is in much better agreement with my Sluice Dock finds than the more or less well-timed May-June highs near Venice.

In Scardovari, T. battagliai has pronounced May 'explosions' whereas T. holothuriae apparently fluctuates unpredictably. This accords with observations in the lagoon of Venice where, unfortunately, T. holothuriae and T. battagliai were not routinely distinguished. As a whole, the Venice pattern for the group (year-round presence with unpredictable outbursts) is not unlike the Sluice Dock situation. The Ostend, Venice and Scardovari data show that for T. holothuriae at least, one should not generalize from one-year sampling programmes. Those available, as could be expected, yield conflicting evidence: a summer maximum was found in Marano (June in the text, May in the table) and a summer bloom in Cook Strait (October-February in New-Zealand!); on the other hand,

Marcotte & Coull (1974) found T. holothuriae (cf. Volkmann, 1979b) to dominate their winter samples and to be absent in those taken in summer in the bay of Piran, N. Adriatic. Most reports agree in considering that T. holothuriae is more favoured in environments subject to physical stress, both on a large (brackish lagoons vs. properly marine habitats: Fava & Volkmann, 1975) and a small scale (supralittoral pools vs. lower tidal levels: Hicks, 1977). The differential distribution of T. holothuriae and T. battagliai in the Sluice Dock repeats the same theme.

T. furcata : The population dynamics

T. furcata is a true inhabitant of the Sluice Dock, occurring year-round on both types of substrates (Figs. 2.4 to 2.12, especially for 1977). Its disappearance from the samples between May 26 and December 4, 1976 is probably related to exceptionally high summer temperatures; though population densities were then reduced below a level that could be detected with the present sampling procedure, downright local extinction appears unlikely.

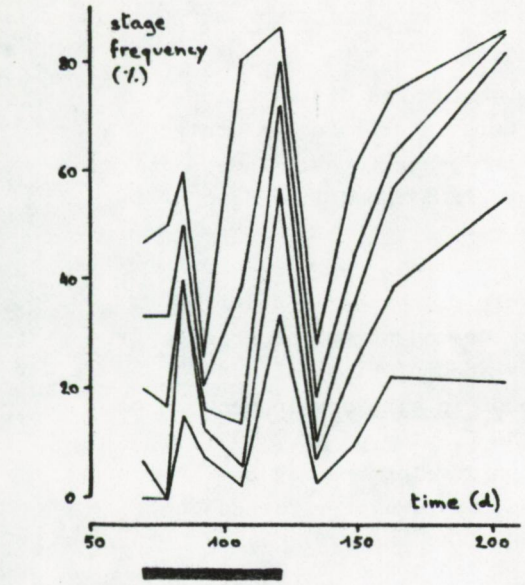
The dynamics of this species are characterized by a highly predictable spring bloom (Fig. 2.11 & 2.12). Vanden Berghe & Bergmans (1981) have hypothesized that the population explosion of T. furcata arises in response to a temporary 'food rain' from the plankton. Bacteria may be involved (ibid.), but the development of T. furcata also parallels (rather than follows) the bloom of the Euglenophyte, Eutreptiella marina (Mommaerts-Billiet et al., 1974). Unfortunately, in no case were data on the phytoplankton and Tisbe populations available for the same year.

The features of the bloom - as observed on the bottom tiles - are summarized in Table 2.1. Realized rates of increase were determined as the slopes of the linear ln N-on-time regression lines. These estimates are less variable from one year to the next, and can be regarded with more confidence, for the adult as compared to the total population. Indeed, individual differences in physiological age within an initially synchronous birth cohort increase as development proceeds (see Figs. 4.1 and 4.2); therefore the rise in adult numbers is smoother and less sensitive to the reproductive pulses characterizing population growth before a stable age structure is reached (cf. Zurlini & Ferrari, 1979). Theory predicts that, if fixed-schedule exponential growth (or, for that matter, stationarity or decline) lasts long enough, the population should eventually converge towards such a stable age distribution. In fact, Taylor (1979) has compiled evidence indicating that for (terrestrial) arthropods with seasonally limited population growth, attainment of the stable age distribution is the exception rather than the rule - too little physiological time being provided during the favourable period. Figs. 2.14 and 2.15 show that damped oscillations converging on the stable stage distribution were not observed during T. furcata blooms (indicated by thick bars).

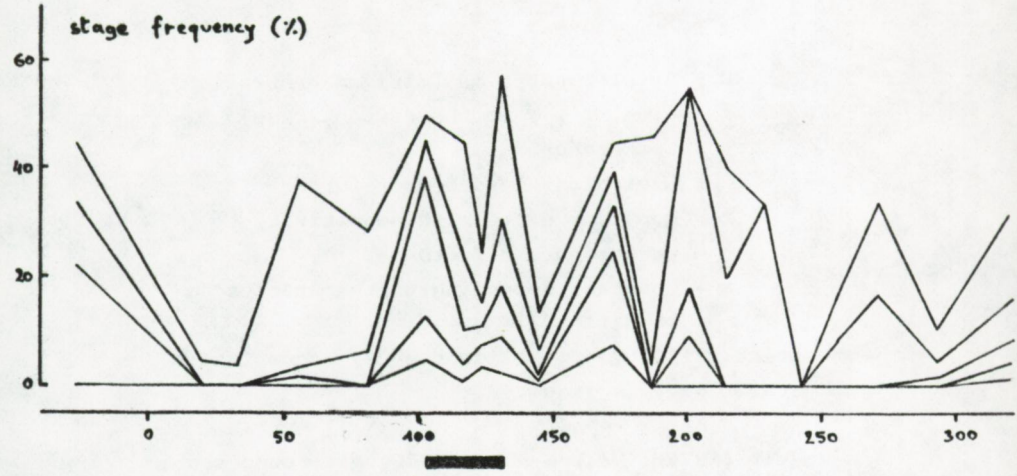
The fact that no s.a.d. was approached outside the bloom either may in part be due to a similar reason, in part also to temporarily low numbers of T. furcata sampled. During the bloom, however, stage structures were derived from fair sample sizes,

Table 2.1. Bloom characteristics of *T. furcata* in the Sluice Dock during three successive years

bloom	spring 75	spring 76	spring 77
minimum duration	March 11 - May 1 (51 d)	April 2 - May 26 (54 d)	April 13 - May 11 (28 d)
# of data points (tiles)	8	4	6
realized rate of increase of the total population (with correlation coefficient of linear regression)	.172 (.982)	.097 (.995)	.127 (.933)
realized rate of increase of the adult population (with correlation coefficient of linear regression)	.141 (.988)	.103 (.999)	.121 (.931)
estimated number of T_{min} (see text)	.93 between peaks of juveniles 1.23 for 'total' bloom	1.84 for 'total' bloom	.85 between peaks of juveniles .88 for 'total' bloom



Stage structure fluctuations in the T. furcata population (bottom tiles).
Fig. 2.14. 1975.
Fig. 2.15. 1977.
Black bars indicate minimum span of bloom.



and the wave running through the age distribution (Figs. 2.14 and 2.15) is here interpreted as truly indicative of two successive generations. Independent support for this view comes from the following considerations.

The speed of life-cycle processes in poikilotherm organisms is largely dependent on temperature. The concept of 'degree-day accumulation' allows fairly accurate prediction of *in situ* development from meteorological records (Varley *et al.*, 1973). An estimation of population development may be attempted by feeding plausible parameter values into Bělehrádek's equation:

$$D = a\,(T - \alpha)^b \qquad (1)$$

where

D = development time (minimum generation time, T_{min}, in the present case)
T = temperature
α = biological zero temperature
b = constant expressing sensitivity to temperature effects
a = constant depending on the species' physiology.

For strict validity of the 'degree-day accumulation' approach, b = -1 is required.

Heip (1974b; Heip & Smol, 1976) has found that, to a first approximation, α may be set to zero for copepods. When this is done, values of b for different species range from about -.5 to about -2.5, and actually have a mean of about -1.0 (Heip & Smol, 1976). When eq. (1) with $\alpha = 0$ is

fitted to published data for Tisbe, the following values are obtained for b: for T. 'dilatata ≠ T. bulbisetosa -1.46 (Muus, 1967); for T. pori -1.74 (Betouhim-El & Kahan, 1972); for T. holothuriae -1.18 to 1.54 (Parise, pers. comm. 1975; Gaudy et al., 1982) but also -1.70 to -2.48 (Parise & Lazzaretto, 1966; Battaglia & Parise, 1967; Gaudy & Guérin, 1978). The physiology of congeners need not, however, be a reliable guide to that of T. furcata. Sarvala (1979; Appendix) reports that of 2 spp. of Moraria co-occurring in the same habitat, the 'summer' species M. mrazeki has b = -1.45 and the 'winter' species M. brevipes has b = -.92. In the Sluice Dock, T. holothuriae and T. bulbisetosa are the warm-water species, T. furcata the cold-water one. (T. pori is a mediterranean species.) Moreover, Epp & Lewis (1980) have argued convincingly, and adduced evidence, that in organisms exploiting seasonal resources, relative metabolic independence of temperature (i.e., b → o) over the T-range encountered should be selected for.

All things considered, α = 0 and b = -1 appears a good 'educated guess' for T. furcata. From D = a/T and the fact that T_{min} at 18°C is about 15 d for the wild population (see chapters 4,5 of the present thesis), the amount of degree-days required to complete the life cycle can then be estimated at 270.

Daily air temperatures at Ostend during the three bloom periods considered have been taken from the Bulletin Mensuel de l'Institut Royal Météorologique de Belgique. I observed the empirical

relationship

(daily mean water T) = .805 (daily mean air T) - 1.303

(n= 11, r = .831). Piecing together the information, the equivalent - in T_{min} units - of the total thermal energy received during each bloom could be calculated (Table 2.1). Given the approximate knowledge of T. furcata's temperature response, and given the fact that blooms may have extended slightly beyond the observed period (which was estimated conservatively), the figures are encourageing.

As a final point of interest, the realized rates of increase observed may be compared to the more nearly optimal or 'intrinsic' values computed for laboratory-raised cohorts. Three such cohorts (see chapters 4,5) yielded values of r = .197 - .279 at 18°C. Taking into account the slower development in situ (peak-to-peak distances in Figs. 2.14 and 2.15: 36 d and 28 d; if these are T_{min}, they are about twice the values at 18°C), optimal r would be in the order of .100 - .140. In other words, 'environmental resistance' during the spring expansion of T. furcata would be almost nil (cf. Table 2.1). A rather close parallel is provided by Heip & Smol's (1976) statement that Tachidius discipes and Paronychocamptus nanus realize (much) more than half their potential for population growth during spring blooms. This leads us naturally to the next topic.

T. furcata: A search for density dependence

The analysis of stage structures may throw light on yet another question, viz. that of density effects c.q. regulation. In the discussion which follows, the term 'regulation' will be restricted to actual control of the population size reached.) As Figs. 2.11 to 2.13 show, *in situ* population growth is never sigmoid. Blooms of the epibenthic population in the centre of the dock consist of a marked exponential rise abruptly followed by a comparable regular decline. Neither phase involves obvious intrinsic density regulation - a conclusion which also follows from the fact that *T. furcata* apparently realizes the major part of its reproductive potential.

To examine the possibility of density effects in a more quantitative way, the regression of ln (number of juveniles) on ln (number of adults) was calculated for all available data points (= individual samples containing at least 1 copepodite and 1 adult). Unlike some classical tests such as regression of N(t+1) on N(t) or k-value analysis (Varley *et al.*, 1973) this approach avoids the problems associated with serial correlation and a lack of statistical independence of data (cf. Benson, 1973). A drawback, on the other hand, is that it does not automatically provide an equilibrium hypothesis (comparable to N(t+1) = N(t)) but, as will be seen below, this can be overcome.

Fig. 2.16 presents the data obtained from tiles - both 'subsurface' and 'bottom', as these two groups completely overlap. The calculated

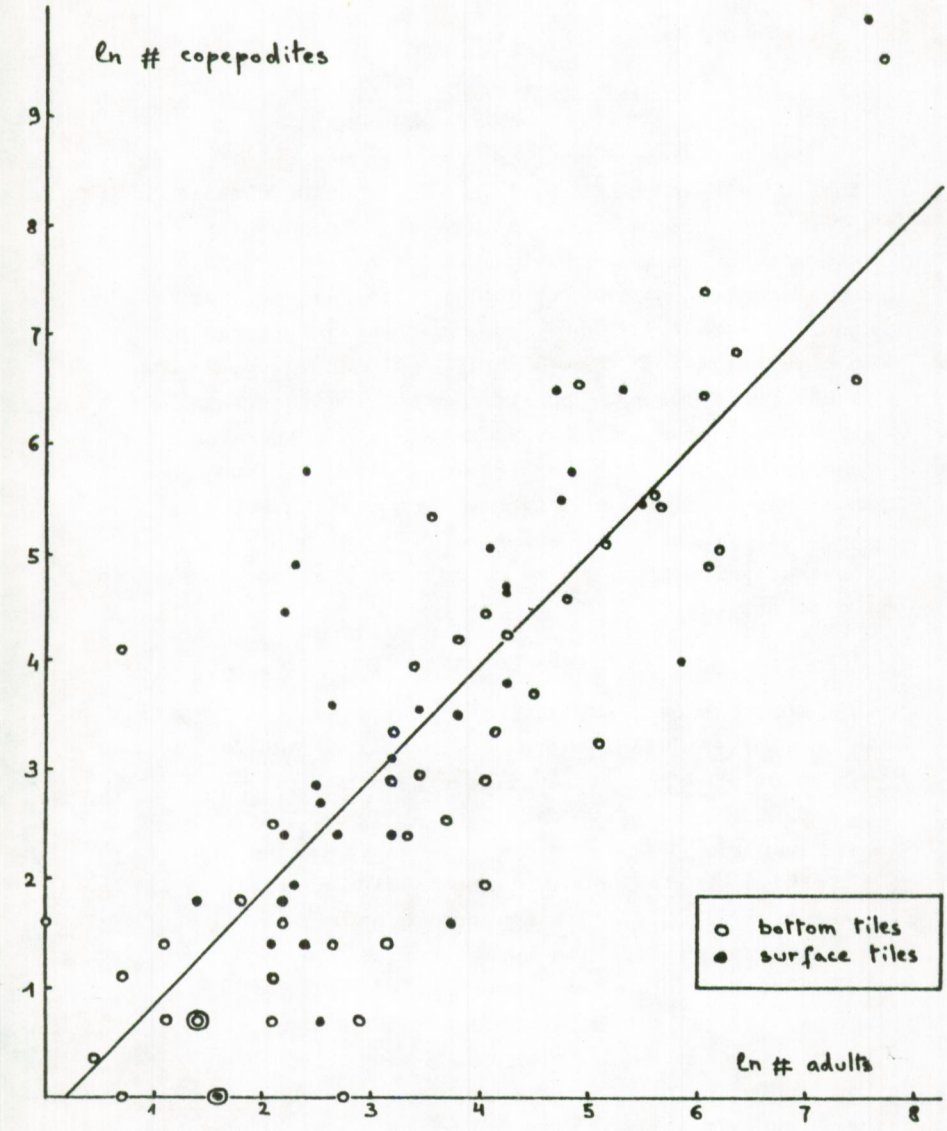


Fig. 2.16. Regression of ln (# copepodites) on ln (# adults) for T. furcata on the tiles.

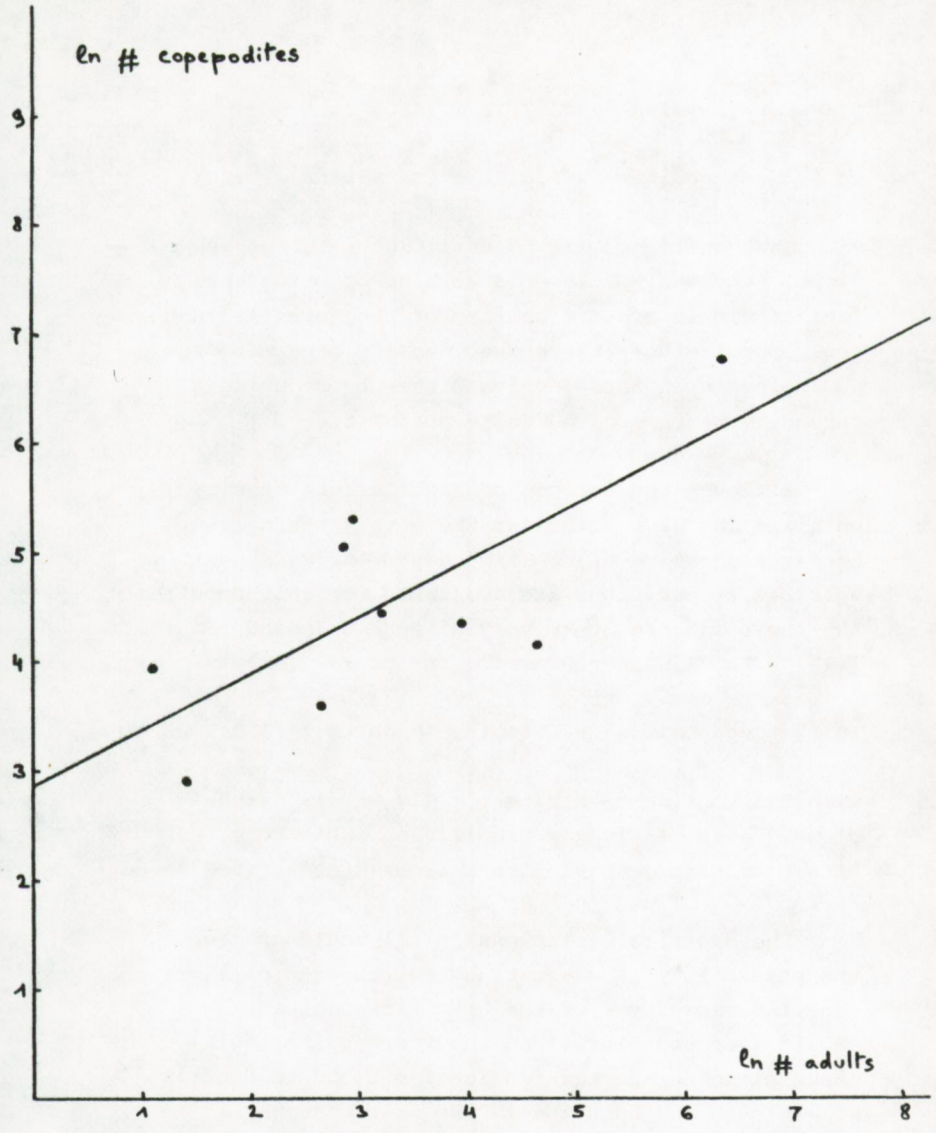


Fig. 2.17. Regression of ln (# copepodites) on ln (# adults) for T. furcata on the Ulva.

linear regression (n = 77, r = .820) is

$$\ln (\Sigma \#\text{copepodites}) = 1.036 \ln (\#\text{ adults}) - .203$$

with 95% confidence limits of $1.036 \pm .166$ on the slope. Obviously, there is nothing opposing the idea of simple proportionality of the juvenile and adult populations; therefore, density does not seem to impinge upon reproduction either by reducing fecundity or raising juvenile mortality.

Although the periods of high furcata density on tiles and Ulva coincide, the Ulva pattern is hardly suggestive of unhampered growth. Far fewer workable observations are available for this population, but their pattern looks very different indeed (Fig. 2.17). The linear regression (n= 9, r= .742) is

$$\ln (\Sigma \#\text{copepodites}) = .514 \ln (\#\text{adults}) + 2.845 \qquad (2)$$

with 95% confidence limits of $.514 \pm .416$ on the slope. A statistically significant inhibitory effect of high densities is thereby demonstrated.

The empirical relationship (2) would open up the possibility of estimating the (theoretical) carrying capacity K of the Ulva microhabitat, should a second 'locus' in the (copepodite,adult) phase plane be known which is also bound to contain K. This second function is the stable stage structure, which may be derived from demographic considerations along the following lines.

The general formula for the stable age distribution (Pielou, 1977)

$$\int_a^b {}_1x e^{-rx} dx \Big/ \int_o^\infty {}_1x e^{-rx} dx \ ,$$

reduces to

$$\int_a^b {}_1x dx \Big/ \int_o^\infty {}_1x dx \qquad (3)$$

in the case of a stationary population. The denominator in the latter equation is nothing but the life expectancy of a newborn. The survival schedule appearing in (3), as it would exist in a density-regulated population, is effectively unknowable; however, it can be determined for a population in a 'density vacuum' - this will be done in chapter 4. It may now usefully be pointed out that density effects in Tisbe are most likely unidirectional, being primarily an effect of adults on juvenile survival (Fava, 1974; Hoppenheit, 1977). If all density-dependent mortality is concentrated on the nauplii, this will alter the relative frequencies of nauplii vs. older stages in the stable age distribution, but leave the relative frequencies of the copepodite stages (including the adult) unaffected, relative to the 'density vacuum' situation. Another likely density effect, viz. reduced adult fertility, is completely neutral with respect to eq. (3).

All this means that the 'density vacuum' observations of chapter 4 may be a fairly reliable guide to the copepodite stage structure under density limitation.

In the cohort of chapter 4, then, life expectancy of newborn females and males was 53.58 d and 60.58 d, respectively. Of these, females spend 9.87 d as juveniles, and of these, 6.52 d as copepodites. The corresponding figures for males are 8.70 d and 5.35 d (see Table 4.1). Assuming a 1:1 sex ratio for the sake of argument, the expected equilibrium proportion (on a total excluding the nauplii) is 11% copepodites, or 1 copepodite to 8 adults. This provides the second relationship required,

$$\ln (\sum \#\text{copepodites}) = \ln (\#\text{adults}) - 2.079 \quad (4).$$

The combination of (3) and (4) yields equilibrium estimates of 25 000 adults + 3 000 juveniles per quantum of Ulva. As can be taken from Fig. 2.15, the maximum total density in an Ulva sample actually observed was about 1400, or only 1/20th of 'carrying capacity'. Fowler (1981) concluded from a survey of the literature that density dependent effects on reproductive performance should be most pronounced far from carrying capacity in species with short life spans, high reproductive rates and densities usually far below resource-determined K. This seems quite applicable to the Ulva population of T. furcata. Though density effects make themselves felt, then, they certainly do not control the population size reached. My findings would seem to lend empirical support to Hicks' (1979) hypothesis

that food is not a limiting factor in phytal harpacticoid populations. Ironically, although Ulva qualifies as an ephemeral substrate, it was among the algae which Hicks (1980) found to be inhabited by relatively 'equilibrium' communities, judging from its harpacticoid species-abundance plot. Still, the association of T. furcata and other Tisbids with (not always clearly substantiated) break-points in the species-abundance curves, considered indicative of temporary unchecked population expansions, finds confirmation here. The findings are of special interest because the question of population regulation in harpacticoids is seldom approached otherwise than intuitively. To my knowledge, only Fleeger (1979) tackled it directly: From a comparison of instantaneous birth and death rate patterns, along with the conjectured (lack of) susceptibility to predation of different species, he could plausibly infer density regulation (resource limitation) in Stenhelia bifidia. Compared to demographic phenomena characterizing the neighbourhood of K, the effects detected in my Ulva data appear quite subtle.

Finally, the analysis may be taken one step further by examining the form of the relationship between 'realized reproduction' and density. If 1 copepodite should be present to 8 adults in a population exactly capable of replacing itself,

$$S = 8 \times (\#\text{copepodites}) / (\#\text{adults})$$

is a measure of the population's 'surplus' capacity for growth. (Its conceptual kinship to the realized

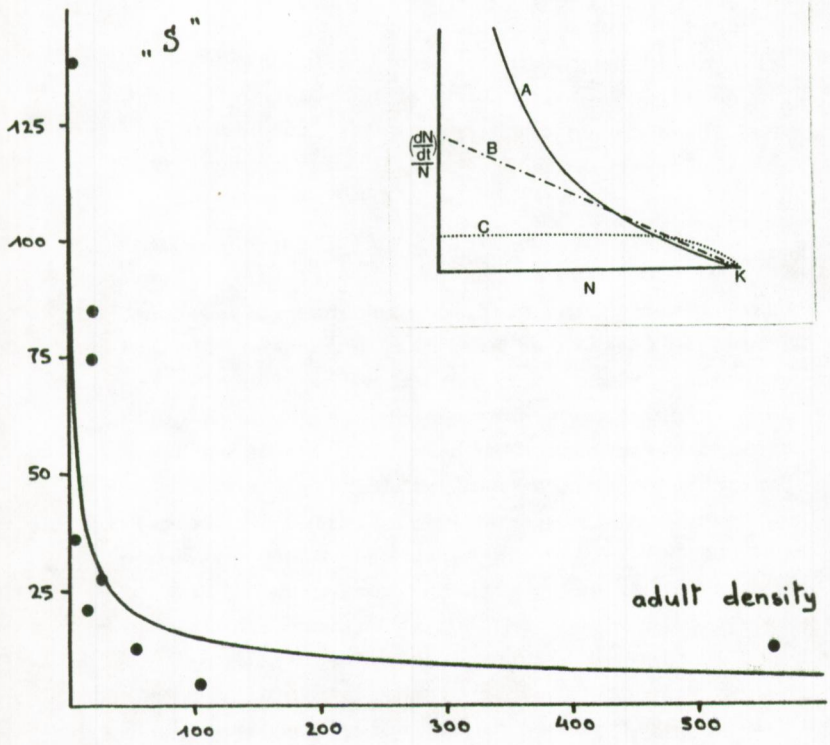


Fig. 2.18. - A, relationship between 'potential for population growth' and adult density for T. furcata (Ulva population).
- B, relationship between realized per capita growth and population density, as taken from Fowler (1981). Curve A refers to quickly-reproducing, short-lived, low-density species.

per capita growth rate, (dN/dt)N, is evident.) Fig. 2.18A displays this measure as a function of adult density. Though it could not a priori be taken for granted that the linear relationship (2) would survive such a drastic change of scale, it is seen that

$$S = 137.6\ (\#\text{adults})^{-.486}$$

(obtained by dividing (2) by (4)) gives a 'satisfactory' description of the data. Clearly, the relationship is concave, as predicted by Fowler (1981) for short-lived, fast-breeding, low-density species : see Fig. 2.16B.

Chapter 3

Prolegomena to harpacticoid demography: A critical look at the state-of-the-art

Abstract

Published studies on the demography and reproductive strategies of harpacticoid copepods are critically examined. At the technical level, the popular approximation $\ln R_o / T_c$ is shown to be inappropriate as an estimate of their intrinsic rate of increase: It leads to a systematic underestimation by 10 - 30 % for parameter values typical of the fast-breeding species. Various home-brewed variants of the r_m and R_o calculations occurring in the literature are also criticised. At the conceptual level, the necessity of a more discriminating approach to life history characteristics is advocated; this applies both to the very assessment of their 'strategic' significance, and to their diagnostic power with regard to the various 'strategies'. Attention is drawn to the non-equivalence of parity and voltinism. Recommendations are made which should promote the construction of a more rigorous cognitive framework.

Introduction

A science comes of age when the purely descriptive approach begins to be complemented with purposeful experimental studies, generated by explicit hypotheses. By this criterion, the field of harpacticoid demography is at present crossing the boundary. (Lopez (1982) provides one example, chapters 5 - 6 of this thesis another.) Lest such developments be based on defective foundations, it appears timely to examine in a critical way the now-existing data and concepts.

The subject matter, of course, is vast. Interpretative reviews of several topics are already available (e.g., phenology and reproductive seasonality: Coull & Vernberg, 1975; reproductive strategies: Hicks, 1979) and a full-length treatment of harpacticoid ecology is forthcoming (Hicks & Coull, in press). In this chapter, no attempt will be made to give a complete coverage of all possibly relevant data scattered throughout the literature. Instead, attention will be focused on selected themes bearing directly on work reported in this thesis, viz., technical aspects concerning the computation of demographic parameters (see chapter 4) and conceptual aspects relating to life histories (see chapters 5 and 6). Biased estimates of demographic parameters may be quite harmless for certain purposes (e.g. establishing the existence of particular environmental effects) but will thwart proper population prediction - which is what demography is about; the effect of loose and inexplicit concepts, though less readily apparent, may prove an even greater handicap in the long run. It is hoped that the present critical

treatment may help eradicate some unfortunate traditions which, being easily remediable, should not be allowed to perpetuate themselves by mere inertia.

Computation of reproductive rates

Fundamental quantities in any demographic analysis include measures of offspring number (e.g. R_o), generation time (e.g. T_{min}) and the distribution of offspring production in time (e.g. r_m). Accurate computational methods applicable to empirical data can be found in textbooks such as Pielou (1977), in those harpacticoid life cycle studies which deal with demographic procedures in didactic detail (Parise & Lazzaretto, 1966; Bergmans, 1981), and in chapter 4. For easy reference, the definitions of the principal parameters and the logical relationships between them have been assembled in Table 3.1.

The intrinsic rate of natural increase

If one were to single out a 'curse' of harpacticoid demography, confusion between r_m (eq. 1) and r_c (eq. 5) would certainly qualify. It shows up in Lazzaretto & Parise (1967), Volkmann-Rocco & Fava (1969), Heip & Smol (1976) - in spite of the lucid remarks in their Material and Methods section -, Gaudy & Guérin (1977, 1978), D'Apolito & Stancyk (1979). In some instances confusion simply stems from the misleading isomorphism between eq. 4 and eq. 5, often in conjunction with ambiguity about the meaning of 'generation time' and/or the illegitimate assumption that T_c will always give a reasonable approximation of T. Sometimes the belief that r_m and r_c can be interchanged

Table 3.1. Principal formulae used in descriptive demography.
Arrows indicate the direction of logical relationships. The life table and fertility schedule provide the fundamental observed quantities l_x and m_x.

Eq. 1

$$\int l_x m_x e^{-rx} dx = 1$$

Defines the intrinsic rate of natural increase, r_m, in terms of the age-specific mortality and fertility schedules.

Eq. 2

$$T_c = \int x l_x m_x dx \Big/ \int l_x m_x dx$$

Defines the cohort generation time, T_c, in terms of the age-specific mortality and fertility schedules.

Eq. 3

$$R_o = \int l_x m_x dx$$

Defines the net reproductive rate, R_o, in terms of the age-specific mortality and fertility schedules.

Eq.4

$$r_m = \ln R_o / T$$

Defines generation time s.s., T, in terms of r_m and R_o.

Eq. 5

$$r_c = \ln R_o / T_c$$

Defines capacity for increase, r_c, in terms of T_c and R_o.

at will is concealed in a delusive Lotkaic presentation: D'Apolito & Stancyk (1979) profess to apply the Lotka formula (eq.1) but proceed quite unnecessarily to lump all reproductive activity into a single age class, thus effectively reducing it to 'r'= $\ln R_o/T_{min}$ -- yet another of the various approximations to eq.1, which, admittedly, performs slightly better than eq.5.

As can easily be checked, $r_c \simeq r_m$ if and only if either 1) $R_o \simeq 1$ or 2) the organism under study is semelparous, all ofspring being produced in a single simultaneous batch. Eq.1 is the only one yielding the correct intrinsic rate (correct within limits imposed by grouping over time intervals) in all cases, and therefore also in the case of iteroparous organisms. In the latter, T is defined in terms of r_m, not vice versa (eq. 4), and as is known at least since Parise (1966), r_c will seriously and systematically underestimate r_m. (Even if one chooses to call the bias 'slight', as do Gaudy et al. (1982), it would seem preferable to call r_c by its own name.) May (1976) gives formulae to estimate or, in the case of simple idealized life tables , compute the relative systematic error $(r_m-r_c)/r_c$. In several species of Tisbe where values of both parameters are available (see Table 4.4) the bias introduced by eq. 5 ranges from 8 to 29 %. Another example is provided by Tachidius discipes, using Heip & Smol's (1976) values at 20°C (6 egg-sacs per female produced on the 18th day and every 3rd day subsequently; 41 eggs per egg-sac, a sex-ratio of 67% ♀♀ and no embryonic or juvenile mortality). The bias involved in applying eq. 5 is an estimated 11%. In fact, Heip & Smol (1976) did not apply

$r_m \simeq \ln R_o / T_c$, as claimed later (Heip et al., 1978) but used $r_m \simeq \ln$ (# eggs in first egg sac) / T_{min} which results in an underestimate by 21 %. (Of course, this does not affect the authors' perfectly valid conclusion regarding the considerable effect of temperature on the rate of increase.

Also in connection with r_m, a comment is due on a somewhat idiosyncratic procedure. Starting from the correct observation that the calculation of r_c does not take into account adult mortality (while that of r_m does), Heip (1972) 'corrected' his previous laboratory estimate by subtracting adult mortality as observed in the field. It is difficult to see how this could result in improving a value which is already an underestimate.

To put matters squarely: the computation of r_m from observed l_x, m_x by eq. 1 is so straightforward that use of r_c as an approximation must be discouraged altogether : eq. 5 introduces an unnecessary bias while not even fully exploiting high-resolution observations of l_x and m_x.

The net reproductive rate

Lack of insight into the nature of R_o may be another problem, as exemplified by D'Apolito & Stancyk's (1979) paper. The fundamental life table parameter l_x, i.e. the probability of survival to age x, is sometimes scaled to 1,000 initial individuals and sometimes to 1 (Pielou, 1977, p.66). Obviously only the latter scaling is appropriate in computing R_o = the number of daughters expected to be born to each newborn female. Choice of the

wrong l_x values led D'Apolito and Stancyk to compute R_o and r_m values which by chance happen to be of an acceptable order of magnitude for harpacticoids, but which nevertheless bear no justifiable relationship to their own data.

Another sore point in the same paper has to do with R_o as the factor by which the population size is multiplied from one generation to the next. Its value remains unaffected by the stage which one chooses to use as o-age class, as long as the x, l_x and m_x adopted encompass one complete life cycle. (The equivalent 'life-history graph method' (Hubbell & Werner, 1979) may be helpful in providing insight into this.) So it makes no sense to have m_x values in terms of nauplii 'corrected' for embryonic mortality (D'Apolito & Stancyk, 1979, table 4) : by thus increasing the m_x by a factor (embryonic mortality)$^{-1}$ without concurrently decreasing the l_x by (embryonic mortality), fertility in terms of eggs is being combined with n_1-to-adult survival. Obviously, transitions to m_x and l_x values linked to any age or stage other than the observed one, always cancel each other out when R_o is computed correctly.

Loose ways with published information

Biased estimates of r_m and R_o are by far the most common, but not the only blemish on the harpacticoid demography literature. Faulty data on the number of ontogenetic stages abound (see chapter 4: Discussion). On this matter one could be inclined to take a lenient view, as there is

something of a historical tradition here. Misuse of correct information is less excusable. Reviewers commonly fail to distinguish 'larval period', 'generation time' (to be defined) and 'minimum generation time' (Gaudy & Guérin, 1977, table 3; D'Apolito & Stancyk, 1979, table 5). Gaudy & Guérin's table itself is further mutilated in Walker (1979). Gaudy & Guérin (1977) wondered at Hoppenheit's (1975b) observing realized rates of increase up to 2.33 for Tisbe holothuriae -- apparently without realizing that the latter figure was expressed on a weekly instead of a daily basis. The same authors approvingly quote Heip's (1972) r_c = 0.237 for Tachidius discipes in the lab, though Heip himself clearly stated that this value becomes 0.193 when sex-ratio among offspring is taken into account. All these instances sadly illustrate the general principle that information can only decay in the course of transmission.

Reproductive strategies

The classical unidimensional r-K-concept has for some time ceased to be the unchallenged paradigm of reproductive strategies (see in particular Stearns (1977) for criticism and Grime (1977) for one possible alternative). For harpacticoids a thought-provoking alternative view - at the very general level of the order as a whole - has in fact already been proposed by Hicks (1979). He suggests that dimensions relevant to such strategies include trophic resource abundance, specificity of dietary requirements and substrate persistence. This approach also leads to a roughly dichotomous pattern, viz. phytal species

(food supposedly never limiting; short life cycles and production of many small eggs) vs. sediment dwellers (resources limiting with one seasonally predictable optimum; annual life cycles and "parsimonious' production of few large eggs). Within each category, however, much residual variation remains which may be related to the second and third factors referred to above.

It would be beyond the scope of this thesis to enter the debate on the utility of the r-K-dichotomy as a description, if only heuristic, of reproductive patterns (though, in chapter 6, an operational alternative to the concept of K-strategy will be considered and tested). Instead, I shall examine whether authors professing to apply the classical concept -whatever its intrinsic merits - have done so in a way unobjectionable on grounds of internal consistency. Unfortunately, this is not always the case.

Choice of criteria

Sometimes invalid criteria have been applied, as by Hoppenheit (1978) when he used increased relative frequency of nauplii per se as evidence for an r-strategy. As pointed out in the next chapter, a 'young' age structure is a demographic epiphenomenon accompanying increased realized growth rates; it is to be expected even when no change in the fecundity function m_x occurs and the differences in realized r are wholly due to the manipulation of mortality (through population density).

Sometimes valid characteristics have been wrongly ascribed to putative r-strategists, as by Hicks (1979, p. 145) when he took univoltinism (the existence of a single population peak annually) to indicate semelparity (the concentration of all reproductive activity into a single age class). Similarly, the existence of more than one generation annually is hardly evidence for iteroparity. The error stems at least in part from the ambiguity of the word 'brood', which sometimes seems to refer to a single egg batch, sometimes to total F_1 (as in Jewett & Feder, 1977). A shift of meaning explains why what was interpreted as 3 generations of Porcellidium dilatatum in Hicks (1977), should have become 3 broods in Hicks (1979) and is there taken to indicate iteroparity. As Fig. 3.1 shows, however, parity and voltinism bear no necessary relationship to each other and all four combinations are logically possible. The distinction between some cases (e.g. the distinction, for univoltinism, between a unique iteroparous generation and a succession of semelparous generations) may be exceedingly difficult on the basis of in situ observations only, yet this distinction is crucial for a correct assessment of hypotheses on reproductive strategies. Without information on generation turnover, current indices such as % ovigerous females are difficult to interpret if not altogether misleading. E.g., long-term presence of nauplii may indicate slow development rather than prolonged recruitment (Feller, 1980b).

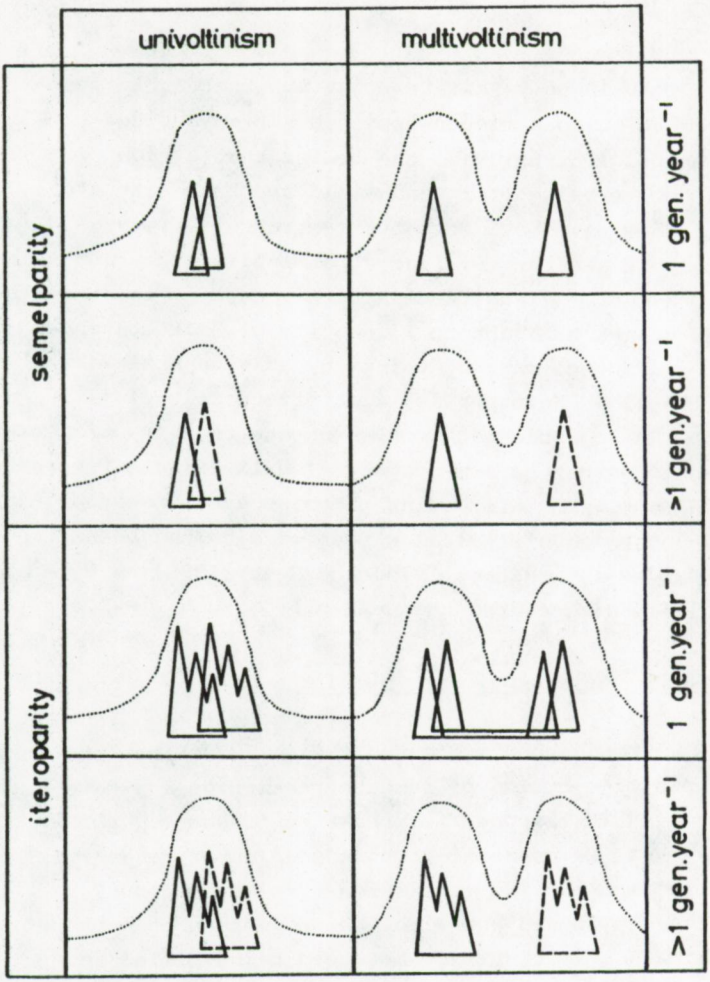


Fig. 3.1. Various possible combinations of voltinism, parity and annual number of generations. Shown are: population density over the course of 1 year (dots), fertility m_x of 1 or 2 ♀♀ of the 1st generation (continuous line) and of 1 ♀ of the 2nd generation where relevant (dashes). Life cycles extending over more than 1 year, as have been reported in freshwater spp. (Rouch, 1968; Sarvala, in press) require a different time scale for their interpretation.

It is only fair to point out that at least one ubiquitous misconception has been avoided by copepodologists, viz. the belief that a high absolute value of r_m and small absolute size are in themselves evidence for r-strategy. This belief, and the corollary that entire high-rank taxa can be classified as either r- or K-strategists, goes back straight to Pianka (1970). It continues to influence current thinking, as when Kozłowski (1980), in an otherwise appropriate criticism of the logistic equation, suggests that 'r-strategists' would merely be a synonym of 'small animal' (whereas in fact, the interesting patterns are those remaining when the physiological effect of size has been removed !). Hicks (1979) and Heip (1980) have wisely dissociated themselves from such views.

Search for evolutionary meaning

It has been suggested (Heip, 1974a) that the short life cycles of some harpacticoids may have evolved in response to predation pressure. This may well be correct, provided one interprets 'life span' as 'minimum generation time' throughout, lest one should end with the suggestion that these animals commit suicide to avoid being killed and eaten. The evidence advanced in support of Heip's view does not, however, bear on this thesis. The fact that a catastrophic population crash ensues whenever a female's expected time to fatal encounter with a predator grows less than T_{min}, is tautological - it holds just as well for even the most extreme K-strategist.

Desire to make evolutionary sense out of every observed reproductive phenomenon led Hoppenheit (1978) to the incongruous suggestion that individuals which find themselves at the K-end of the r-K-spectrum may adopt the 'strategy' of being unsuccessful breeders (i.e., of producing sterile egg sacs). Apart from attributing adaptive value to an obviously undesirable waste of energy, this interpretation ignores the fundamental distinction between unavoidable proximal effects (of temperature, food limitation, exploitation and interference competition, ...) and 'active' adaptations.

The moral

Experience and know-how in the culturing of harpacticoid copepod species, representing a broad spectrum of life histories, have steadily increased in recent years. They have thus become excellent material for quantitative studies, especially with regard to the temporal aspects of reproduction. That is why demographic research on harpacticoid copepods holds promises of new insights, perhaps even of broad ecological significance . Clearly, the data will not yield these under torture.
So if there is a message to be brought home from the above, let it be a plea for strictness. Three points at least seem especially worthy of consideration:

1. All calculations and interpretations should duly respect demographic theory (and logic).
2. Grandiloquent but facile and potentially fallacious analogies with disciplines such as thermodynamics and cybernetics would profitably be omitted,

especially in otherwise interesting population dynamics papers (e.g. Walker, 1979).

3. The term 'strategy' should not be used unless some stringent conditions are met. This remark does not refer to the fashionable if somewhat sterile discussion on its semantic appropriateness (Louw, 1979): many initial misnomers eventually became consacrated by usage without ill effects. ('Demography' is one of these: Cole, 1957.) The real danger does not lie in the unlikely suggestion of deliberating capacities in lower organisms; rather, it lies in the erosion of a concept turned into a blanket for phenomena the adaptive nature of which is sometimes far from obvious. Not only should every 'strategy' contribute to some evolutionarily desirable property (fitness) of the individual in a specified ecological context; above all, the phenomena cited as evidence for it must not be the mere expression of environmental influences on the organism. An animal's response to particular conditions can only be part of a 'strategy' when it demonstrably transcends physiological necessity, and a <u>different</u> response (entailing lower fitness) is at least theoretically possible.

Chapter 4

Ontogeny and life cycle of *Tisbe furcata* : A demographic study

Abstract

The life-cycle of *Tisbe furcata* 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 = 0.236 day^{-1}; net reproductive rate R_o = 94; minimum generation time T_{min} = 14.9 days; parameters related to 'generation time': T = 19.2 days, $\bar{T}$ = 16.4 days, T_c = 25.4 days. These observations are helpful in reassessing the taxonomic identity of the material used in some of the older 'classics' of the *Tisbe* literature.

Introduction

As pointed out in chapter 1, earlier studies of Tisbe 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, 1972b; Volkmann, 1975) and a good deal is already known about its ecology (Fava & Volkmann, 1975), demography (Hoppenheit, 1975a, b, 1976, 1977, 1978) and ecological genetics (Lazzaretto-Colombera et al., 1976; Fava et al., 1976).

However, Tisbe nearly always occurs as multi-species guilds in the field (see chapter 1 for my findings and chapter 2 for other references). Western-European samples such as those of Sars (1911) nearly always contain true T. furcata in addition to other congenors (Volkmann, pers. comm. 1979). A redescription of this apparently common species has been published (Bergmans, 1979) but no body of information comparable to that on T. holothuriae has become available so far. Only a qualitative life-cycle study exists (Johnson & Olson, 1948), and in fact, as will be shown below, it is evident that even this work does not relate to the species T. furcata.

In an attempt to fill this gap, I have studied the reproductive ecology of this species in the light of demographic principles. Although demographic and 'life history' 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. In this chapter, I present quantitative data on postembryonic development and on the age-specific mortality and fertility schedules of one particular cohort. In doing so, I also introduce the demographic methodology to be used in chapters 5 and 6.

Material and Methods

On April 24, 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 (# 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 (# females $\geq$ 40 yielding 151 nauplii). Culture conditions were based on standard methods for Tisbe (Battaglia, 1970). As previous experience has 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.

To compute the schedules and parameters discussed below, as well as some other standard demographic variables, I wrote a Fortran IV program which was run on the CDC of the V.U.B./U.L.B. Computer Centre. An annotated listing may be found in Appendix 2. Small differences between some time-related parameters as reported here and in Bergmans (1981) stem from the fact that this automated routine corrects for an incomplete first observation interval (time between birth and first census less than 24 h); in Bergmans (1981), this interval was assumed to be 1 day.

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 = 0.5 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. 4.1, 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. 4.2).

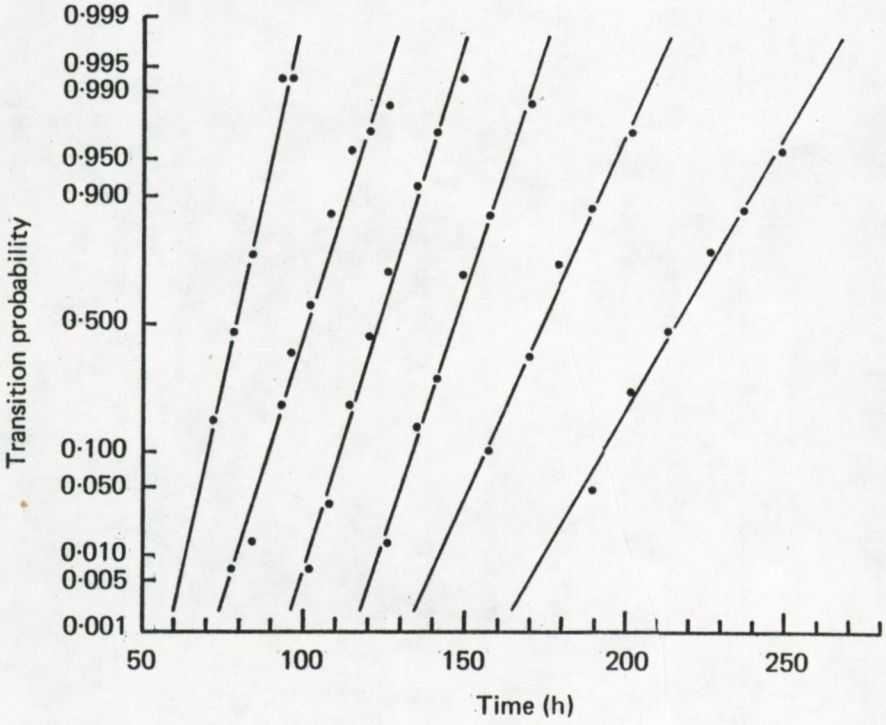


Fig. 4.1. Tisbe furcata (18°C). Cumulative distributions of transition times between successive ontogenetic stages: nauplii (considered together), five copepodite stages and the adult. (Second cohort.)

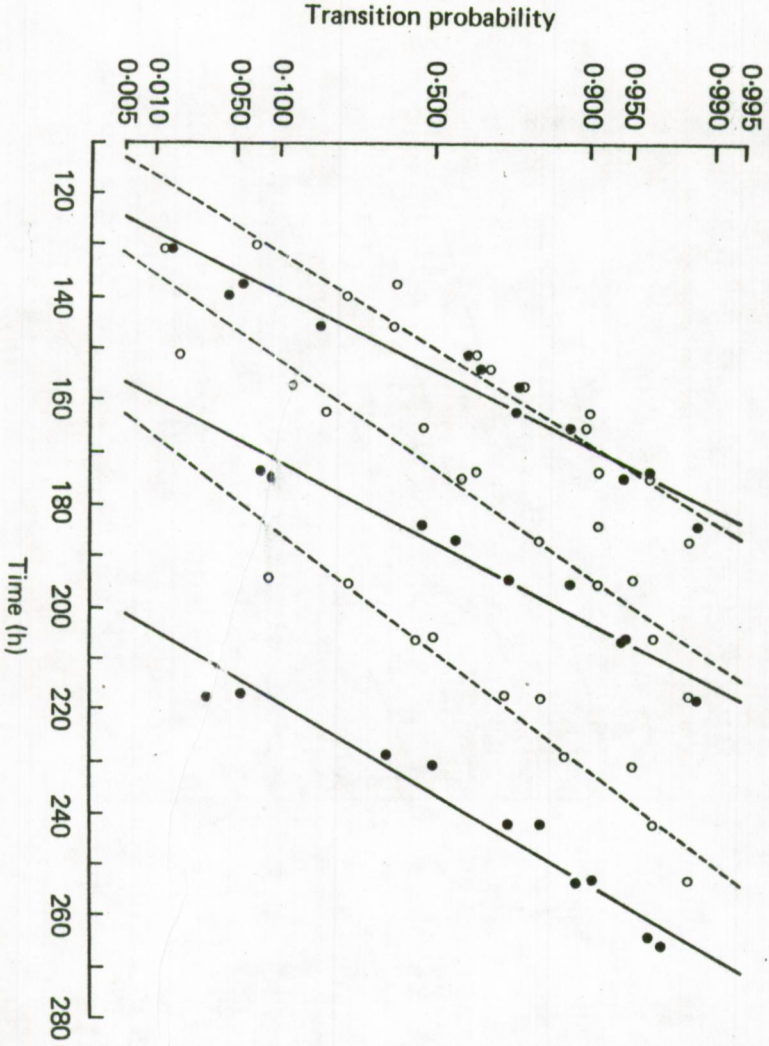


Fig. 4.2. Tisbe furcata (18°C). Sex-specific cumulative transition time distributions. O --- O, males; ●——●, females. (Data from first cohort moved forward and those from second cohort moved backward by 4.5 h for better coincidence.)

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,

$$\int_{x=o}^{\infty} \varphi_s(x)dx$$

equals the duration of stage s ($\varphi_s(x)$ 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. 4.3). Values obtained by the second method differed from those of the first by only 3% on the average. Table 4.1 lists durations and asynchrony values for both cohorts.

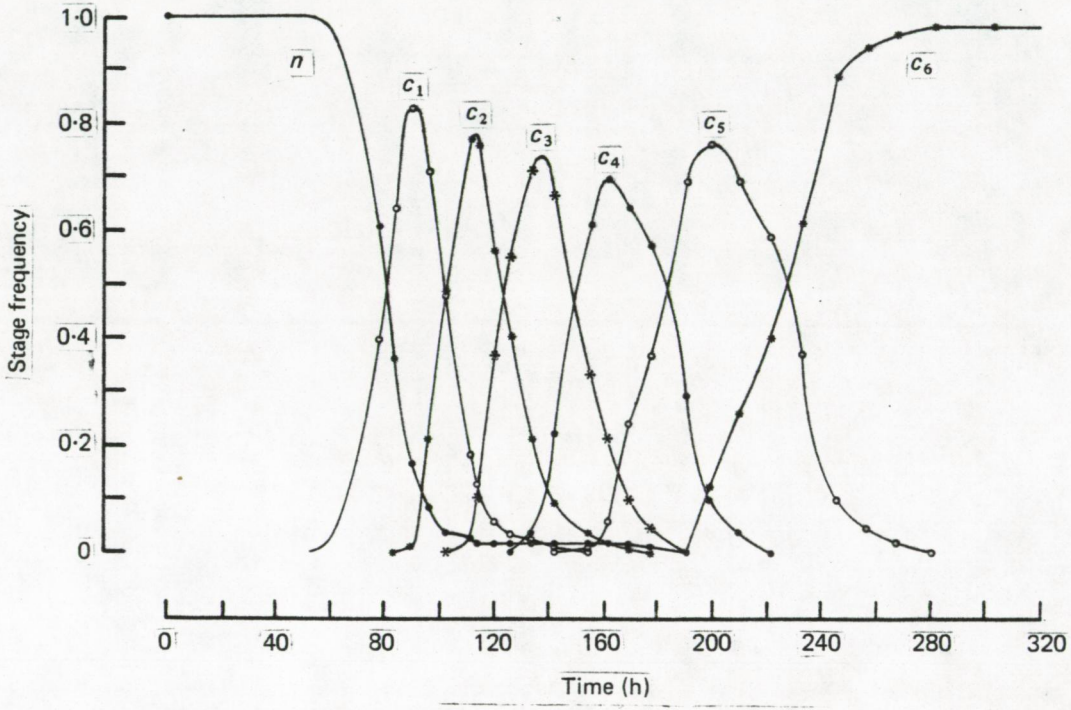
Cohort life-table, fecundity table and demographic parameters

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 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

Table 4.1. 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									
$n \rightarrow c_1$	9·5	—	—	6·7	—	—	8·1	—	—
$c_1 \rightarrow c_2$	8·9	—	—	9·4	—	—	9·2	—	—
$c_2 \rightarrow c_3$	12·8	—	—	9·4	—	—	11·1	—	—
$c_3 \rightarrow c_4$	12·8	11·0	17·1	10·1	11·7	11·1	11·4	11·3	14·1
$c_4 \rightarrow c_5$	13·6	10·3	16·7	13·7	12·5	12·0	13·7	11·4	14·3
$c_5 \rightarrow$ ad.	20·3	13·7	20·3	17·8	13·4	12·0	19·1	13·6	16·2

Fig. 4.3. 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.


1·0
0·8
0·6
0·4
0·2
0
Stage frequency
n
c1
c2
c3
c4
c5
c6
0
40
80
120
160
200
240
280
320
Time (h)

across generations) and dividing by $(1+l_1) / 2$ to allow for naupliar mortality prior to harvesting. U_x and l_x schedules are presented in Fig. 4.4.

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 = 0.236 for T. furcata at 18°C. The net reproductive rate is

$$R_o = \sum_{x=0}^{\infty} U_x = 93.9.$$

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 $T = \ln R_o / r = 19.2$. The age of the mother of an average newborn in an exponentially growing population is

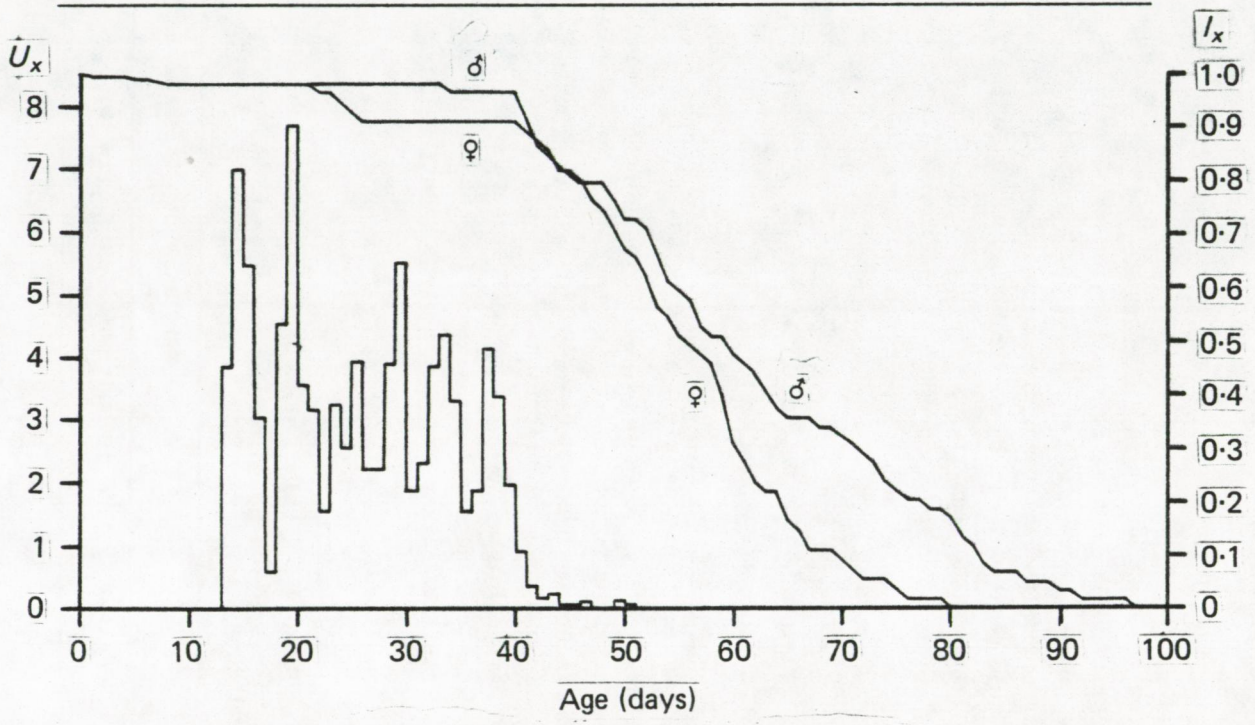
$$\bar{T} = \sum_{x=0}^{\infty} (x+0.5)U_x e^{-rx} = 16.4 .$$

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

$$T_C = \frac{1}{R_o} \sum_{x=0}^{\infty} (x+0.5)U_x = 25.4.$$

(The 0.5 in the last two formulae is a correction for grouping by 1-day intervals.)

Fig. 4.4. Tisbe furcata (18°C). Age-specific survival (l_x) and fertility (U_x)



Stable stage 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

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

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 4.2. lists the stable stage distribution thus obtained.

Table 4.2. 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	52.2	9.8	7.8	7.3	6.5	6.3	10.1
Males	52.2	9.8	7.8	6.2	5.1	5.5	13.4

Table 4.3. 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
T. brevicornis, 15 °C (Harris, 1973)	1·5	1·5	1	1	2·5		2	2	2	3	7
Tisbe furcata, 18 °C (this work)	← 15 →						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, 1980a)	← 3·4 →						9·6	7·6	8·4	8·4	11·9
	← 37·6 →										

* 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.

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, 1980a, 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 Amphiascoides sp. (Walker, 1979), Harpacticus littoralis (Castel, 1976), Tigriopus brevicornis (Fraser, 1936; Harris, 1973 - but see Itô, 1970, on its congener T. japonicus) and even Tisbe holothuriae (Hoppenheit, 1975a, b - but see Johnson & Olson, 1948; Battaglia, 1957b; Battaglia & Talamini, 1957; Vilela, 1969; Chua, 1975; Lopez, 1980, on six other species of the genus).

Table 4.3, 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 et al. (1977) for species of the calanoid genus Acartia. (Compare also development of Cyclops abyssorum from n_1 through c_2 : Whitehouse & Lewis, 1973, Fig. 2.) The other

harpacticoids in Table 4.3 , 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 referrred 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 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 4.1). Similar observations - or inferences - have been made on Euterpina acutifrons (Haq, 1972; Zurlini, et al., 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 in 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. 4.4 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, 1980a). 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 4.4). The Huntemannia and Euterpina

Table 4.4. 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		15·9–18·0, mean 16·8	17·5–19·0, mean 18·4				Parise & Lazzaretto (1966), Battaglia & Parise (1967), Lazzaretto & Parise (1967), Lazzaretto-Colombera (1970), Braioni & Parise (1971), Parise (personal communication, 1975), Gaudy & Guérin (1977)†
			0·254–0·282, mean 0·268			11·2–11·9, mean 11·5	0·77–0·95, mean 0·87	32–63, mean 49	
(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 (1962b), Volkmann-Rocco (1972c) 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).

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

This study is the first one 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 (1975b) 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 has been considered in chapter 3. 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 4.4 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 $r_c = \ln R_o / T_c$; 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 4.4) 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, 1972c).

All data in Table 4.4 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 of a much higher R_o and correspondingly longer T_c. This may reflect the fact that, like my own T. furcata data, they were determined using the F_1 offspring of wild-caught animals. (All other data in Table 4.4 refer to laboratory-adapted populations.) If laboratory populations are relatively inbred, lower R_o may result (Lazzaretto & Parise, 1967; Lazzaretto-Colombera et al., 1976). However, in chapter 6 I will argue that adaptation should lead to the opposite effect.

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_{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.

Chapter 5

Does 'life-history' evolve in the course of a bloom ?

Abstract

A possible genetic effect of the yearly predictable bloom, considered a special kind of seasonality, upon T. furcata's life cycle was investigated. To this effect, relevant features of 2 cohorts collected early and late in the 1979 bloom were compared. The hypothesis of r-selection correctly predicted increases in r, developmental speed and fecundity, and decreases in life expectancy and offspring viability. Due to sampling of related individuals (genotypes), however, the true magnitude of these effects has probably been overestimated.

Introduction

Many if not a majority of organisms are faced with environmental seasonality. When life cycles are short and offspring grow up in a different environment from their parents', a problem of adaptation arises which could theoretically be solved in two different ways: either by individual plasticity ('general purpose'genotypes) or by a cyclical process of selection among 'specialist'genotypes. Which mechanism should be favoured may not always be evident, though obviously the range of environmental variation and its predictability play an essential rôle. Some authors (e.g. Johnson, 1976 p. 149) have been very sceptical about the second alternative, argueing that it would entail a heavy substitutional load. From the viewpoint of population genetics, the amount of variability which a population is able to hold is certainly determinative. Asexual reproduction may obviate the problem and, in fact, rapid evolution during blooms, and cyclical selection with a 1-year period, have been observed in essentially clonal populations (Gallagher, 1980). Even in sexual populations, though, polymorphism at loci specifying the form of the net maternity function $U_x = l_x m_x$ may be maintained at no cost if fluctuations in the population's growth rate occur - as they are bound to do (Giesel, 1972). But if such loci exist at all, any phase of unresisted population expansion must necessarily result in increased frequencies of alleles specifying more pronounced r-strategist phenotypes. Data in Fujiie (1980) are highly suggestive of such a process but were collected under poorly controlled circumstances. The above

considerations provided the impetus for a search of life history shifts arising in situ in T. furcata. The recurring exponential growth phase (chapter 2) guaranteed both a reliable demographic background, and unambiguous predictions as to the expected direction of change.

Material and Methods

Observations were conducted on 'birth' cohorts using the experimental procedure described in chapter 4. To examine the genetic influence of demographic antecedents, cohorts were derived from the samples taken on March 14 ('early') and April 17, 1979 ('late'). Cohort initiation followed 3-4 days after collection of the ovigerous females. Numbers of nauplii obtained within a 6 h -span were 250 from 21 ♀♀ and 155 from ⩾40 ♀♀, respectively.

Methods, being virtually identical to those used for the 1978 cohort (chapter 4) will not be repeated here. In addition to survival/fecundity schedules and classical population parameters for each cohort (as described ibid.), the procedure allowed the calculation of individual fitness parameters for each female. (The variability of both life expectancy and reproductive effort was assumed to have a genetic component, with both traits potentially interdependent. Therefore actual performance of each individual was considered a better estimate of its 'expected' life history than any composite value involving cohort statistics.) The following parameters were considered:

R_o, the number of daughters per mother, defined as the corresponding population parameter but using the individual fecundity pattern and assuming $l(x)=1$ throughout reproductive life.

r, the intrinsic rate of increase of a hypothetical population where all females would have the said female's phenotype.

T_{min}, or minimum generation time. As offspring in Tisbe are produced in batches, T_{min} was defined as the time lapse between release of the cohort to which the female belongs, and the average time of release calculated over all nauplii of her first batch.

Period, the time lapse between the production of two successive batches. It was operationally defined as the local maximum in the power spectrum resulting from Fourier analysis of the individual m_x schedules.

Life span, being the time lapse (to the nearest half day) between the female's release as a 'newborn' nauplius and its death.

Results and Discussion

Evidence for r-selection

A summary of demographic traits for the two cohorts considered here may be found in table 5.1. The reader is referred to chapter 6 for a general discussion of the interrelationships between the cohorts studied in chapter 4-6. Here, comparison of the 1979 'early' and 'late' accessions will be restricted to traits for which the hypothesis of r-selection generates explicit predictions:

The intrinsic rate of increase is, in a general way, proportional to ln (fecundity) and to 'speed of reproduction' (cf. Table 3.1, eq. 4). Accordingly, r-selection should lead to higher r through higher R_o and/or shorter generation times.

As R_o appears as a logarithm in the formula, the second effect may be expected to be more efficient (Lewontin, 1965). Moreover, generation time T is affected by the form of the net maternity function $l_x m_x$ (Table 3.1, eqs.1 & 4), so that altering the pdf of the latter also influences r (Mertz, 1971). Specifically, the weighting factor e^{-rx} of age-specific reproduction is such that small positive effects on early reproduction (shorter T_{min} and higher early fecundity) may override large adverse effects later in life (Lewontin, 1965; Charlesworth, 1980). Reduced life span may thus be selectively neutral - or even favoured if it accompanies increased early reproduction (cf. Sokal, 1970). If changes as predicted here occur by selection acting on genetic variability, the (additive genetic) variance of the traits under selection is bound to decrease. Finally, resources available for reproduction being in limited supply, no single investment strategy can simultaneously maximize offspring quantity and quality; r-strategists are then expected to emphasize productivity at the expense of, e.g., offspring viability (Pianka, 1970).

As Table 5.1 and Figs 5.1 to 5.3 show, most of the above predictions are very well met. No quantitative-genetic analysis was carried out, and therefore the variance reported is 'total' rather than 'additive genetic'; however, the latter must be contained in the former and, the 'environmental' contribution from laboratory handling being probably very similar between cohorts, the large reduction in total variance certainly speaks in favour of a selective process. The comparatively small reduction

Table 5.1. Traits of demographic importance as observed in the 'early' 1979 (1) and 'late' 1979 (2) bloom cohorts.

	1979 (1)			1979 (2)		
	aggregate cohort value	mean for reproducing females	variance	aggregate cohort value	mean for reproducing females	variance
r	.197	.204	58.10^{-5}	.279	.279	20.10^{-5}
T_{min}	16.9	17.1	2.40	14.5	14.5	0.17
'period'	5.0	4.5	1.48	3.8	3.9	.33
R_o	91.1	111.2	1756	172.2	174.8	1541
% of sterile ♀♀	18.1			1.5		
life span (♀)		52.9	128		48.3	39
survival to adult-hood	.98			.87		

Next pages:

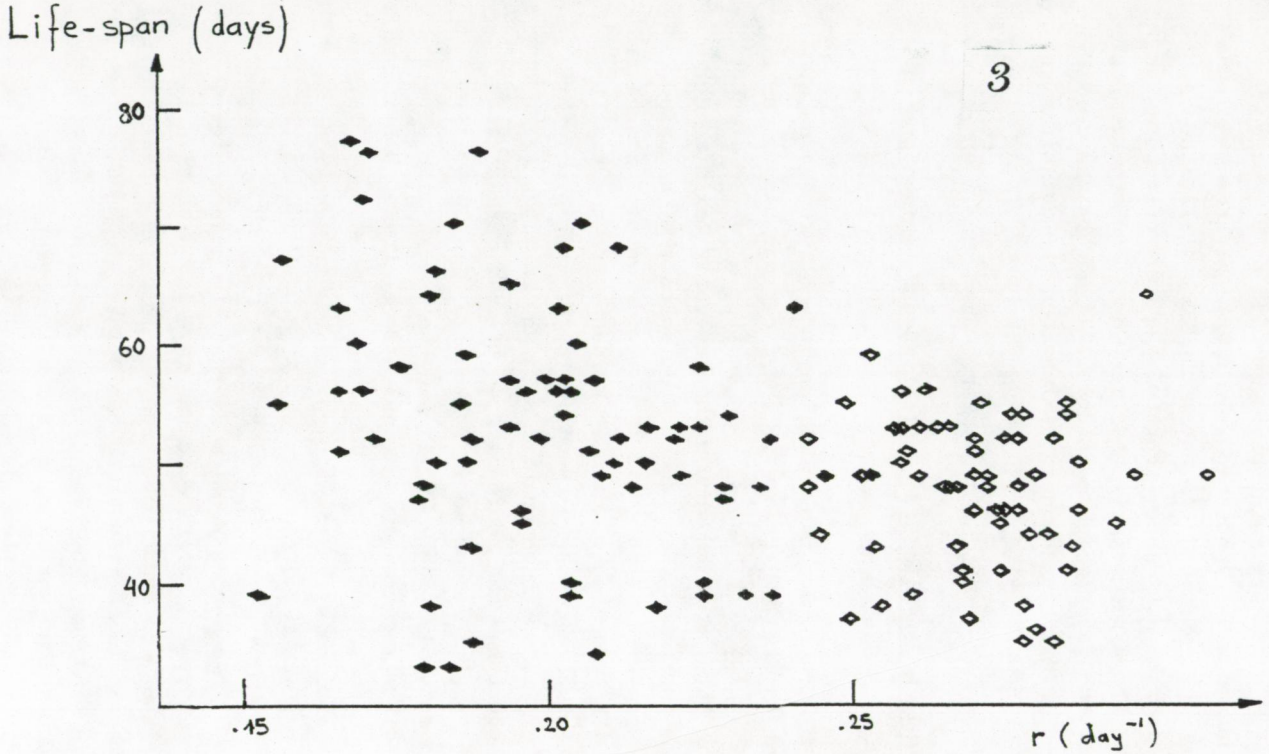
Fig. 5.1. Fecundity and life table for the 'early' bloom cohort of T. furcata (1979).

Fig. 5.2. Fecundity and life table for the 'late' bloom cohort of T. furcata (1979).

Fig. 5.3. Individual r and life-span values recorded for females of the 'early' and 'late' bloom cohorts of 1979.

SURVIVAL
0
.2
.4
.6
.8
1
AGE (DAYS)
0
20
40
60
80
100
♂
♀
2
0
4
8
12
16
20
U_x

SURVIVAL
0
.2
.4
.6
.8
1
♂
♀
1
4
8
12
16
20
U_x


Life-span (days)
80
60
40
.15
.20
.25
r (day⁻¹)

of R_o variance as compared to that of T_{min} also agrees with expectation; in fact, only the magnitude of increase in R_o is unexpected. Overall, then findings would seem to rate as a fine corroboration of the hypothesis -- had there not been other aspects of the data which cast doubt, if not on the reality of life cycle changes, at least on the quantitative representativity of the second cohort. These will now be considered.

Why the 'r-selection' effect should be interpreted with caution.

There are two anomalies in the 1979 (2) data, which are interrelated. The first one has to do with its very high R_o. In chapter 6, where a cohort is studied which should theoretically maximize R_o, it is argued that it could do so only by delaying reproduction: it would then avoid the cost associated with early reproduction. Evidence for the reality of such a cost was found in the distribution of T_{min} values (see chapter 6). Now the 1979 (2) cohort has the shortest T_{min} of all, yet it ranks a very close second in terms of R_o (Table 6.1). Admittedly, the 1979 (2) had the lowest life expectancy; this may certainly be considered a 'cost', but it was not passed on in R_o. In a word, fecundity in 1979 (2) was singularly insensitive towards the cost of reducing T_{min}.

The second problem is that the gain achieved by 1979 (2) relative to the 1979 (1) situation is rather too good to be true. Some quick calculations may serve to illustrate the point. It must be kept in mind that the time elapsing between the two accessions was 34 d, or about 1 generation in the field (cf. chapter 2).

First, a Gedanken experiment may be performed in which two clones compete in a growth 'race'; these clones are given the (aggregate) characteristics of the 1979 (1) and 1979 (2) cohorts, respectively. After 34 d, the second clone would have increased

$$\exp((.279 - .197) \times 34) \simeq 16$$

times faster than the first. Clearly, this is insufficient to explain the complete absence in 1979 (1) of individuals with r typical of 1979 (2), and vice versa (Fig. 5.3).

It may be objected that r is itself a composite trait, and that the feasibility of fast evolution should be examined on the 'raw material' (i.e., on R_o and T_{min} rather than on r). Genetic, and, *a fortiori*, phenotypic variance sets an upper limit to the gain that may theoretically be achieved. Response to selection in artificial situations is described by

$$R = h^2 S$$

where R = selective gain or response
h^2 = heritability
S = selection differential = difference between population mean and selected-subpopulation mean.

Now even if h^2 were given the unattainable value of 1, and the unrealistic extremism of the model (non-selected individuals are not allowed to contribute to the next generation in any way) is disregarded, improbably high selective differentials are still required ($\sim$1.7 s.d. for T_{min} and $\sim$ 1.5 s.d. for R_o, as taken from Table 5.1).

Granting the anomalous nature of 1979 (2), an explanation is called for. Several may be considered.

1. Imprinting. It is conceivable that eggs produced in exponential populations should give rise to animals with phenotypically faster life cycles. Hoppenheit (1976) observed such imprinted acceleration in exploited populations of T. holothuriae ; the effect was, however, short-lived and did not extend beyond embryonic development (see also discussion in chapter 6).
2. Recombination. Sudden spurts have sometimes been observed in the response to directional selection for quantitative traits (e.g. Thoday & Boam, quoted in Bodmer & Parsons, 1962); these are due to a release of genetical variability, previously locked up into tight linkage groups, and which all at once provides new material for selection to act upon. In the present case, this explanation will not work, as the new variants could not possibly have arisen and be strongly selected for in the course of a single generation.
3. Cyclomorphosis. In aphids, pre-programmed (fixed, non-heritable) fecundity differences are known to exist between different generations within a year, which are well tuned to the phenology of resource quality and quantity (Wellings et al., 1980). Aphids are, however, very special genetic systems, in which prolonged phases of parthenogenetic reproduction (and therefore, non-disruption of genotypes) singularly facilitate the origin of such programmed features. Tisbe hardly qualifies as a parallel.

4. Nonrandom sampling. In a study of seasonal electromorph frequency changes in the heteropteran Gerris lacustris, Varvio-Aho (1981) concluded that the shifts observed between samples were caused by neutral processes; random binomial sampling could not, however, account for their magnitude, and it was hypothesized that cohorts or sibling groups had been collected. This explanation appears especially plausible with respect to the wild T. furcata cohorts of 1979. In my experimental procedure, the contribution of founding females to the pool of newborns is inevitably unequal; consideration of the numbers of nauplii available to initiate each cohort suggests that 1979 (2) may indeed have been most subject to sampling bias of genotypes.

Summing up, the hypothesis of bloom-induced r-selection correctly predicted the direction of change in demographic parameters between 'early' and 'late' bloom accessions. The magnitude of the effects is best accounted for by assuming less-than-representative sampling of a real selective process. If so, of course, the reduction in parameter variances between 1979 (1) and 1979 (2) must be viewed with more caution.

Chapter 6

Life history adaptation to demographic regime in laboratory-cultured *Tisbe furcata*

Abstract

A laboratory population of *Tisbe furcata* with a 35-generation history of stable population size was examined for life history adaptations to demographic stationarity (a standard being provided by the wild source population). *T. furcata* responded to density regulation by increasing its potential net reproductive rate, R_o. This result is in agreement with the theory of fitness in age-structured populations, though in contradiction with intuitions based on the r-K-paradigm. The physiological mechanisms through which R_o is raised are high age-specific fecundity, delayed senescence and, primarily, increased frequency of egg sac production. The reasons for the adoption of the latter mechanism rather than other alternatives are analyzed. The cost of early reproduction is held responsible for differences between cohorts in the distributions of individual minimum generation times : (indirect) truncation-type selection in the case of R_o - selection is opposed to a (direct) symmetric pattern in the case of r-selection. This is one of the first reports of adaptive fine-tuning of the $l_x m_x$ schedule in an equilibrium rather than r-selected population.

Introduction

Whenever the characteristics of laboratory stocks are compared to those of conspecific wild populations, negative aspects such as reduced 'vigor' and the loss of genetic variability tend to receive emphasis. Only rarely have differences between wild and domesticated populations been investigated which speak for adaptation in the latter; and even when observations have been so interpreted (e.g. Salt, 1969), the very basis of the adaptation has remained a matter of faith. This may be partly due to the failure of current ecological theory to yield specific criteria for life history adaptation when $N \simeq K$ (Stearns, 1977, p. 155). The vagueness surrounding the nature of K-strategy is symptomatic. Whereas it is fairly obvious that protracted exponential growth should lead to selection for greater r_m, no such pleasingly simple principle has been suggested for populations remaining at carrying capacity; not much progress seems to have been made since the time when the characteristics ascribed to K-strategists were simply the opposite of those of r-strategists (Pianka, 1970). More sophisticated models may prove to be at variance with this intuitive symmetry. As Stearns (1977) puts it, 'the logic of comparison is weaker than the logic of prediction, which should be used wherever feasible'. Recent theoretical analyses, to be examined below, predict that a higher net reproductive rate, R_o, will be selected for in stationary populations.

Predictions

By deriving an expression for the population birth rate in age-structured populations, Charlesworth (1976, 1980) was able to identify

$$w_{ij} = \int_x l_{ij}(x)m_{ij}(x) \exp(-r_p x)dx$$

as the fitness of a genotype ij, defined by its demographic phenotype $l_{ij}(x)$, $m_{ij}(x)$ when present in a population growing at exponential rate r_p. (The model presupposes that the stable age distribution has been reached and that the mating system obeys certain restrictions; nonrandomness of matings with respect to age does not, however, materially alter its conclusions: see Charlesworth and Charlesworth, 1973: Appendix). Obviously, when $r_p = 0$, $w_{ij} = \int l_{ij}(x)m_{ij}(x)dx = R_{o\ ij}$. In other words: maximizing fitness in a stationary population amounts to maximizing the realized net reproductive rate.

In addition, Charlesworth (1973) could show that under density regulation, the probability for a mutant allele j to invade a stationary population of ii individuals, as measured by the initial rate of change of its frequency, is proportional to the root s of

$$1 = \int_x l_{ij}(x)m_{ij}(x) \exp(-sx)dx \quad .$$

Here, $l_{ij}(x)$ and $m_{ij}(x)$ characterize the heterozygote life history under the density conditions prevalent in the stationary ii population. For s to be > 0, $\int l_{ij}m_{ij}dx$ clearly must be >1, i.e. the invading allele must cause the heterozygote to have a higher R_o than the common homozygote. Essentially the same

point, viz. that the invasibility of a density-regulated population depends only on the R_o, was proved by Hastings (1978) using a completely different, non-genetic, approach.

A methodological caveat

When life history strategies are studied, it is of obvious interest to distinguish between genetically fixed responses, phenotypic plasticity and passive (non-adaptive) effects, respectively. At the same time it is necessary to establish, in the first and second instances, that the 'strategy' actually involves a choice between alternatives (see chapter 3), which can most easily be done by observing a control group in identical circumstances. Finally, information on individual organisms is to be preferred to aggregate measurements. Previous studies of density effects in harpacticoids (Braioni & Parise, 1971; Fava & Crotti, 1979; Walker, 1979) always involved observation of animals either directly experiencing density effects, or at least having experienced them during their entire prereproductive life. While useful information on the nature and extent of phenotypical responses, including imprinting, is thus provided, these studies do not permit the detection of evolutionary/genetic rather than immediate/physiological effects. Also, all but a few reports concern aggregate measurements, and controls - in the form of a population expected to lack certain adaptations - were never provided.

These considerations have influenced the

choice of experimental conditions in the present study. The search for 'strategic' life history differences of the first kind resulting from different demographic regimes presupposes the elimination of all direct effects - including that of population density itself. The procedure adopted (the same as in chapter 4 & 5) was, moreover, designed to monitor the reproductive performance of individual females. As such, it involves conditions closely approximating a 'density vacuum' and may be expected to yield appropriate parameter values for animals from exponential population phases. On the other hand, the performance thus recorded for the culture specimens is definitely not the same as would have been realized under actual density regulation. (The difficulty is inherent to all similar studies: cf. Law et al., 1977). It seems, though, that the loss of information on actual density-regulated performance is a small price to pay for the earlier-mentioned advantages. Indeed, although the assumption cannot be tested in organisms that cannot be cloned, it may reasonably be assumed that the reproductive performance of a given genotype under different density regimes is well correlated: several authors searched for, but failed to detect, a trade-off in per capita growth rate at low and high densities (Luckinbill, 1979; Mueller & Ayala, 1981; cf. also Stearns, 1977 p. 155).

Similarly, the observed distribution of fecundity over ages cannot be back-transformed to the pattern under density regulation, as for

any given genotype the relationship between both patterns is unknown. As a first approximation, though, one may assume that the probability density function of age-specific reproduction does not vary too much between both situations. Then (letting a prime indicate a density vacuum and an asterisk the N = K case),

$$m_x^* = m_x' / R_o' \quad .$$

A fixed p.d.f. of reproduction is a common feature in models of density regulation, as well as other dynamic trends in fertility patterns (Charlesworth & Giesel, 1972a, b; Oeppen, 1981); it will be implicit in the calculations of the Results section.

Material and Methods

The prediction that a higher R_o should be selected for in equilibrium populations was tested as follows.

Observations were again conducted on a 'birth' cohort. This one consisted of 140 nauplii, taken at random from 280 born within a 5h span on December 19, 1978. The nauplii-carrying females used to supply these newborns had been obtained two days earlier from a mass laboratory population; the latter had been founded on May 26, 1976 using wild-caught animals from the Sluice Dock. Through regular addition of a fixed amount of food (Dunaliella sp.) every 3rd day, it had presumably (see Appendix 2) been maintained in a quasi-steady state for at least 35 generations (cohort generation time $T_{coh} = \sum x l_x m_x / R_o$ = 26.4 d, T_{min} = 17.2 d, both computed from results below).

Results

As Table 6.1 shows, the prediction that a stationary population regime favours a high R_o is borne out. Two separate mechanisms contribute to a higher reproductive rate: first, increased frequency of egg-sac production throughout reproductive life (Table 6.1 , 'period'); second, an apparent delay of senescence, revealed by increased life span (Table 6.1). Although there is no corresponding lengthening of reproductive activity (Fig. 6.1; compare with Figs 4.4, 5.1 and 5.2), reproduction is more intense in the older age-classes: The contribution to R_o of individuals older than 40 d ($\sum l_x m_x$ for $x \geq 40$) is 10.3 in the culture cohort and 4.8, 1.9 and 1.5 in the 1979 (1), 1978 and 1979 (2) wild cohorts, respectively. Supporting this interpretation is the fact that R_o and life span are significantly correlated in the culture cohort (Spearman rho = . 395, P = .002) while they are not in any of the wild cohorts.

The existence of a physiological cost associated with reproduction, and with early reproduction in particular, has been repeatedly established (Mertz, 1975; Law, 1979; Rose & Charlesworth, 1980, 1981 b; Browne, 1982). (From the negative relationship between life span and 'last-day' reproduction observed by Snell & King (1977), their conclusion that reproduction at old age is more costly than early reproduction explicitly does not follow). Accordingly, maximizing R_o should be incompatible with minimizing generation time and, given the preponderant influence of T_{min} on r, a trade-off

Table 6.1. Population parameters for the four cohorts considered in chapters 4-6 (female individuals)

	N	survival to adulthood	r	R_o	T_{min}	period	average life span
wild, 1978	54	.981	.236	93.9	14.9	4.8	54.3
wild, 1979(1)	94	.980	.197	91.1	16.9	5.0	52.9
wild, 1979(2)	67	.871	.279	172.2	14.5	3.8	48.3
culture, 1979	66	.972	.241	183.7	17.2	3.7	58.7

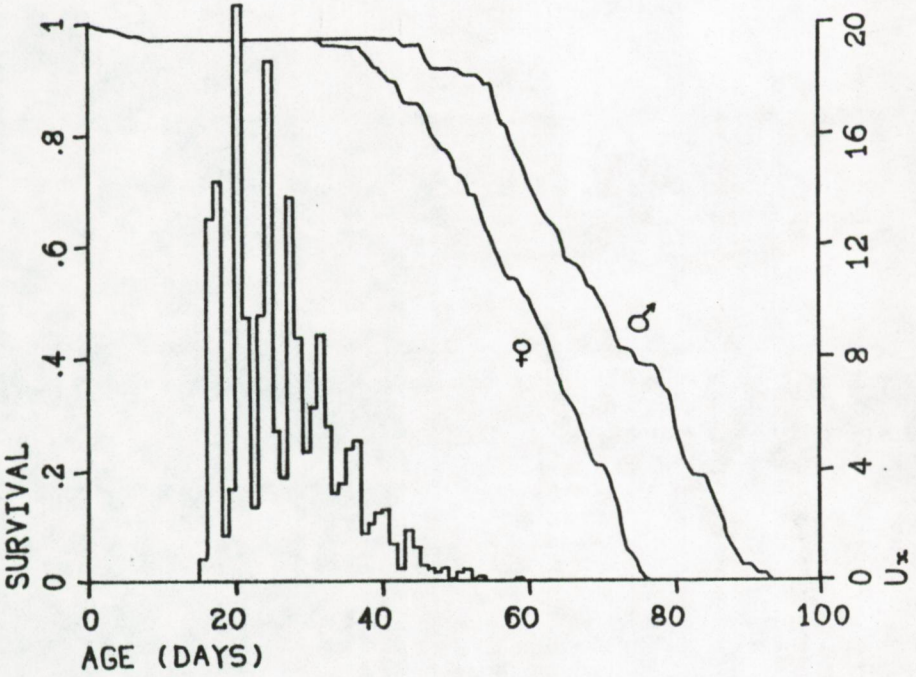
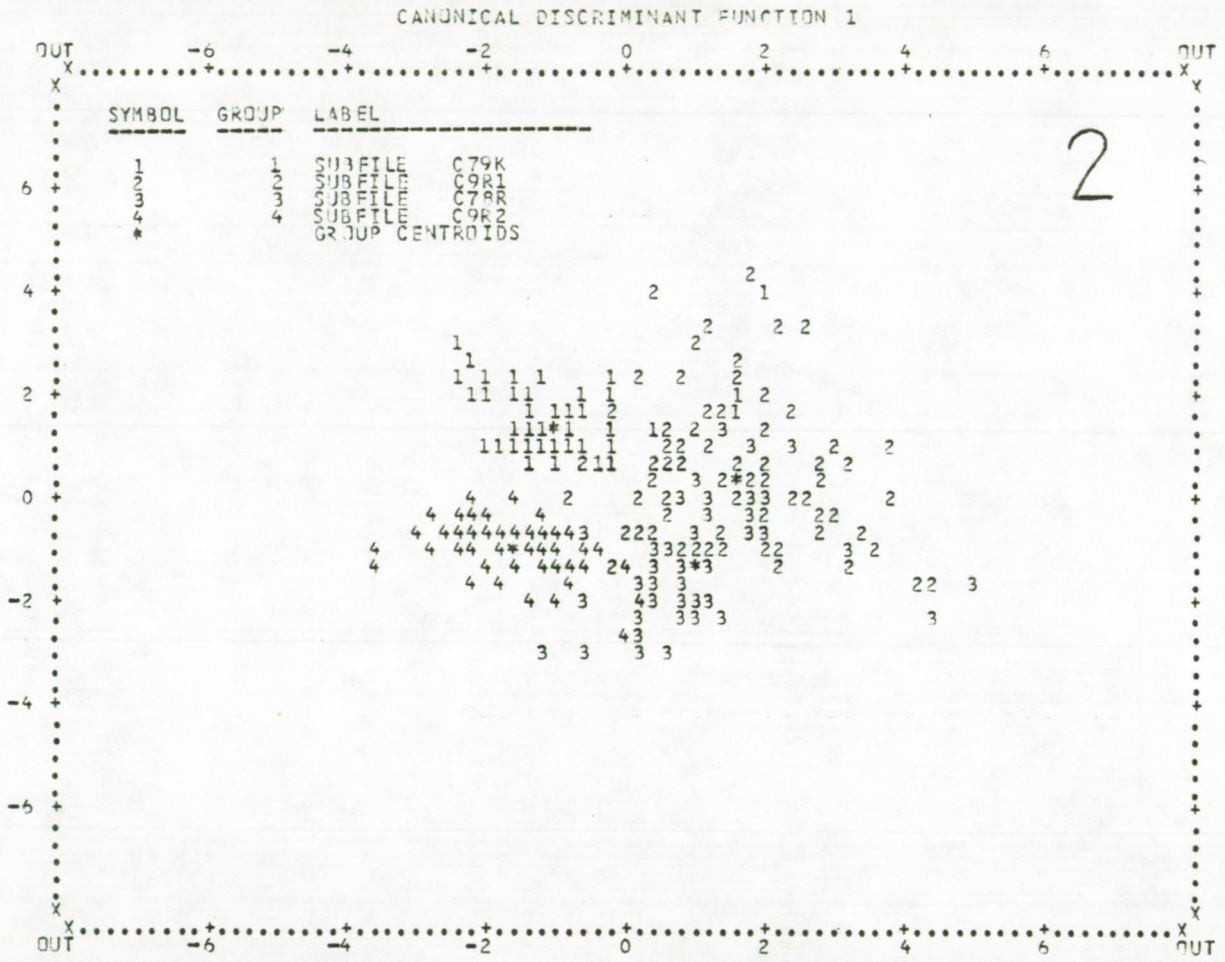


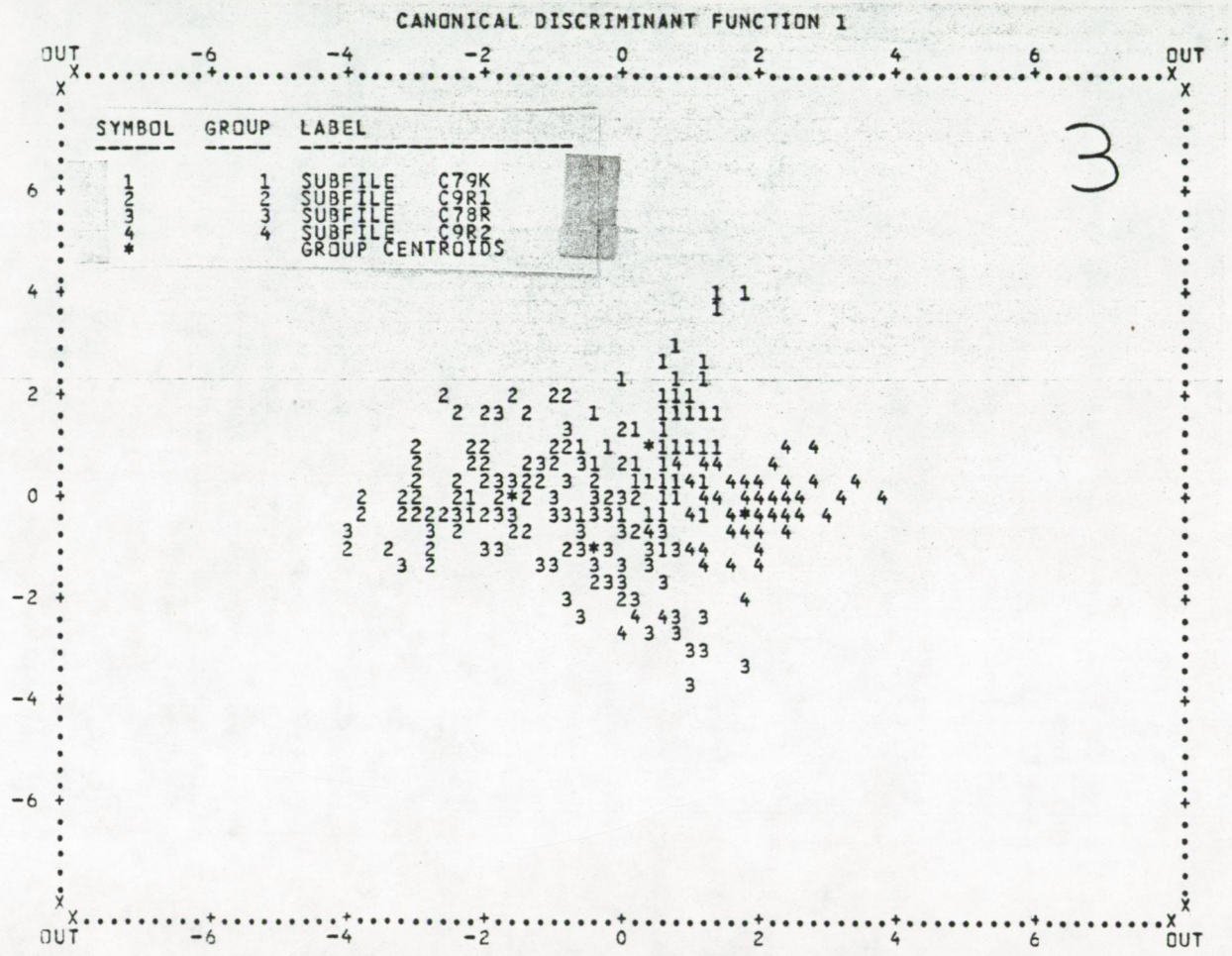
Fig. 6.1. Fecundity and life table for laboratory-cultured T. furcata.

Next pages:

Fig. 6.2. Discriminant analysis of the 4 cohorts using all 5 demographic parameters described in the Material and Methods section (SPSS printout). Symbols: 1 = culture, 2 = 1979 early bloom, 3 = 1978 Ulva, 4 = 1979 late bloom.

Fig. 6.3. Discriminant analysis performed on the basis of R_o and r only. Symbols as in Fig. 6.2.


CANONICAL DISCRIMINANT FUNCTION 1
CANONICAL DISCRIMINANT FUNCTION 2
SYMBOL GROUP LABEL
1 1 SUBFILE C79K
2 2 SUBFILE C9R1
3 3 SUBFILE C78R
4 4 SUBFILE C9R2
* GROUP CENTROIDS
2
OUT
-6
-4
-2
0
2
4
6
OUT


CANONICAL DISCRIMINANT FUNCTION 1
CANONICAL DISCRIMINANT FUNCTION 2
SYMBOL GROUP LABEL
1 1 SUBFILE C79K
2 2 SUBFILE C9R1
3 3 SUBFILE C78R
4 4 SUBFILE C9R2
* GROUP CENTROIDS
3
OUT
-6
-4
-2
0
2
4
6

between R_o and r is to be expected. Inspection of Table 6.1 suggests that such a mechanism may have operated: the culture specimens maximize R_o whereas their intrinsic rate of increase, resulting from the combination of high T_{min} and high R_o, assumes a rather average value. Clearly, then, the high R_o of the culture population is an end in itself rather than just another (presumably rather inefficient: Lewontin, 1965) means of increasing r.

The data on the 1979 (2) wild cohort would appear to belie the existence of a penalty on early reproduction . The low susceptibility of this cohort to the cost may, however, be a sampling error artifact (see chapter 5). Synchronous parturient females to found the cohorts were always available in low numbers only; moreover their contribution to the pool of newborns must inevitably have been unequal. Consideration of the numbers of nauplii that were available for initiation of the cohorts suggests that sampling bias of genotypes may have been greatest in 1979 (2).

Because of its influence on r, T_{min} strongly correlates with fitness in freely expanding populations. As a result, Lewontin (1965) could predict that 'very little genetic variance in development time ought to be found in species with a history of colonization'. As pointed out in chapter 5, this is borne out by comparison of the 'early' and 'late' bloom accessions of 1979 (but see discussion there). Variability in the culture cohort is, however, also surprisingly low (Table 6.2). A plausible explanation is that

Table 6.2. Distribution of individual minimum generation times.

	N	mean	s.d.	C.V.(%)	skewness
wild, 1978	54	15.15	1.22	8.0	.52
wild, 1979(1)	77	17.05	1.55	9.1	.97
wild, 1979(2)	66	14.47	.42	2.9	-.96
culture, 1979	64	17.25	.92	5.3	2.35

selection for high R_o entails indirect selection against early reproduction, the cost of the latter setting a lower - but no upper - limit on T_{min}. As a corollary, there should be a contrast between the asymmetric (truncation-type) selection on T_{min} under R_o-selection and the more symmetric (stabilizing) selection on T_{min} under r-selection, in which case both high cost and delayed reproduction must be avoided. The marked positive skewness of the individual T_{min}-value distribution, in the culture cohort only (Table 6.2), strongly supports this hypothesis.

In order to investigate the relationships between the four cohorts, discriminant analyses were carried out using the data on those 259 females (in the 4 cohorts) which actually reproduced. The five demographic parameters considered, were ranked according to their 'separating power' by the SPSS stepwise discriminant procedure (Klecka, 1975). By any of the available criteria, r proved to be the best single discriminator, with the other variables adding their partial (conditional) contribution in the order $r > T_{min} > R_o >$ life span $\geq$ period. As early as the inclusion of T_{min}, the Mahalonobis distances between any two cohorts become highly significant (pairwise $F's \geq 44.2$, $P < .001$).

It is interesting to observe that two rather than three discriminant functions are sufficient to separate the four cohorts (the first two canonical variates account for 96.5 % of the eigenvalue sum). This suggests that the populations are differentiated mainly along two

Table 6.3. Discriminant analysis of the four cohorts

	discriminant axes		
	I	II	III
associated eigenvalue	1.90 (60%)	1.17 (37%)	.11 (3%)
canonical correlation	.81	.73	.32
standardized discriminant function coefficients			
r	-1.04	.11	-.46
T_{min}	- .38	1.00	-.17
R_o	- .29	.37	.61
period	.22	-.03	.36
life span	-.06	.02	-.93

Table 6.4. Discriminating power of the Ist and IInd canonical variates with respect to the four cohorts. Overall correct classification: 83.8%. (As Box's M test signals significant heterogeneity of within-cohort covariances, separate covariance matrices were used for each cohort in the classification) .

actual cohort membership	culture 1979	predicted cohort membership: wild 1979 (1)	wild 1978	wild 1979(2)
culture 1979	92.2	6.3	0	1.6
wild 1979(1)	5.2	71.4	20.8	2.6
wild 1978	0	22.6	77.4	0
wild 1979(2)	0	0	4.6	95.4

dimensions, which can be identified by their associated variables (Fig. 6.2, Table 6.3). Together, these two canonical variates possess excellent classification properties (Table 6.4).

Although all versions of the stepwise procedure agree in indicating r with T_{min} as the best two-parameter combination for discrimination purposes, it should be pointed out that T_{min} with R_o (preferable on physiological grounds) or r with R_o (preferable on demographic grounds) provide extremely satisfactory descriptions, leading to an overall 74% and 75% of individuals correctly classified, respectively. The latter, although inferior to the full-data-set analysis with respect to group separation, yields a more appealing visualization (Fig. 6.3) of the selection processes as envisaged here.

Discussion

Intraspecific life history variation in Copepoda

Although the existence of life history differences between geographic populations of certain harpacticoids was reported two decades ago (Battaglia, 1962b; Battaglia & Parise, 1967), studies placing such differences in their proper ecological context have only recently begun to appear. Palmer (1980) reported *in situ* differences in clutch size and realized birth and death rates between spatially adjacent populations of *Microarthridion littorale*. She acknowledged, though, that these might more readily and parsimoniously be explained as the proximal effects of different competition/predation regimes. I argued in chapter 3 that the concept of 'strategy'

presupposes a fitness-enhancing 'choice' transcending physiological necessity and the passive subjection to environmental influences. A 'strategic' element is more clearly involved in the life cycle differentiation which Elgmork et al. (1978) observed in the cyclopoid Cyclops scutifer. In this instance, however, the biotic force (predation) moulding life cycles is still extraneous to the populations concerned, as Nilssen (1980) documents. (In contrast, the life cycle variation in T. furcata described here arose under purely internal demographic control.) Also, the marked seasonality experienced by C. scutifer within an individual's lifetime has resulted in life cycle variations (e.g. diapause, fractionation of the population into cohorts developing according to divergeing time patterns) of a wholly different nature from the fine-tuning of $l(x)m(x)$ considered in the present study.

Nature of the life history syndromes

A survey of life history strategies at both the inter- and intraspecific levels (Stearns, 1977) discloses the existence of recurrent 'syndromes' or associations of traits: late-reproducing, long-lived species or individuals with low reproductive effort per time unit stand in contrast to those displaying early, intense and occasionally lethal (big-bang) reproduction. While there is a partial parallellism with 'culture' vs. 'wild' specimens in the present study, an important distinction should not go unnoticed. The combination of iteroparity and low reproductive effort per time unit is usually taken to reflect a risk-spreading mechanism associated with uncertain juvenile survival (e.g. Stearns & Crandall, 1981). In the culture

specimens of T. furcata, however, the very high m_x values throughout reproductive life speak for a high offspring number as a goal in its own right. Paradoxical as this may seem within the framework of classical r-K-dichotomy, it contributes to the high R_o which is an explicit feature of Charlesworth's theory of fitness (see 'Predictions'). Spreading of risk is, of course, automatically achieved at the same time, but would not be expected to enhance fitness to any significant extent in a stationary population.

While the notion that density limitation favors increased net fecundity has not yet achieved general recognition, it is not altogether without supporting evidence. Cyclops abyssorum, when adequately fed, responds (phenotypically) to increased density by producing more eggs per clutch and more clutches per female (Whitehouse & Lewis, 1973). In what appears to be the only previous 'natural selection' experiment involving life history evolution under crowding (Taylor & Condra, 1980), the 'K-selected' lines of Drosophila pseudoobscura had R_o-values twice those of their R-selected counterparts.

The syndromes described above, or elements thereof, are sometimes realized through individual plasticity (e.g. Mertz, 1971). Probable instances of phenotypic responses have been described in Tisbe (although alternative explanations were, or could be, offered) : Hoppenheit (1976) noticed an increased rate of egg sac production in female T. holothuriae artificially r-selected by regular harvesting of the source population. (As noted by the author, this 'imprinted' response, which quickly faded away under the very conditions needed to study it, could have been an artifact of

different female ages). In T. cucumariae, Lopez (1982) found that exhaustion of a food patch may be accompanied by delayed development. (The possibility that the stage structure stabilized because demographic stationarity was reached was not, however, ruled out).

In contrast, the individuals whose life cycle I observed never experienced the particular demographic regime which they represent. Indeed, observations were conducted on the F_1 of 'wild' or 'culture' females rather than on these females themselves. Except for 1978, cohorts were constituted at the earliest two days after collection of the females, at which time the F_1 individuals could not have developed beyond the stage of the newly-extruded egg. Consequently, a genetic factor is almost certainly involved in the differences detected. The number of generations during which the laboratory population was subjected to the stationary regime (at least 35 generations: cf. 'Material and Methods' section is amply sufficient for genetic adaptation to occur: significant responses of reproductive schedule parameters were obtained after as few as 8 - 12 generation of selection in other studies (Mertz, 1975; Rose & Charlesworth, 1980; Mueller & Ayala,1981).

Of course, non-genetic maternal influences cannot a priori be excluded. In heritability studies of the calanoids Eurytemora herdmani and Pseudocalanus sp., appreciable maternal effects on survival, female size and rate of early development

have been observed (McLaren, 1976; McLaren & Corkett, 1978). Could such effects also have contributed to the differences between wild and culture cohorts, which are of interest here? Female size as a determinant of fecundity may safely be dismissed, culture specimens being, if anything, smaller than wild ones. Survival to adulthood was found to be the same in the culture, 1978 and 1979 (1) cohorts (Table 1), so that even if this trait were under exclusive maternal control it could not account for the differences in realized fecundities either. Maternal effects on developmental rates are least readily predictable: The proximal effect of crowding would be production of smaller eggs of lower energetic content, whereas an adaptive response could result in fewer but larger eggs (cf. Cooney & Gehrs, 1980a). Egg size and embryonic duration are correlated (Steele, 1977), but a straightforward causal relationship cannot be assumed (cf. Hart & McLaren, 1978; Cooney & Gehrs, 1980b). In the only pertinent study of a Tisbe species, Hoppenheit (1976 p. 125-127) observed an increase in T_{min} for eggs produced under 4-fold population density, which was both modest (6h or 3%) and virtually limited to the embryonic phase; this effect would have been obviated in the present newborn-initiated life cycles.

Formal genetic analyses of the mode of inheritance of life history variations are quite rare up to the present (but see Derr, 1980; Rose & Charlesworth, 1981a; Giesel et al., 1982; and for copepods McLaren, 1976; McLaren & Corkett, 1978). Indeed, these few studies indicate that both the genetic architecture of life history variation and its interaction with different environments may be of considerable complexity.

What has been established beyond doubt, on the other hand, is that sufficient genetic variability is available in natural populations to permit the adaptive fine-tuning of life cycles (Law et al., 1977; Snell & King, 1977; Burdon, 1980). The present evidence that such autogenous fine-tuning actually occurs provides a necessary link between the natural variability on the one hand, and research demonstrating the effectiveness of selection for life history traits on the other.

A number of studies have succeeded in altering the net fecundity distribution by artificially manipulating the fitness value of reproduction at specific ages (Sokal, 1970; Mertz, 1975; Taylor & Condra, 1980 [r-line]; Rose & Charlesworth, 1980, 1981b). Others have simulated 'natural selection' situations where exploitation mimics r-selection (Doyle & Hunte, 1981a, b) or stage-specific mortality (Barclay & Gregory, 1982). Apart from Taylor & Condra's (1980) study, the observations reported here constitute the first such 'natural selection' experiment focusing on a resource-limited rather than expanding or exploited population.

It has been observed in some studies (e.g. McLaren, 1976; Giesel et al., 1982) that measures of heritability, genetic variance and covariance of life-history traits at one temperature correlate poorly with the same measures at other temperatures. Giesel et al. (1982) even hypothesized that different portions of the genome may be

responsible for phenotypic response at different temperatures. The culture specimens in the present study experienced their usual temperature regime (constant at 18°C). With regard to the wild cohorts, however, it could be objected that the experimental temperature was not representative of the conditions under which their adaptations evolved : During the bloom period of T. furcata, i.e. from early March to late May, rising water temperatures in the Sluice Dock barely reach 18°C (Polk, 1966; my Fig. 2.1). Nevertheless the observed distribution of the different life history parameters does not suggest any appreciable rôle of such confounding temperature influences: e.g., the C.V. of T_{min} and r was smaller in the most r-selected wild cohort than in the culture cohort, showing that the expected trimming effect of natural selection was not overridden by any possible effect of temperature regime.

The mechanism for raising R_o

From $R_o = \sum_x l_x m_x$, three non-exclusive alternative ways to increase R_o can be suggested: increased survival, increased fecundity, and reduced prereproductive lag. The rationale behind the latter possibility is this : If the cost of reproduction in terms of survival probability is expressed with a long time lag, l_x may be considered independent of m_x. (In the T. furcata cohorts, there is indeed no evidence that reproduction induces any except senescent mortality). 'Decreasing prereproductive lag' may then conveniently be modeled by shifting m_x forward relative to l_x (e.g. Mertz, 1971 p. 372 'case 5') rather than shifting $l_x m_x$ in concert (e.g.

Lewontin, 1965; Mertz, 1971 'case 3'). The net result is the combination of each m_x with a higher l_x.

Having established that a stationary population regime should select for higher R_o, the question naturally arises which of the three mechanisms will be adopted. Life expectancy is indeed higher in the culture cohort (see 'Results'); since in the 1978 and 1979 (1) wild cohorts, however, l_x during most of the reproductive period (up to day 40) is only 2.6 % and 1.8 % below that of the culture cohort, there is little advantage to be gained from the first alternative. The relative merits of the second and third possibilities were shown by Caswell & Hastings (1980) to depend on $\lambda/\tilde{P}$, where λ = finite growth rate and $\tilde{P}$ = age-specific survival during reproduction. Time shifts of the fecundity function are ineffective iff $\lambda/\tilde{P} \simeq 1$ (see Appendix 3). In each of the T. furcata cohorts studied, after a phase of juvenile mortality, $P_x = l_{x+1}/l_x$ is virtually 1 throughout reproduction. (This holds for other Tisbe spp. as well: consult Bergmans, 1981 for a review). In the culture population, where $\lambda = 1$, there is thus no incentive for speeding up reproduction.

Consequently, R_o in the culture population could only be raised by increasing fecundity. There is an upper limit to the amount of eggs which an animal can contain, and therefore discharge, at any one time; so the rate of egg sac production must be the proximal target of selection. This, then, is exactly what was observed (Table 6.1). In copepod species which carry the

eggs until the nauplii become independent, embryonic development inside the sac is the rate-limiting step in clutch production. It has been suggested (Watras & Haney, 1980) that premature dislodging of partly developed egg masses could be a mechanism to increase this rate. In Tisbe, little opportunity for such mechanism seems available, as egg sacs up to the 'embryonic nauplius' stage (Lwoff, 1927 Fig. X 11; Witschi, 1934 Fig. 12) fail to develop when no longer carried around by the mother - either when dislodged or after death of the female (unpubl. obs.). The minimal interval of 3.7 days between successive egg sacs observed in the present study may therefore well correspond to a physiological minimum for the species.

At this point it could legitimately be asked why a higher R_o value under density regulation should not be achieved by reproductive investment in offspring quality rather than quantity. (This, in fact, is the main objection raised by Caswell & Hastings (1980) against their own model, which predicts increased fecundity rather than the classical 'K-selected' reproductive parsimony in certain equilibrium populations). The answer may be that both mechanisms are not mutually exclusive. Offspring quality was not monitored in the present study, but it has been known for a long time (Wesenberg-Lund quoted in Hutchinson, 1951) that egg size is variable in certain copepods, and larger (though in fact fewer) eggs are produced as a phenotypic response to food stress (Cooney & Gehrs, 1980a). Also, egg size correlates with nauplius size and presumably with nauplius 'quality' (Cooney & Gehrs, 1980b). An upper bound to offspring size

may, however, be dictated by other constraints (e.g. morphology of the female reproductive tract). In cases where offspring quality has already been pushed to some upper limit, as the present study underscores, mere fecundity is still expected to yield an appreciable contribution to a female's expected number of surviving offspring.

Appendix 1

Annotated listing of the Fortran IV program for demographic computations

```
      PROGRAM LIFTAB (INPUT,OUTPUT,TAPE1,TAPE2)
      DIMENSION UNAUPI(120,80),MORTF(120),MORTM(120)
      DIMENSION LD(120),UNAUP(80),UMI(80)
      DIMENSION TAVI(120,10),VITA(120,4),FITPAR(120,8)
      DIMENSION STABF(120),STABM(120),FRF(7),FRM(7)
      DIMENSION WAVE(80),A(40),B(40),P(40)
      DIMENSION VX1(120),VX2(240),VY1(120),VY2(240)
C
CC    A MAXIMUM OF 120 FF ; # OF MM UNLIMITED
CC    MAX. LIFE SPAN 120 DAYS ; MAX. FERTILE AGE 80
CC    UNAUPI = # NAUPLII PER FEMALE AND PER DAY
CC    MORTF, MORTM = # DEAD FOUND EACH DAY
CC    LD = LIFE SPAN = NR. DAY WHEN FOUND DEAD IF * = 0
CC    SURVIVAL TO ADULTHOOD, % FF, # FF EN MM
CC    TT = AMOUNT BY WHICH 1ST OBSERVATION INTERVAL IS SHORTER
C                                                        THAN 1 DAY
      READ(1,101)STA,PERFEM,NF,NM,TT
      READ(1,102)(MORTF(J),J=1,40)
      READ(1,102)(MORTF(J),J=41,80)
      READ(1,102)(MORTF(J),J=81,120)
      READ(1,102)(MORTM(J),J=1,40)
      READ(1,102)(MORTM(J),J=41,80)
      READ(1,102)(MORTM(J),J=81,120)
      READ(1,102)(LD(I),I=1,40)
      READ(1,102)(LD(I),I=41,80)
      READ(1,102)(LD(I),I=81,120)
      DO 1 I=1,NF
      READ(1,200)(UNAUPI(I,J),J=1,20)
      READ(1,200)(UNAUPI(I,J),J=21,40)
      READ(1,200)(UNAUPI(I,J),J=41,60)
      READ(1,200)(UNAUPI(I,J),J=61,80)
1     CONTINUE
      DO 2 J=1,80
      UNAUP(J)=0.0
2     UMI(J)=0.0
      DO 103 J=1,120
      STABF(J)=0.0
103   STABM(J)=0.0
C
CC    COMPUTE IN UNAUP THE TOTAL # OF NAUPLII HARVESTED
C
      DO 3 J=1,80
      DO 3 I=1,NF
      UNAUP(J)=UNAUP(J)+UNAUPI(I,J)
3     CONTINUE
```

```
C
CCC     COMPUTE LX IN TAVI(*,1) AND LX IN TAVI(*,2)
C       DURATION LARVAL STAGES = 9(.2) DAYS, SEXES POOLED
C
        MORTCU=0
        SUR=STA**0.11111111
        TAVI(1,1)=1.0
        TAVI(120,2)=0.0
        DO 4 J=1,119
        MORTCU=MORTCU+MORTF(J)
        IF(J.LT.9)TAVI(J+1,1)=SUR**J
        IF(J.GE.9)TAVI(J+1,1)=STA*FLOAT(NF-MORTCU)/FLOAT(NF)
        TAVI(J,2)=(TAVI(J,1)+TAVI(J+1,1))/2.0
4       CONTINUE
C
CCC     COMPUTE PX IN TAVI(*,3), EX IN TAVI(*,4),
CC      UX IN TAVI(*,5) AND MX IN TAVI(*,6)
C
        DO 47 K=3,7
        TAVI(120,K)=0.0
47      CONTINUE
        DO 5 J=1,119
        IF(TAVI(J,2).EQ.0.0)TAVI(J,3)=0.0
        IF(TAVI(J,2).NE.0.0)TAVI(J,3)=TAVI(J+1,2)/TAVI(J,2)
        ORDAYS=0.0
        DO 6 K=J,120
        ORDAYS=ORDAYS+TAVI(K,2)
6       CONTINUE
        IF(TAVI(J,1).EQ.0.0)TAVI(J,4)=0.0
        IF(TAVI(J,1).NE.0.0)TAVI(J,4)=ORDAYS/TAVI(J,1)
        IF(J.GE.81)TAVI(J,5)=0.0
        IF(J.LT.81)TAVI(J,5)=UNAUP(J)*PERFEM*STA/
     C       (FLOAT(NF)*TAVI(1,2))
        IF(TAVI(J,1).EQ.0.0)TAVI(J,6)=0.0
        IF(TAVI(J,1).NE.0.0)TAVI(J,6)=TAVI(J,5)/TAVI(J,1)
5       CONTINUE
CC
CCC     COMPUTE FX IN TAVI(*,7)
C
        DO 7 J=1,119
        IF(TAVI(J,2).EQ.0.0)TAVI(J,7)=0.0
        IF(TAVI(J,2).EQ.0.0)GO TO 7
        TAVI(J,7)=(TAVI(J,5)+TAVI(J+1,5))*TAVI(1,2)/(2.0*TAVI(J,2))
7       CONTINUE
CC
CCC     COMPUTE R IN R
C
        EST=0.0
        CREM=1.0
9       EST=EST+CREM
        SUM=0.0
        DO 8 J=1,80
        SUM=SUM+TAVI(J,5)*EXP(-EST*(FLOAT(J-1)-TT))
8       CONTINUE
        IF(ABS(SUM-1.0).LT.0.0000001)GO TO 10
        IF(SUM.LT.1.0)EST=EST-CREM
        IF(SUM.LT.1.0)CREM=CREM/10.0
        GO TO 9
10      R=EST
C
CCC     COMPUTE CLASSICAL POPULATION PARAMETERS : RO IN RO
CCC     LAMBDA IN FINRAT, T IN T, T- IN TBARR, TC IN TCOH
C
        SUMRO=0.0
        SUMTB=0.0
        SUMTC=0.0
        DO 11 J=1,80
        FJ=FLOAT(J)
        SUMRO=SUMRO+TAVI(J,5)
        SUMTC=SUMTC+(FJ-.5-TT)*TAVI(J,5)
        SUMTB=SUMTB+(FJ-.5-TT)*EXP(-R*(FJ-1.-TT))*TAVI(J,5)
11      CONTINUE
        RO=SUMRO
        FINRAT=EXP(R)
        T=ALOG(RO)/R
        TBARR=SUMTB
        TCOH=SUMTC/RO
```

```
C
C       COMPUTE DISCRETE P.D.F.  OF UX IN TAVI(*,8) AND
C       "ENTROPY FOR ARBITRARY AGE DISTRIB." IN HBARR
C
        SUMT=0.0
        SUMN=0.0
        DO 12 J=1,120
        FJ=FLOAT(J)
        TAVI(J,8)=TAVI(J,5)/R0
        IF(TAVI(J,8).LE.0.0)GO TO 12
        SUMT=SUMT+TAVI(J,8)*ALOG(TAVI(J,8))
        SUMN=SUMN+(FJ-.5-TT)*TAVI(J,8)
12      CONTINUE
        HBARR=-SUMT/SUMN
C
C       COMPUTE REPROD.  VALUE IN TAVI(*,9) AND
C       RESID.  REPROD.  VALUE IN TAVI(*,10)
C
        DO 13 J=1,80
        SUMV=0.0
        DO 14 K=J,80
        SUMV=SUMV+TAVI(K,5)*EXP(R*(FLOAT(J-K)+TT))
14      CONTINUE
        IF(TAVI(J,1).LE.0.0)TAVI(J,9)=0.0
        IF(TAVI(J,1).GT.0.0)TAVI(J,9)=SUMV/TAVI(J,1)
        TAVI(J,10)=TAVI(J,9)-TAVI(J,6)
13      CONTINUE
999     DO 998 K=81,120
        TAVI(K,9)=0.0
        TAVI(K,10)=0.0
998     CONTINUE
C
C       PRINT KNOWN LIFE- AND FECUNDITY-TABLE
C
        WRITE(2,204)
        WRITE(2,104)
        DO 15 J=1,120
        WRITE(2,105)J-1,TAVI(J,1),TAVI(J,2),TAVI(J,3),TAVI(J,4),
     C      TAVI(J,5),TAVI(J,6),TAVI(J,7),TAVI(J,8),
     C      TAVI(J,9),TAVI(J,10)
15      CONTINUE
C
C       DO HARMONIC ANALYSIS OF MX; FIRST DETERMINE
C       SIZE OF THE ARRAY TO BE ANALYSED; PUT USEFUL
C       PART OF TAVI(*,6) INTO WAVE; DO ANALYSIS OF WAVE
C
        DO 16 J=1,80
        IF(TAVI(J,6).EQ.0.0)GO TO 16
        N1=J
        GO TO 18
16      CONTINUE
18      CONTINUE
        DO 17 J=1,80
        IF(TAVI(81-J,6).EQ.0.0)GO TO 17
        N2=J
        GO TO 181
17      CONTINUE
181     NUM=82-N1-N2
        DO 19 K=1,NUM
        WAVE(K)=TAVI(N1-1+K,6)
19      CONTINUE
        NH=FLOAT(NUM)/2.0
        CALL HARMAN(WAVE,NUM,NH,1,ESPER,A,B,P)
C
C       PRINT FITNESSPARAMETERS FOR THE POPULATION
C
        WRITE(2,206)
        WRITE(2,106)R
        WRITE(2,107)R0
        WRITE(2,108)FINRAT
        WRITE(2,109)T
        WRITE(2,110)TBARR
        WRITE(2,111)TCOH
        WRITE(2,112)HBARR
        WRITE(2,113)ESPER
C
C       COMPUTE LIFE TABLE FOR MM
C
        MORTCU=0
        VITA(1,1)=1.0
        VITA(120,2)=0.0
```

```
      DO 20 J=1,119
      MORTCU=MORTCU+MORTM(J)
      IF(J.LT.9)VITA(J+1,1)=SUR**J
      IF(J.GE.9)VITA(J+1,1)=STA*FLOAT(NM-MORTCU)/FLOAT(NM)
      VITA(J,2)=(VITA(J,1)+VITA(J+1,1))/2.0
20    CONTINUE
      VITA(120,3)=0.0
      VITA(120,4)=0.0
      DO 21 J=1,119
      IF(VITA(J,2).EQ.0.0)VITA(J,3)=0.0
      IF(VITA(J,2).NE.0.0)VITA(J,3)=VITA(J+1,2)/VITA(J,2)
      ORDAYS=0.0
      DO 22 K=J,120
      ORDAYS=ORDAYS+VITA(K,2)
22    CONTINUE
      IF(VITA(J,1).EQ.0.0)VITA(J,4)=0.0
      IF(VITA(J,1).NE.0.0)VITA(J,4)=ORDAYS/VITA(J,1)
21    CONTINUE
C
C     PRINT LIFE TABLE MM
C
      WRITE(2,214)
      WRITE(2,114)
      DO 23 J=1,120
      WRITE(2,115)J-1,VITA(J,1),VITA(J,2),VITA(J,3),VITA(J,4)
23    CONTINUE
C
C     PLOT UX, LXF, LXM
C     PLOT EXF, VX, EXM
C
      NIET=0
      IF(NIET.EQ.0)GO TO 12121
      CALL DTITRE("*OEFTERM*       COHORTE 1978 MIDDENBLOOM ")
      CALL DECHGLO(1.5)
      CALL DORIGIN(5.,2.)
      CALL DCENACT(0.,-1.,0.,.5,.5,
     C"0          20          40          60          80          100          120")
      CALL DCENACT(0.,-2.,0.,.5,.5,"AGE (DAYS)")
      CALL DCENACT(-1.,0.,90.,.5,.5,
     C    "0 .1 .2 .3 .4 .5 .6 .7 .8 .9 1.")
      CALL DCENACT(-2.,0.,90.,.5,.5,"SURVIVAL")
      CALL DCENACT(25.,0.,90.,.5,.5,
     C    "0       4       8       12      16      20")
      CALL DCENACT(26.,0.,90.,.5,.5,"U(X)")
      CALL DAXE(0.,0.,0.,24.,.3,24)
      CALL DAXE(0.,0.,90.,15.,.3,10)
      CALL DAXE(24.,0.,90.,15.,.3,10)
      DO 991 J=1,120
      VX1(J)=FLOAT(J-1)*0.2
      VX2(2*J-1)=FLOAT(J-1)*0.2
      VX2(2*J)=FLOAT(J)*0.2
      VY1(J)=TAVI(J,1)*15.0
      VY2(2*J-1)=TAVI(J,5)*.75
      VY2(2*J)=TAVI(J,5)*.75
991   CONTINUE
      CALL DVECABS(VX1,VY1,120)
      CALL DVECABS(VX2,VY2,240)
      DO 992 J=1,120
      VX1(J)=FLOAT(J-1)*0.2
      VY1(J)=VITA(J,1)*15.0
992   CONTINUE
      CALL DVECABS(VX1,VY1,120)
      CALL DFENTRE(0.,0.,24.,15.,101)
      CALL DFENTRE(-5.,-5.,70.,48.,100)
      CALL DORIGIN(5.,22.)
```

```
      CALL DTRAIT(1)
      CALL DCENACT(0.,-1.,0.,.5,.5,
     C   "0          20          40          60          80          100         120")
      CALL DCENACT(0.,-2.,0.,.5,.5,"AGE (DAYS)")
      CALL DCENACT(-1.,0.,90.,.5,.5,
     C   "0    10    20    30    40    50    60    70    80")
      CALL DCENACT(-2.,0.,90.,.5,.5,"LIFE EXPECTANCY")
      CALL DCENACT(25.,0.,90.,.5,.5,
     C   "0     5    10    15    20    25    30    35    40")
      CALL DCENACT(26.,0.,90.,.5,.5,"REPRODUCTIVE VALUE")
      CALL DAXE(0.,0.,0.,24.,.3,24)
      CALL DAXE(0.,0.,90.,20.,.3,8)
      CALL DAXE(24.,0.,90.,20.,.3,8)
      DO 993 J=1,120
      VX1(J)=FLOAT(J-1)*0.2
      VY1(J)=TAVI(J,4)*0.25
993   CONTINUE
      CALL DVECABS(VX1,VY1,120)
      DO 994 J=1,120
      VX1(J)=FLOAT(J-1)*0.2
      VY1(J)=TAVI(J,9)*0.5
994   CONTINUE
      CALL DVECABS(VX1,VY1,120)
      DO 995 J=1,120
      VX1(J)=FLOAT(J-1)*0.2
      VY1(J)=VITA(J,4)*0.25
995   CONTINUE
      CALL DVECABS(VX1,VY1,120)
      CALL DFENTRE(0.,0.,24.,20.,101)
12121 CONTINUE
C
C     COMPUTE STABLE AGE DISTRIBUTION
C
777   SSF=0.0
      SSM=0.0
      DO 37 J=1,120
      STABF(J)=TAVI(J,2)*EXP(-R*(FLOAT(J-1)-TT))
      STABM(J)=VITA(J,2)*EXP(-R*(FLOAT(J-1)-TT))
37    CONTINUE
      STABF(1)=STABF(1)*(1.-TT)
      STABM(1)=STABM(1)*(1.-TT)
      DO 38 J=1,120
      SSF=SSF+STABF(121-J)
      SSM=SSM+STABM(121-J)
      IF(J.EQ.110)SHF=SSF
      IF(J.EQ.110)SHM=SSM
38    CONTINUE
      FRF(1)=3.2*STABF(10)/24.0+SHF
      FRF(2)=(20.8*STABF(10)+24.0*STABF(9)+4.0*STABF(8))/24.0
      FRF(3)=(20.0*STABF(8)+13.4*STABF(7))/24.0
      FRF(4)=(10.6*STABF(7)+17.4*STABF(6))/24.0
      FRF(5)=(6.6*STABF(6)+16.6*STABF(5))/24.0
      FRF(6)=(7.4*STABF(5)+15.6*STABF(4))/24.0
      FRF(7)=8.4*STABF(4)/24.0+STABF(3)+STABF(2)+STABF(1)
      FRM(1)=7.3*STABM(9)/24.0+STABM(10)+SHM
      FRM(2)=(16.7*STABM(9)+18.0*STABM(8))/24.0
      FRM(3)=(6.0*STABM(8)+18.2*STABM(7))/24.0
      FRM(4)=(5.8*STABM(7)+17.4*STABM(6))/24.0
      FRM(5)=(6.6*STABM(6)+16.6*STABM(5))/24.0
      FRM(6)=(7.4*STABM(5)+15.6*STABM(4))/24.0
      FRM(7)=8.4*STABM(4)/24.0+STABM(3)+STABM(2)+STABM(1)
45    CONTINUE
      DO 44 K=1,7
      FRF(K)=FRF(K)/SSF
      FRM(K)=FRM(K)/SSM
44    CONTINUE
      WRITE(2,140)
      WRITE(2,240)
      WRITE(2,40)(FRF(K),K=1,7)
      WRITE(2,41)(FRM(K),K=1,7)
      IF(FRF(7).EQ.0.0)GO TO 46
      SSF=1.0-FRF(7)
      SSM=1.0-FRM(7)
      FRF(7)=0.0
      FRM(7)=0.0
      GO TO 45
46    CONTINUE
```

```
C
CC      COMPUTE INDIVIDUAL FITNESS PARAMETERS
C       TO THAT END,  FIRST TRANSFORM ALL UNAUPI INTO UX
C       FIRST COMPUTE THOSE PARAMETERS BASED ON
CC         WEIGHTED SUMS OF UX
C
        DO 24 I=1,NF
        SUMRO=0.0
        SUMTC=0.0
        SUMW=0.0
        DO 25 J=1,80
        UNAUPI(I,J)=UNAUPI(I,J)*PERFEM*STA/TAVI(1,2)
        SUMRO=SUMRO+UNAUPI(I,J)
        SUMTC=SUMTC+UNAUPI(I,J)*(FLOAT(J)-.5-TT)
        SUMW=SUMW+UNAUPI(I,J)*EXP(-R*(FLOAT(J-1)-TT))
25      CONTINUE
        FITPAR(I,1)=SUMRO
        IF(SUMRO.EQ.0.0)FITPAR(I,2)=99.99
        IF(SUMRO.NE.0.0)FITPAR(I,2)=SUMTC/FITPAR(I,1)
        FITPAR(I,3)=SUMW
        IF(SUMRO.NE.0.0)GO TO 43
        FITPAR(I,4)=-99.99
        FITPAR(I,5)=99.99
        FITPAR(I,6)=99.99
        FITPAR(I,7)=99.99
        GO TO 42
C
CC      COMPUTE INDIVIDUAL R
C
43      EST=0.0
        CREM=1.0
26      EST=EST+CREM
        SUM=0.0
        DO 27 J=1,80
        SUM=SUM+UNAUPI(I,J)*EXP(-EST*(FLOAT(J-1)-TT))
27      CONTINUE
        IF(ABS(SUM-1.0).LT.0.0000001)GO TO 28
        IF(SUM.LT.1.0)EST=EST-CREM
        IF(SUM.LT.1.0)CREM=CREM/10.0
        GO TO 26
28      FITPAR(I,4)=EST
C
CC      HARMONIC ANALYSIS OF UX
C
        DO 29 J=1,80
        IF(UNAUPI(I,J).EQ.0.0)GO TO 29
        N1=J
        GO TO 31
29      CONTINUE
31      CONTINUE
        DO 30 J=1,80
        IF(UNAUPI(I,81-J).EQ.0.0)GO TO 30
        N2=J
        GO TO 311
30      CONTINUE
311     NUM=82-N1-N2
        IF(NUM.LT.3)FITPAR(I,5)=99.99
        IF(NUM.LT.3)GO TO 39
        DO 32 K=1,NUM
        WAVE(K)=UNAUPI(I,N1-1+K)
32      CONTINUE
        NHI=FLOAT(NUM)/2.0
        CALL HARMAN(WAVE,NUM,NHI,0,ESPER,A,B,P)
        FITPAR(I,5)=ESPER
39      CONTINUE
C
C       DETERMINE INDIVIDUAL TMIN,  AND DRAW UP
CC      "UX" WHICH ALLOWS CALCULATION OF THE POPULATION TMIN
C
        SUMT=0.0
        ES1=0.0
        Q=1.0
        DO 33 J=1,80
        IF(UNAUPI(I,J).GT.0.0)Q=0.0
        IF(UNAUPI(I,J).EQ.0.0.AND.Q.EQ.0.0)GO TO 34
        SUMT=SUMT+(FLOAT(J)-.5-TT)*UNAUPI(I,J)
        ES1=ES1+UNAUPI(I,J)
        UMI(J)=UMI(J)+UNAUPI(I,J)
33      CONTINUE
34      FITPAR(I,6)=SUMT/ES1
```

```
C
CC      COMPUTE H- AFTER TRANSFORMING ALL UX(IND) INTO GX(IND)
C
        SUM1=0.0
        SUM2=0.0
        DO 35 J=1,80
        UNAUPI(I,J)=UNAUPI(I,J)/FITPAR(I,1)
        IF(UNAUPI(I,J).LE.0.0)GO TO 35
        SUM1=SUM1+UNAUPI(I,J)*ALOG(UNAUPI(I,J))
        SUM2=SUM2+(FLOAT(J)-.5-TT)*UNAUPI(I,J)
35      CONTINUE
        FITPAR(I,7)=-SUM1/SUM2
C
CC      INDIVIDUAL LIFE SPAN
C
42      FITPAR(I,8)=FLOAT(LD(I))-.5-TT
C
CC      END OF COMPUTATION INDIVIDUAL FITNESS PARAMETERS; PRINT THEM
C
24      CONTINUE
        WRITE(2,216)
        WRITE(2,116)
        DO 36 I=1,NF
        WRITE(2,117)I,FITPAR(I,1),FITPAR(I,2),FITPAR(I,3),
     C      FITPAR(I,4),FITPAR(I,5),FITPAR(I,6),
     C      FITPAR(I,7),FITPAR(I,8)
36      CONTINUE
        IF(NIET.EQ.0)GO TO 21212
        CALL DORIGIN(50.,5.)
        CALL DFENTRE(-5.,-5.,50.,48.,100)
        CALL DCENACT(0.,-1.,0.,.5,.5,
     C   "0          20          40          60          80          100")
        CALL DCENACT(0.,-2.,0.,.5,.5,"LIFE SPAN (DAYS)")
        CALL DCENACT(-1.,0.,90.,.5,.5,
     C   "0          100         200         300")
        CALL DCENACT(-2.,0.,90.,.5,.5,"NET FECUNDITY")
        CALL DAXE(0.,0.,0.,20.,.3,20)
        CALL DAXE(0.,0.,90.,17.5,.3,7)
        DO 996 L=1,NF
        XP=FITPAR(L,8)*0.2
        YP=FITPAR(L,1)*0.05
        CALL DCENACT(XP,YP,0.,.2,.2,"0")
996     CONTINUE
        CALL DORIGIN(50.,30.)
        CALL DCENACT(0.,-1.,0.,.5,.5,
     C   "0          20          40          60          80          100")
        CALL DCENACT(0.,-2.,0.,.5,.5,"LIFE SPAN (DAYS)")
        CALL DCENACT(-1.,0.,90.,.5,.5,
     C   "          1           2           3")
        CALL DCENACT(-2.,0.,90.,.5,.5,"      RATE OF INCREASE")
        CALL DAXE(0.,0.,0.,20.,.3,20)
        CALL DAXE(0.,2.5,90.,12.5,.3,5)
        DO 997 L=1,NF
        XP=FITPAR(L,8)*0.2
        YP=(FITPAR(L,4)-.05)*50.0
        CALL DCENACT(XP,YP,0.,.2,.2,"0")
997     CONTINUE
        CALL DFINSAV
21212   CONTINUE
C
CC      COMPUTE AND PRINT POPULATION TMIN
C
        SUM1=0.0
        SUM2=0.0
        DO 48 J=1,50
        SUM1=SUM1+(FLOAT(J)-.5-TT)*UMI(J)
        SUM2=SUM2+UMI(J)
48      CONTINUE
        TMIN=SUM1/SUM2
        WRITE(2,118)TMIN
101     FORMAT(2F7.5,213,F5.2)
102     FORMAT(40I2)
200     FORMAT(20F4.0)
```

```
204    FORMAT(*FEMALE LIFE-TABLE AND FECUNDITY SCHEDULE*)
104    FORMAT(*AGE      L(X)      L(X)      P(X)      E(X)*,4X,
     C       *U(X)      M(X)      F(X)      PDFU      V(X)*,3X,
     C       *V#(X)*)
105    FORMAT(I3,10F8.3)
206    FORMAT(*FITNESSPARAMETERS VAN COHORTE ALS GEHEEL*)
106    FORMAT(*INTRINSIC RATE =*,F5.3 )
107    FORMAT(*NET FECUNDITY =*,F5.1)
108    FORMAT(*FINITE RATE =*,F7.3)
109    FORMAT(*MEAN GENERATION TIME =*,F4.1)
110    FORMAT(*AGE MOTHER OF AVERAGE NEWBORN =*,F4.1)
111    FORMAT(*COHORT GENERATION TIME =*,F4.1)
112    FORMAT(*ENTROPY OF FECUNDITY SCHEDULE =*,F8.3)
113    FORMAT(*PERIOD OF E.S. PRODUCTION =*,F4.1)
214    FORMAT(*MALE LIFE-TABLE*)
114    FORMAT(*AGE      L(X)      L(X)      P(X)      E(X)*)
115    FORMAT(I3,4F8.3)
140    FORMAT(*STABLE STAGE DISTRIBUTION*)
240    FORMAT(15X,*ADULT*,6X,*COP5*,6X,*COP4*,6X,
     C       *COP3*,6X,*COP2*,6X,*COP1*,6X,*NAUP*)
40     FORMAT(* FEMALES   *,7F10.3)
41     FORMAT(* MALES     *,7F10.3)
216    FORMAT(*INDIVIDUELE FITNESSPARAMETERS*)
116    FORMAT(*INDIVIDU       RO       TCOH      FITNESS*,
     C       *       R        PERIOD    TMIN        *,
     C       *ENTROPY    LIFESPAN*)
117    FORMAT(I5,F9.1,F9.2,2F9.3,2F9.2,F12.6,F9.1)
118    FORMAT(*POPULATION TMIN =*,F4.1)
       CALL EXIT
       END
       SUBROUTINE HARMAN(Y,N,NH,INDEX,PERIO,ALFA,BETA,POWER)
       DIMENSION Y(N)
       DIMENSION ALFA(NH),BETA(NH),POWER(NH)
       CALL MEAN(Y,N,YMEAN,YVAR,YSD)
       FF=6.2831854/FLOAT(N)
       SPOWER=0.0
       GP=0.0
       IGP=0
       SP=0.0
       ISP=0
       IF(INDEX.EQ.1)WRITE(2,200)
       DO 10 I=1,NH
       ELEMA=0.0
       ELEMB=0.0
       DO 20 K=1,N
       ARG=FF*FLOAT(K-1)*FLOAT(I)
       ELEMA=ELEMA+Y(K)*COS(ARG)
       ELEMB=ELEMB+Y(K)*SIN(ARG)
20     CONTINUE
       ALFA(I)=ELEMA*2/FLOAT(N)
       BETA(I)=ELEMB*2/FLOAT(N)
       POWER(I)=ALFA(I)**2+BETA(I)**2
       SPOWER=SPOWER+POWER(I)
       PERIOD=FLOAT(N)/FLOAT(I)
       IF(INDEX.EQ.1)WRITE(2,201)ALFA(I),BETA(I),
     C       POWER(I),I,PERIOD
       PO=POWER(I)
       II=I
       IF(PO.LE.GP.OR.I.EQ.1)GO TO 50
       PO=GP
       II=IGP
       IGP=I
       GP=POWER(I)
50     IF(PO.LE.SP.OR.I.EQ.1)GO TO 10
       ISP=II
       SP=PO
10     CONTINUE
       IF(INDEX.EQ.1)WRITE(2,999)IGP,ISP
```

```
999   FORMAT(*DE GEKOZEN PERIODICITEITEN ZIJN 1,*,I3,* EN*,I3)
      PERIO=FLOAT(N)/FLOAT(IGP)
      IF(INDEX.EQ.0)GO TO 40
      WRITE(2,100)
      DO 30 K=1,N
      ARG1=FF*FLOAT(K-1)
      YEST=YMEAN+ALFA(1)*COS(ARG1)+BETA(1)*SIN(ARG1)
     C       +ALFA(IGP)*COS(ARG1*FLOAT(IGP))
     C       +BETA(IGP)*SIN(ARG1*FLOAT(IGP))
     C       +ALFA(ISP)*COS(ARG1*FLOAT(ISP))
     C       +BETA(ISP)*SIN(ARG1*FLOAT(ISP))
      WRITE(2,101)Y(K),YEST
30    CONTINUE
40    CONTINUE
200   FORMAT(10X,*ALFA*,10X,*BETA*,10X,*POWER*,
     C       10X,*HARMONIC*,10X,*PERIOD*)
201   FORMAT(4X,F10.3,4X,F10.3,5X,F10.3,15X,I3,10X,F5.2)
300   FORMAT(*TOTAL VARIANCE =*,F10.3,5X,*SUM POWERS =*,F10.3)
100   FORMAT(*SIMULATION BY 3 PERIODICITIES :   OBS      EST*)
101   FORMAT(32X,F6.2,2X,F6.2)
      RETURN
      END
      SUBROUTINE MEAN(X,N,XMEAN,XVAR,XSD)
      DIMENSION X(N)
      SUMX=0.0
      DO 10 I=1,N
      SUMX=SUMX+X(I)
10    CONTINUE
      XMEAN=SUMX/FLOAT(N)
      SS=0.0
      DO 20 I=1,N
      SQDEV=(X(I)-XMEAN)**2
      SS=SS+SQDEV
20    CONTINUE
      XVAR=SS/FLOAT(N-1)
      XSD=SQRT(XVAR)
      RETURN
      END
```

Appendix 2

Demography of laboratory-husbanded Tisbe

Density fluctuations in my laboratory culture of T.furcata were not monitored - in fact, it had been maintained for no other purpose than as a future source of reference material. One could therefore object that such cultures may perhaps not come sufficiently close to the ideal of true demographic stationarity. Hence it is useful to examine published data on similarly-husbanded populations of two closely related species : T,reticulata (Battaglia & Lazzaretto, 1960; Battaglia, 1962; Lazzaretto, 1964) and T.clodiensis (Fava, 1973, 1975). These papers report census figures taken about 1 generation apart in otherwise undisturbed mass cultures; censused individuals were returned to their bowls. I have computed instantaneous inter-census rates of increase, and these show the following features (Fig. A2.1) : they are

1. similar among species (Kolmogorov-Smirnov two-sample test n.s.);
2. normally distributed (Kolmogorov-Smirnov one-sample test n.s.) with mean = -.0003 and s.d. = .022 (which means that they do not normally exceed .04);
3. if anything, negatively autocorrelated ($P < .05$ in 2 out of 14 runs tests).

These results would seem to validate extrapolation to T.furcata, and to vindicate the contrast between laboratory and bloom animals (cfr chapter 2 : rates of increase $\geq .10$ for two consecutive generations in the latter).

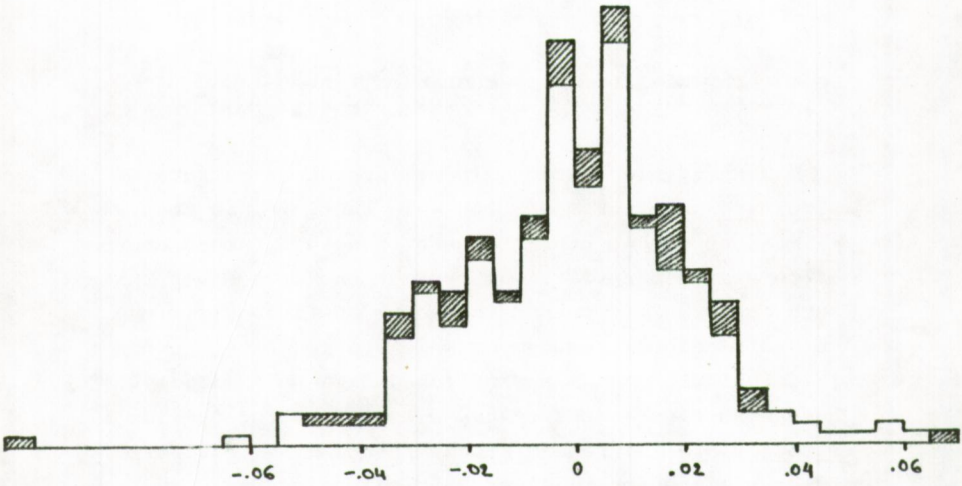


Fig. A2.1. Distribution of instantaneous rates of increase (over one generation) in laboratory-husbanded T. clodiensis (plain) and T. reticulata (cross-hatched).

Appendix 3

When m-selection?

The relative impact on the population growth rate λ, of time shifts vs. proportional increase of the fecundity function m_x depends on the demographic regime already prevalent in the population. In a recent paper, Caswell & Hastings (1980) deduced the relationship

$$k_q \simeq (\lambda / \breve{P})^q \qquad (1)$$

where

k_q = the increase in fecundity which duplicates the effect of a forward shift of m_x over q time units, and

$\breve{P}$ = the average age-specific survival during the reproductive period (assumed near-constant).

As a corollary, it was concluded that selection for high reproductive output must occur in equilibrium and declining populations. The purpose of this appendix is to show that the latter conclusion, although valid in the case of T. furcata considered in chapter 6, does in general need some qualification.

Fig. 1 of Caswell & Hastings (right half of my Fig. A3.1) tells one that when $\lambda/\breve{P} < 1$, fecundity must be multiplied by a factor < 1 to duplicate a forward shift over q time units. While this is mathematically correct, it is not biologically informative. Indeed, in many declining populations (viz. those where $\lambda < \breve{P}$), it is delaying reproduction (q negative) which will increase λ and is therefore desirable from the organism's viewpoint (Mertz, 1971; Charlesworth & Giesel, 1972; Charlesworth,

1980 p. 225; Caswell, 1982). For a biologically meaningful parallel to the $\lambda/\tilde{P} > 1$ case developed by Caswell & Hastings, it suffices to note that

$$(k_q \mid \lambda/\tilde{P} = a) = (k_{-q} \mid \lambda/\tilde{P} = 1/a)$$

(see Fig. A3.1). It then becomes obvious that fecundity increases in the above-mentioned declining populations will be relatively inefficient, and time shifts will be preferred, for the same reason which Caswell & Hastings quote in relation to increasing populations, viz. the steepness of the $k_q(q)$ relationship whenever $\lambda/\tilde{P}$ is not $\simeq 1$. The claim that 'as λ decreases, the relative importance of fecundity goes up' (Caswell, 1982) is not generally valid. On the other hand, iff $\lambda/\tilde{P} = 1$, fitness can only be increased by increasing the m_x (for any subset of x).

It remains to be clarified which demographic conditions correspond to variations of the somewhat abstract key parameter, $\lambda/\tilde{P}$. Unless $\tilde{P} \simeq 1$, $\lambda/\tilde{P}$ does not strictly reflect the dynamic behaviour of the population. In particular, $\tilde{P}$ always being ≤ 1, $\lambda/\tilde{P} < 1$ implies a declining population but the reverse does not hold true, the concordance being:

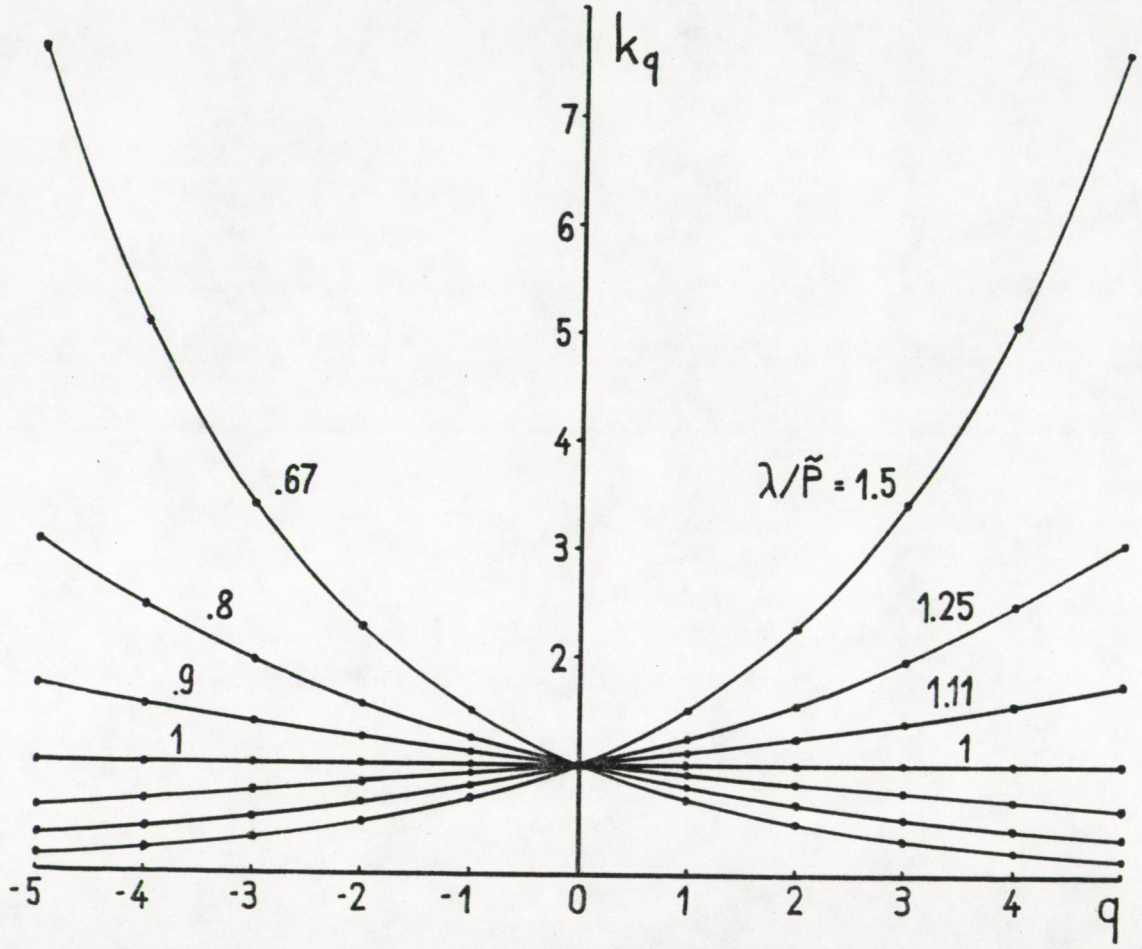
λ	>1	$=1$	<1
$\lambda/\tilde{P}$	>1	$\geqslant 1$	$\gtrless 1$

Caswell & Hastings' own Discussion of stationary and declining populations involves the tacit assumption that $\tilde{P} \simeq 1$. In practice, this may often be realistic, as density regulation is generally achieved by pre-adult (larval) mortality. Nevertheless, their ensueing identification of stationary ($\lambda = 1$) populations with 'K-strategists' does, in a way, beg the question: cases such as a highly fecund population kept in check by heavy predation on the adults, are not thus considered. In the latter (perhaps somewhat theoretical) equilibrium populations, selection for early reproduction still goes on (Mertz, 1971, p. 372). Moreover, Caswell & Hastings (1980) include oft-declining populations in the 'K-selected' category (in the wide sense), e.g. when Gymnogyps californianus is quoted as an example of a K-selected species; Caswell (1982) reiterates that declining populations should be 'even more intensely K-selected' than stationary ones. In declining populations, however, any value of $\lambda/\tilde{P}$ is theoretically possible so that speeding up development may be harmful, ineffective or even desirable according as $\tilde{P} >, =$ or $< \lambda$.

Summing up : while it is correct that there exist stationary and declining populations wherein fitness can only be increased by increasing fecundity, it should be noted that in other stationary c.q. declining regimes, selection will still favour shifts in the age of reproduction. In each case, the optimal distribution of m_x over time is known to be mediated by the stable age structure, $l_x e^{-rx}$, which turns up as a weighting factor for the age-specific fecundities (Charlesworth & Giesel, 1972; Giesel,

1976; Charlesworth, 1980 p. 145 sqq). To see how this relates to Caswell & Hastings' result, let l_x equal Ce^{-dx}, i.e. assume a constant survival rate $\tilde{P} = e^{-d}$ during reproduction; it follows at once that $l_x e^{-rx}$ is nothing else but $(\lambda / \tilde{P})^q$ in a different guise.

Fig. A3.1. Illustration of the relative merits of increasing fecundity and speeding up development as mechanisms to raise the population growth rate. See text for explanation.


k_q
7
6
5
4
3
2
.67
.8
.9
1
$\lambda/\tilde{P} = 1.5$
1.25
1.11
1
-5
-4
-3
-2
-1
0
1
2
3
4
q

References

Ayala, F.J. (1971). Competition between species : Frequency dependence. Science 171, 820-824.

Ayala, F.J., M.E. Gilpin & J.G. Ehrenfeld (1973). Competition between species : Theoretical models and experimental tests. Theor. Pop. Biol. 4, 331-356.

Barclay, H.J. & P.T. Gregory (1982). An experimental test of life history evolution using Drosophila melanogaster and Hyla regilla. Amer. Natur. 120, 26-40.

Barnett, P.R.O. (1970). The life cycles of two species of Platychelipus Brady (Harpacticoida) on an intertidal mudflat. Int. Rev. Ges. Hydrobiol. 55, 169-195.

Battaglia, B. (1957a). Ecological differentiation and incipient intraspecific isolation in marine copepods. Année Biol. 33, 259-268.

----- (1957b). Ricerche sul ciclo biologico di Tisbe gracilis (T. Scott),(Copepoda, Harpacticoida), studiato in condizioni di laboratorio. Archo Oceanogr. Limnol. 11, 29-46.

----- (1958). Selezione e rapporto dei sessi nel Copepode Harpacticoide Tisbe gracilis (T. Scott). Atti Accad. Naz. Lincei, Rend. Cl. Sci. Fis. Mat. Nat. 24, 327-335.

----- (1961). Rapporti tra geni per la pigmentazione e la sessualità in Tisbe reticulata. Atti Ass. Genet. Ital. 6, 439-447.

----- (1962a). Osservazioni preliminari sugli equilibri di popolazioni sperimentali a diversa composizione iniziale, nel Copepode Tisbe reticulata. Atti Accad. Naz. Lincei, Rend. Cl. Sci. Fis. Mat. Nat. 32, 711-715.

----- (1962b). Controllo genetico della velocità di sviluppo in popolazioni geografiche del copepode marino Tisbe furcata (Baird). Nota preliminare. Atti Ist. Veneto Sci. Lett. Arti 120, 83-91.

----- (1970). Cultivation of marine copepods for genetic and evolutionary research. Helgoländer Wiss. Meeresunters. 20, 385-392.

Battaglia, B. & I. Lazzaretto (1960). Prime osservazioni sulla genetica e l'ecologia di popolazioni sperimentali del copepode Tisbe reticulata. Atti Accad. Naz. Lincei, Rend. Cl. Sci. Fis. Mat. Nat. 28, 502-506.

Battaglia, B. & L. Malesani (1962). Gli effetti della selezione operata in assenza di inincrocio sugli spostamenti del rapporto-sessi in Tisbe gracilis (Copepoda, Harpacticoida). Atti Accad. Naz. Lincei, Rend. Cl. Sci. Fis. Mat. Nat. 32, 251-257.

Battaglia, B. & A. Parise (1967). Ricerche sulla "fitness" in razze geografiche del Copepode Tisbe furcata (Baird) (Harpacticoida). Boll. Zool. 34, 88-89.

Battaglia, B. & P. Talamini (1957). Osservazioni sullo sviluppo larvale di Tisbe reticulata Bocquet (Copepoda, Harpacticoida). Archo Oceanogr. Limnol. 11, 63-68.

Battaglia, B. & B. Volkmann-Rocco (1973). Geographic and reproductive isolation in the marine harpacticoid copepod Tisbe. Mar. Biol. 19, 156-160.

Benson, J.F. (1973). Some problems of testing for density-dependence in animal populations. Oecologia 13, 183-190.

Bergmans, M. (1979). Taxonomic notes on species of Tisbe (Copepoda, Harpacticoida) from a Belgian sluice dock. Zool. Scr. 8, 211-220.

----- (1981). A demographic study of the life cycle of Tisbe furcata (Baird, 1837) (Copepoda: Harpacticoida). J. Mar. Biol. Ass. U.K. 61, 691-705.

Betouhim-El, T. & D. Kahan (1972). Tisbe pori n.sp. (Copepoda: Harpacticoida) from the Mediterranean coast of Israel and its cultivation in the laboratory. Mar. Biol. 16, 201-209.

Bocquet, C. (1951). Recherches sur Tisbe (= Idyaea) reticulata, n.sp. Essai d'analyse génétique du polychromatisme d'un Copépode Harpacticoïde. Archs Zool. Exp. Gén. 87, 335-416.

Bodmer, W.F. & P.A. Parsons (1962). Linkage and recombination in evolution. Adv. Genet. 11, 1 -100.

Braioni, G.M. & A. Parise (1971). Affollamento e dinamica di popolazioni di Tisbe (Copepoda, Harpacticoida). Boll. Zool. 38, 500-501.

Browne, R.A. (1982). The costs of reproduction in brine shrimp. Ecology 63, 43-47.

Burdon, J.J. (1980). Intra-specific diversity in a natural population of Trifolium repens. J. Ecol. 68, 717-735.

Castel, J. (1976). Développement larvaire et biologie de Harpacticus littoralis Sars 1910 (Copépode, Harpacticoïde) dans les étangs saumâtres de la région d'Arcachon. Cah. Biol. Mar. 17, 195-212.

Caswell, H. 1982. Life history theory and the equilibrium status of populations, Am. Nat. 120, 317-339.

Caswell, H. & A. Hastings (1980). Fecundity, developmental time, and population growth rate: An analytical solution. Theor. Pop. Biol. 17, 71-79.

Charlesworth, B. (1973). Selection in populations with overlapping generations. V. Natural selection and life histories. Amer. Natur. 107, 303-311.

----- (1976). Natural selection in age-structured populations. Lect. Math. Life Sci. 8, 69-87.

----- (1980). Evolution in Age-Structured Populations. Cambridge Univ. Press, Cambridge.

Charlesworth, B. & D. Charlesworth (1973). The measurement of fitness and mutation rate in human populations. Ann. Hum. Genet. 37, 175-187.

Charlesworth, B. & J.T. Giesel (1972a). Selection in populations with overlapping generations. II. Relations between gene frequency and demographic variables. Amer. Natur. 106, 388-401.

----- (1972 b). Selection in populations with overlapping generations. IV. Fluctuations in gene frequency with density-dependent selection. Amer. Natur. 106, 402-411.

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

Cole, L.C. (1957). Sketches of general and comparative demography. Cold Spring Harbor Symp. Quant. Biol. 22, 1-15.

Cooney, J.D. & C.W. Gehrs (1980a). Effects of varying food concentration on reproduction in Diaptomus clavipes Schacht. Amer. Midl. Natur. 104, 63-69.

-----.(1980b). The relationship between egg size and naupliar size in the calanoid copepod Diaptomus clavipes Schacht. Limnol. Oceanogr. 25, 549-552.

Coull, B.C. & B.W. Dudley (1976). Delayed naupliar development of meiobenthic copepods. Biol. Bull. Mar. Biol. Lab. Woods Hole 150, 38-46.

Coull, B.C. & W.B. Vernberg (1975). Reproductive periodicity of meiobenthic copepods: Seasonal or continuous? Mar. Biol. 32, 289-293.

D'Apolito, L.M. & S.E. Stancyk (1979). Population dynamics of Euterpina acutifrons (Copepoda: Harpacticoida) from North Inlet, South Carolina, with reference to dimorphic males. Mar. Biol. 54, 251-260.

Derr, J.A. (1980). The nature of variation in life history characters of Dysdercus bimaculatus (Heteroptera: Pyrrhocoridae), a colonizing species. Evolution 34, 548-557.

Dhondt, A.A. (1977). Interspecific competition between great and blue tit. Nature 268, 521-523.

Doyle, R.W. & W. Hunte (1981a). Genetic changes in 'fitness' and yield of a crustacean population in a controlled environment. J. Exp. Mar. Biol. Ecol. 52, 147-156.

----- (1981b). Demography of an estuarine amphipod (Gammarus lawrencianus) experimentally selected for high 'r': A model of the genetic effects of environmental change. Can. J. Fish. Aquat. Sci. 38, 1120-1127.

Elgmork, K., J.P. Nilssen, T. Broch & R. Øvrevik (1978). Life cycle strategies in neighbouring populations of the copepod Cyclops scutifer Sars. Verh. Internat. Verein. Limnol. 20, 2518-2523.

Epp, R.W. & W.M. Lewis, Jr. (1980). Metabolic uniformity over the environmental temperature range in Brachionus plicatilis (Rotifera). Hydrobiologia 73, 145-147.

Fava, G. (1973). Effetti selettivi della temperatura in Tisbe clodiensis (Copepoda Harpacticoida). Atti Accad. Naz. Lincei, Rend. Cl. Sci. Fis. Mat. Nat. 53, 186-191.

----- (1974). Competizione intraspecifica in Tisbe clodiensis (Copepoda Harpacticoida). Atti Ist. Veneto Sci. Lett. Arti, Cl. Sci. Mat. Nat. 132, 75-85.

----- (1975). Studies on the selective agents operating in experimental populations of Tisbe clodiensis (Copepoda,Harpacticoida). Genetica 45, 289-305.

-----(1980). Osservazioni ecologiche sulle specie di Tisbe (Copepoda, Harpacticoida) nella laguna di Marano. Atti Ist. Veneto Sci. Lett. Arti, Cl. Sci. Fis. Mat. Nat. 138, 39-51.

Fava, G. & E. Crotti (1979). Effect of crowding on nauplii production during mating time (sic) in Tisbe clodiensis and T. holothuriae (Copepoda, Harpacticoida). Helgoländer Wiss. Meeresunters. 32, 466-475.

Fava, G., I. Lazzaretto-Colombera & M. Cervelli (1976). Carico genetico in Tisbe (Copepoda, Harpacticoida). II. T. holothuriae e T. bulbisetosa della laguna di Venezia. Atti Accad. Naz. Lincei, Rend. Cl. Sci. Fis. Mat. Nat. 60, 699-708.

Fava, G. & B. Volkmann (1975). Tisbe (Copepoda: Harpacticoida) species from the lagoon of Venice. I. Seasonal fluctuations and ecology. Mar. Biol. 30, 151-165.

----- (1977). Tisbe (Copepoda: Harpacticoida) species from the estuarine embayment of Scardovari. Archo Oceanogr. Limnol. 19, 55-64.

Feller, R.J. (1980a). Development of the sand-dwelling meiobenthic harpacticoid copepod Huntemannia jadensis Poppe in the laboratory. J. Exp. Mar. Biol. Ecol. 46, 1-15.

----- (1980b). Quantitative cohort analysis of a sand-dwelling meiobenthic harpacticoid copepod. Est. Coast. Mar. Sci. 11: 459-476.

Fleeger, J.W. (1979). Population dynamics of three estuarine meiobenthic harpacticoids (Copepoda) in South Carolina. Mar. Biol. 52, 147-156.

Fowler, C.W.(1981). Density dependence as related to life history strategy. Ecology 62, 602-610.

Fraser, J.H. (1936). The occurrence, ecology and life history of Tigriopus fulvus (Fischer). Mar. Biol. Ass. U.K. 20, 523-536.

Fujiie, A. (1980). Ecological studies on the population of the pear leaf miner, Bucculatrix pyrivorella Kuroko (Lepidoptera: Lyonetiidae) III. Fecundity fluctuation from generation to generation within a year. Appl. Ent. Zool. 15, 1-9.

Gallagher, J.C. (1980). Population genetics of Skeletonema costatum (Bacillariophyceae) in Narragansett Bay. J. Phycol. 16, 464-474.

Gaudy, R. & Guérin, J.P. (1977). Dynamique des populations de Tisbe holothuriae (Crustacea: Copepoda) en élevage sur trois régimes artificiels différents. Mar. Biol. 39, 137-145.

----- (1978). Etude expérimentale de la respiration, de la croissance et de la fécondité de Tisbe holothuriae (Copépode: Harpacticoïde) élevé à des températures différentes. In : McLusky, D.S. & A.J. Berry (eds.), Physiology and Behaviour of Marine Organisms. Pergamon Press, Oxford & New York, pp. 31-38.

Gaudy, R., J.P. Guérin & M. Moraïtou-Apostolopoulou (1982). Effect of temperature and salinity on the population dynamics of Tisbe holothuriae Humes (Copepoda : Harpacticoida) fed on two different diets. J. Exp. Mar. Biol. Ecol. 57, 257-271.

Gehrs, C.W. & A. Robertson (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: Persoone, G. & E. Jaspers (eds.), Proceedings of the 10th European Symposium on Marine Biology, vol. 1, Research in Mariculture at Laboratory and Pilot scale. Universa Press, Wetteren (Belgium), pp. 143-159.

Giesel, J.T. (1972). Maintenance of genetic variability in natural populations - An alternative implication of the Charlesworth-Giesel hypothesis. Amer. Natur. 106, 412-414.

----- (1976). Reproductive strategies as adaptations to life in temporally heterogeneous environments. Annu. Rev. Ecol. Syst. 7, 57-79.

Giesel, J.T., P.A. Murphy & M.N. Manlove (1982). The influence of temperature on genetic interrelationships of life history traits in a population of Drosophila melanogaster : What tangled data sets we weave. Amer. Natur. 119, 464-479.

Ginsburger-Vogel, T. (1975). Température et différenciation sexuelle chez les crustacés. Bull. Soc. Zool. Fr. 100, 95-115.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Natur. 111 : 1169- 1194.

Haq, S.M. (1972). Breeding of Euterpina acutifrons, a harpacticid copepod, with special reference to dimorphic males. Mar. Biol. 15, 221-235.

Harris, R.P. (1973). Feeding, growth, reproduction and nitrogen utilization by the harpacticoid copepod, Tigriopus brevicornis. J. Mar. Biol. Ass. U.K. 53, 785-800.

Hart, R.C. & I.A. McLaren (1978). Temperature acclimation and other influences on embryonic duration in the copepod Pseudocalanus sp. Mar. Biol. 45, 23-30.

Hastings, A. (1978). Evolutionarily stable strategies and the evolution of life history strategies: I. Density dependent models. J. Theor. Biol. 75, 527-536.

Hauspie, R. & Polk, P. (1973). Swimming behaviour patterns in certain benthic harpacticoids (Copepoda). Crustaceana 25, 95-103.

Heip, C. (1972). The reproductive potential of copepods in brackish water. Mar. Biol. 12, 219-221.

----- (1974a). A note on the life-span of r-strategists. Biol. Jb. Dodonaea 42, 117-120.

----- (1974b). A comparison between models describing the influence of temperature on the development rate of copepods. Biol. Jb. Dodonaea 42, 121-125.

----- (1980). The influence of competition and predation on production of meiobenthic copepods. In : Tenore, K.R. & B.C. Coull. (eds.), Marine Benthic Dynamics. Univ. South Carolina Press, Columbia, pp. 167-177.

Heip, C. & N. Smol (1976). Influence of temperature on the reproductive potential of two brackish-water harpacticoids (Crustacea : Copepoda). Mar. Biol. 35, 327-334.

Heip, C., N. Smol & V. Absillis (1978). Influence of temperature on the reproductive potential of Oncholaimus oxyuris (Nematoda : Oncholaimidae). Mar. Biol. 45, 255-260.

Hicks, G.R.F. (1977). Breeding activity of marine phytal harpacticoid copepods from Cook Strait. N.Z.J.Mar.Freshwater Res. 11, 645-666.

----- (1979). Pattern and strategy in the reproductive cycles of benthic harpacticoid copepods. In : Naylor, E. & R.G. Hartnoll (eds.), Cyclic Phenomena in Marine Plants and Animals. Pergamon Press, Oxford & New York, pp. 139-147.

----- (1980). Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. J. Exp. Mar. Biol. Ecol. 44, 157-192.

Hoppenheit, M. (1975a). Zur Dynamik exploitierter Populationen von Tisbe holothuriae (Copepoda, Harpacticoida). I. Methoden, Verlauf der Populationsentwicklung und Einfluss der Wassererneuerung. Helgoländer Wiss. Meeresunters. 27, 235-253.

----- (1975b). Zur Dynamik exploitierter Populationen von Tisbe holothuriae (Copepoda, Harpacticoida). II. Populationsdichte, Alterszusammensetzung, Wachstum und Ausbeute. Helgoländer Wiss. Meeresunters. 27, 377-395.

----- (1976). Zur Dynamik exploitierter Populationen von Tisbe holothuriae (Copepoda, Harpacticoida). III. Reproduktion, Geschlechtsverhältnis, Entwicklungsdauer und Überlebenszeit. Helgoländer Wiss. Meeresunters. 28, 109-137.

----- (1977). On the dynamics of exploited populations of Tisbe holothuriae (Copepoda, Harpacticoida). V. The toxicity of cadmium: Response to sub-lethal exposure. Helgoländer Wiss. Meeresunters. 29, 503-523.

----- (1978). On the dynamics of exploited populations of Tisbe holothuriae (Copepoda, Harpacticoida). VI. Response to perturbation by temporarily elevated mortality. Helgoländer Wiss. Meeresunters. 31, 285-297.

Hubbell, S.P. & P.A. Werner (1979). On measuring the intrinsic rate of increase of populations with heterogeneous life histories. Amer. Natur. 113, 277-293.

Huizinga, H.W. (1971). Cultivation, life history and salinity tolerance of the tidepool copepod, Tigriopus californicus Baker 1912, in artificial sea water. Trans. Illinois State Acad. Sci. 64, 230-236.

Humes, A.G. (1957). Deux copépodes harpacticoïdes nouveaux du genre Tisbe, parasites des holothuries de la Méditerranée. Vie Milieu 8, 9-22.

Hutchinson, G.E. (1951). Copepodology for the ornithologist. Ecology 32, 571-577.

Itô, T. (1970). The biology of a harpacticoid copepod, Tigriopus japonicus Mori. Fac. Sci. Hokkaido Univ. (Zool.) 17, 474-500.

----- (1976). Descriptions and records of marine harpacticoid copepods from Hokkaido. VI. J. Fac. Sci. Hokkaido Univ. (Zool.) 20, 448-567.

Ivester, M.S. & B.C. Coull (1977). Niche fractionation studies of two sympatric species of Enhydrosoma (Copepoda, Harpacticoida). Mikrofauna Meeresboden 61, 137-151.

Jewett, S.C. & H.M. Feder (1977). Biology of the harpacticoid copepod, Harpacticus uniremis Krőyer on Dayville Flats, Port Valdez, Alaska. Ophelia 16, 111-129.

Johnson, C. (1976). Introduction to Natural Selection. Univ. Park Press, Baltimore.

Johnson, M.W. & J.B.Olson (1948). The life history and biolgoy of a marine harpacticoid copepod, Tisbe furcata (Baird). Biol. Bull. Mar. Biol. Lab. Woods Hole 95, 320-332.

Klecka, W.R. (1975). Discriminant analysis. In : Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner & D.H. Bent (eds.), SPSS. Statistical Package for the Social Sciences, 2nd ed. McGraw-Hill, N.Y., pp. 434-467.

Klie, W. (1949). Harpacticoida (Cop.) aus dem Bereich von Helgoland und der Kieler Bucht 1. Kieler Meeresforsch. 6, 90-128.

Kozłowski, J. (1980). Density dependence, the logistic equation, and r- and K-selection : A critique and an alternative approach. Evol. Theor. 5, 89-101.

Lang, K. (1948). Monographie der Harpacticiden, 2 vols. Håkan Ohlssons Boktryckeri, Lund.

Law, R. (1979). The cost of reproduction in annual meadow grass. Amer. Natur. 113, 3-16.

Law, R., A.D. Bradshaw & P.D. Putwain (1977). Life-history variation in Poa annua. Evolution 31, 233-246.

Lazzaretto, I. (1964). Influenza della temperatura sul valore adattativo di alcuni genotipi in popolazioni artificiali di Tisbe reticulata. Boll. Zool. 31, 1125-1131.

Lazzaretto, I. & A. Parise (1967). Effetto dell' inincrocio protratto su alcuni parametri di popolazione in Tisbe furcata (Baird) (Copepoda Harpacticoida). Boll. Zool. 34, 128-129.

Lazzaretto-Colombera, I. (1970). Effetti della diluizione su alcuni parametri di popolazione in razze geografiche del copepode Tisbe holothuriae Humes (Harpacticoida). Archo Oceanogr. Limnol. 16, 263-274.

Lazzaretto-Colombera, I., G. Fava & M. Gradenigo-Denes (1976). Carico genetico in Tisbe (Copepoda, Harpacticoida). I. Tisbe holothuriae di due popolazioni del Mediterraneo occidentale. Atti Accad. Naz. Lincei, Rend. Cl. Sci. Fis. Mat. Nat. 60, 691-698.

Lazzaretto-Colombera, I. & G. Polo (1969). Polimorfismo e superiorità degli eterozigoti nel copepode harpacticoide Tisbe clodiensis. Atti Ist. Veneto Sci. Lett. Arti, Cl. Sci. Mat. Nat. 127, 383-392.

Leloup, E. & P. Polk (1967). La flore et la faune du Bassin de Chasse d'Ostende (1960-1961). III. -Etude zoologique. Mém. Inst. Roy. Sci. Natur. Belg. 157, 1-114.

Lewontin, R.C. (1965). Selection for colonizing ability. In: Baker, H.G. & G.L. Stebbins (eds.), The Genetics of Colonizing Species. Academic Press, N.Y., pp. 77-94.

Lopez, G.W. (1980). Description of the larval stages of Tisbe cucumariae (Copepoda: Harpacticoida) and comparative development within the genus Tisbe. Mar. Biol. 57, 61-71.

----- (1982). Short- term population dynamics of Tisbe cucumariae (Copepoda: Harpacticoida). Mar. Biol. 68, 333-341.

Louw, G. (1979). Biological "strategies". Science 203 : 955.

Luckinbill, L.S. (1979). Selection and the r/K continuum in experimental populations of Protozoa. Amer. Natur. 113, 427-437.

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. Bull. Biol. Fr. Belg. 61, 193-240.

Marcotte, B.M. & B.C. Coull (1974). Pollution, diversity and meiobenthic communities in the North Adriatic (Bay of Piran, Yugoslavia). Vie Milieu 24, 281-300.

May, R.M. (1976). Estimating r: A pedagogical note. Amer. Natur. 110, 496-499.

McLaren, I.A. (1976). Inheritance of demographic and production parameters in the marine copepod Eurytemora herdmani. Biol. Bull. Mar. Biol. Lab. Woods Hole 151, 200-213.

McLaren, I.A. & C.J. Corkett (1978). Unusual genetic variation in body size, development times, oil storage, and survivorship in the marine copepod Pseudocalanus. Biol. Bull. Mar. Biol. Lab. Woods Hole 155, 347-359.

Mertz, D.B. (1971). Life history phenomena in increasing and decreasing populations. In: Patil, G.P., E.C. Pielou & W.E. Waters (eds.), Statistical Ecology, vol. 2, Sampling and Modeling Biological Populations and Population Dynamics. Pennsylvania State Univ. Press, University Park, pp. 361-399.

----- (1975). Senescent decline in flour beetle strains selected for early adult fitness. Physiol. Zool. 48, 1-23.

Miller, C.B., J.K. Johnson & D.R. Heinle (1977). Growth rules in the marine copepod genus Acartia. Limnol. Oceanogr. 22, 326-335.

Mommaerts, J.P. (1978). Systeemnadering van een Gesloten Marien Milieu, met de Nadruk op de Rol van het Fytoplankton. Ph. D. thesis, Vrije Univ. Brussel.

Mommaerts-Billiet, F., J.P. Mommaerts & M.H. Daro (1974). Seasonal variation of phytoplankton populations and primary production in the Sluice Dock at Ostend (Belgium). Br. Phycol. J. 9, 297-305.

Monk, C.R. (1941). Marine harpacticoid copepods from California. Trans. Amer. Microscop. Soc. 60, 75-99.

Mueller, L.D. & F.J. Ayala (1981). Trade-off between r-selection and K-selection in Drosophila populations. Proc. Nat. Acad. Sci. USA 78, 1303-1305.

Muus, B.J. (1967). The fauna of Danish estuaries and lagoons. Medd. Danmarks Fisk. Havunders (N.S.) 5, 1-316.

Neunes, H.W. & G.-F. Pongolini (1965). Breeding a pelagic copepod, Euterpina acutifrons (Dana), in the laboratory. Nature 208, 571-573.

Nilssen, J.P. (1980). When and how to reproduce: A dilemma for limnetic cyclopoid copepods. In: Kerfoot, W.C. (ed.), Evolution and Ecology of Zooplankton Communities. Univ. Press of New England, Hanover, N.H., pp. 418-426.

Nordby, Ø.& G. Nordby (1976). Measurement of division stage durations and degree of synchrony during meiosis. Exp. Cell Res. 103, 31-38.

Oeppen, J. (1981). Aggregative back projection. In: Wrigley, E.A.& R.S. Schofield, The Population History of England 1541 - 1871. A reconstruction. Edward Arnold, London, pp. 715-738.

Palmer, M.A. (1980). Variation in life-history patterns between intertidal and subtidal populations of the meiobenthic copepod Microarthridion littorale. Mar. Biol. 60, 159-165.

Parise, A. (1966). Ciclo sessuale e dinamica di popolazioni di Euchlanis (Rotatoria) in condizioni sperimentali. Archo Oceanogr. Limnol. 14, 387-411.

----- (1978). Population dynamics and food supply in a copepod of the genus Tisbe. Boll. Zool. 45, 375-381.

Parise, A. & I. Lazzaretto (1966). Misure di popolazione sul copepode Tisbe furcata (Baird) (Harpacticoida). Mem. Accad. Patavina Sci. Lett. Arti 79, 3-11.

Persoone, G. (1967). Oecologische Studie van de Aangroei op Ondergedompelde Substraten in de Haven van Oostende, 2 vols.. Ph.D. thesis, Rijksuniv. Gent.

Pianka, E.R. (1970). On r- and K-selection. Amer. Natur. 104, 592-597.

Pielou, E.C. (1977). Mathematical Ecology. Wiley-Interscience, New-York.

Podamo, J. (1976 a, b, c, d, e). Ecometabolism of a shallow marine lagoon at Ostend (Belgium). I. Phytoplankton and phytobenthos dynamics. II. Zooplankton dynamics. III. The role of the planktonic heterotrophic bacteria. IV. The role of microbial activity in sediments in the carbon and nitrogen cycles. V. General discussion. In: Persoone, P. & E. Jaspers (eds.), Proceedings of the 10th European Symposium on Marine Biology, vol. 2, Population Dynamics of Marine Organisms in Relation with Nutrient Cycling in Shallow Waters. Universa Press, Wetteren (Belgium), pp. 485-499, 501-515, 517-530, 531-548, 549-562.

Polk, P. (1963). Bijdrage tot de kennis der mariene fauna van de Belgische kust. V. Some observations on the crustacean fauna of the Sluice-dock (Bassin de Chasse) of Ostend. Bull. Inst. Roy. Sci. Nat. Belg. 39 (20), 1-8.

----- (1966). Zooplancton et invertébrés. In: Leloup, E. (ed.), Recherches sur l'Ostréiculture dans le Bassin de Chasse d'Ostende en 1964. Ministère de l'Agriculture, Bruxelles, pp. 28-52.

Rao, G.C. (1967). On the life-history of a new sand dwelling harpacticoid copepod. Crustaceana 13, 129-136.

Renzoni, A. (1974). Influenza delle acque di scarico di un effluente industriale su alcuni organismi marini. Mem. Biol. Mar. Oceanogr. (N.S.) 4, 495-516.

Rieper, M. (1978). Bacteria as food for marine harpacticoid copepods. Mar. Biol. 45, 337-345.

Rose, M. & B. Charlesworth (1980). A test of evolutionary theories of senescence. Nature 287, 141-142.

----- (1981a). Genetics of life history in Drosophila melanogaster. I. Sib analysis of adult females. Genetics 97, 173-186.

----- (1981b). Genetics of life history in Drosophila melanogaster. II. Exploratory selection experiments. Genetics 97, 187-196.

Rouch, R. (1968). Contribution à la connaissance des harpacticides hypogés (Crustacés - Copépodes). Ann. Spéléol. 23, 5-167.

Salt, G.W. (1969). A measure of culture-induced changes in a laboratory population of Protozoa. Ecology 50, 135-137.

Sars, G.O. (1911). An Account of the Crustacea of Norway with short Descriptions and Figures of all the Species, Vol. V., Copepoda Harpacticoida. The Bergen Museum, Bergen.

Sarvala, J. (1977). The naupliar development of six species of freshwater harpacticoid Copepoda. Ann. Zool. Fennici 14, 135-161.

----- (1979). Effect of temperature on the duration of egg, nauplius and copepodite development of some freshwater benthic Copepoda. Freshw. Biol. 9, 515-534.

----- (in press). Life history of a freshwater benthic harpacticoid species: An example of a complex but flexible pattern. Crustaceana Suppl. 00 : 000-000.

Scott, T. (1895). Additions to the fauna of the Firth of Forth. Part VII. Rep. Fish. Bd. Scotl. 13, 165-173.

Scudo, F.M. (1967). Criteria for the analysis of multifactorial sex determination. Monit. Zool. Ital. 1, 1-21.

Sharpe, P.J.H., G.L. Curry, D.W. DeMichele & C.L. Cole (1977). Distribution model of organism development times. J. Theor. Biol. 66, 21-38.

Smol, N. & C. Heip (1974). The culturing of some harpacticoid copepods from brackish water. Biol. Jb. Dodonaea 42, 159-169.

Snell, T.W. & C.E. King (1977). Lifespan and fecundity patterns in rotifers: The cost of reproduction. Evolution 31, 882-890.

Sokal, R.R. (1970). Senescence and genetic load: Evidence from Tribolium. Science 167, 1733-1734.

Stearns, S.C. (1977). The evolution of life history traits: A critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. 8, 145-171.

Stearns, S.C. & R.E. Crandall (1981). Bet-hedging and persistence as adaptations of colonizers. In: Scudder, G.G.E. & J.L. Reveal (eds.), Evolution Today. Proceedings of the 2nd International Congress of Systematic and Evolutionary Biology. Carnegie-Mellon Univ., Pittsburgh, pp. 371-383.

Steele, D.H. (1977). Correlation between egg size and developmental period. Amer. Natur. 111, 371-372.

Taylor, C.E. & C. Condra (1980). r- and K-selection in Drosophila pseudoobscura. Evolution 34, 1183-1193.

Taylor, F. (1979). Convergence to the stable age distribution in populations of insects. Amer. Natur. 113, 511-530.

Vanden Berghe, W. & M. Bergmans (1981). Differential food preferences in three co-occurring species of Tisbe (Copepoda, Harpacticoida). Mar. Ecol. Prog. Ser. 4, 213-219.

Varley, G.C., G.R. Gradwell & M.P. Hassell (1973). Insect Population Ecology. An Analytical Approach. Blackwell, Oxford.

Varvio-Aho, S.-L. (1981). On the causes of seasonal genetic changes in Gerris lacustris. Hereditas 94, 139-142.

Vilela, M.H. (1969). The life cycle of Tisbe sp. (Copepoda, Harpacticoida) under laboratory conditions. Notas Estud. Inst. Biol. Mar. 36, 1-16.

Volkmann, B. (1975). Tisbe remanei (Copepoda, Harpacticoida) a new sibling species of the holothuriae group. Archo Oceanogr. Limnol. 18, 147-157.

----- (1979a). Tisbe (Copepoda, Harpacticoida) species from Bermuda and zoogeographical considerations. Archo Oceanogr. Limnol. 19 (suppl.), 1-76.

----- (1979b). A revision of the genus Tisbe (Copepoda, Harpacticoida). Part I. Archo Oceanogr. Limnol. 19 (suppl.), 121-283.

Volkmann-Rocco, B. (1969). Tisbe pontina n.sp., a harpacticoid copepod from the island Ponza. Archo Oceanogr. Limnol. 16, 117-128.

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

----- (1972a). Species of Tisbe (Copepoda, Harpacticoida) from Beaufort, North Carolina. Archo Oceanogr. Limnol. 17, 223-258.

----- (1972b). Tisbe battagliai n.sp., a sibling species of Tisbe holothuriae Humes (Copepoda, Harpacticoida). Archo Oceanogr. Limnol. 17, 259-273.

----- (1972c). The effect of delayed fertilization in some species of the genus Tisbe (Copepoda, Harpacticoida). Biol. Bull. Mar. Biol. Lab. Woods Hole 142, 520-529.

----- (1973a). Etude de quatre espèces jumelles du groupe Tisbe reticulata Bocquet (Copepoda, Harpacticoida). Archs Zool. Exp. Gén. 114, 317-348.

----- (1973b). Tisbe biminiensis (Copepoda, Harpacticoida), a new species of the gracilis group. Archo Oceanogr. Limnol. 18, 71-90.

Volkmann-Rocco, B. & B. Battaglia (1972). A new case of sibling species in the genus Tisbe (Copepoda, Harpacticoida). In: Battaglia B. (ed.), Proceedings of the Fifth European Marine Biology Symposium. Piccin, Padova, pp. 67-80.

Volkmann-Rocco, B. & G. Fava (1969). Two sibling species of Tisbe (Copepoda, Harpacticoida) : Tisbe reluctans and T. persimilis n. sp. Research on their morphology and population dynamics. Mar. Biol. 3, 159-164.

Walker, I. (1979). Mechanisms of density-dependent population regulation in the marine copepod Amphiascoides sp. (Harpacticoida). Mar. Ecol. Prog. Ser. 1, 209-221.

Watras, C.J. & J.F. Haney (1980). Oscillations in the reproductive condition of Diaptomus leptopus (Copepoda: Calanoida) and their relation to rates of egg-clutch production. Oecologia 45, 94-103.

Wellings, P.W., S.R. Leather & A.F.G. Dixon (1980). Seasonal variation in reproductive potential: A programmed feature of aphid life cycles. J. Anim. Ecol. 49, 975-985.

Whitehouse, J.W. & B.G. Lewis (1973). The effect of diet and density on development , size and egg production in Cyclops abyssorum Sars, 1863 (Copepoda, Cyclopoida). Crustaceana 25,225-236.

Witschi, E. (1934). On determinative cleavage and yolk formation in the harpacticid copepod Tisbe furcata (Baird). Biol. Bull. Mar. Biol. Lab. Woods Hole 67, 335-340.

Zurlini, G. & I. Ferrari (1979). Growth of marine copepod populations in excess food supply. Boll. Zool. 46, 225-228.

Zurlini, G., I. Ferrari & A. Nassogne (1978). Reproduction and growth of Euterpina acutifrons (Copepoda: Harpacticoida) under experimental conditions. Mar. Biol. 46, 59-64.

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