Differential Food Preferences in Three Co-Occurring Species of *Tisbe* (Copepoda, Harpacticoida)

W. Vanden Berghe[1] and M. Bergmans[2]

[1] Zoology Unit, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium
[2] Ecology and Systematics Laboratory, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium

ABSTRACT: Killed samples of a monoclonal bacterial strain and an axenic alga were offered in different proportions to *Tisbe holothuriae*, *T. battagliai* and *T. furcata*. Incorporation of carbon ranged from 0.05 to 0.39 μg C (adult male)$^{-1}$ d^{-1}. Using a radiolabelling technique, the ratio in which the two food types were assimilated was compared to the ratio in which they were offered. Neither *T. holothuriae* nor its sibling species fed selectively under our conditions, but *T. furcata* showed a clear preference for bacteria. These findings constitute the first evidence for intrageneric dietary differentiation in harpacticoids. The results of the feeding experiments parallel observed differences in mandible structure. They render all the more acute the problem of resource partitioning between *T. holothuriae* and *T. battagliai*.

INTRODUCTION

Traditionally, phytal and epibenthic harpacticoids have been collectively considered to feed on 'microalgae, bacteria and detritus' (e.g. Noodt, 1971; Coull, 1973). Such a generalization obviously does not imply that all species are indiscriminate feeders – much as the 'year-round reproduction' of meiobenthic copepods was shown not to imply that all, or even most, species behave as generalists along the time axis of the niche (Coull and Vernberg, 1975). Indeed, recent reviews (Coull, 1973; Lee et al., 1975) surmise that many meiofaunal organisms are specialists with regard to nutritional requirements, nutritional preferences, and ability to utilize specific food species – a point already forcefully made by Provasoli et al. as early as 1959. So even now, 'we still do not know exactly what the meiofauna consume' (Coull and Bell, 1979).

A particularly promising test system to tackle the question of food preferences is provided by the genus *Tisbe* (Copepoda, Harpacticoida) which occurs as multispecies assemblages in coastal ecosystems all around the world (Fava and Volkmann, 1975, 1977; Bergmans, 1979). Table 1 lists published information on food known to be accepted by several *Tisbe* species (considering only those reports where food sources were adequately checked). The situation is rendered more complicated, as well as more interesting, by the fact that

the genus abounds in morphologically similar and even sibling species, which has resulted in scores of misidentifications in both the ancient and recent literature (Volkmann-Rocco, 1971). Is *Tisbe* a guild of generalists or of specialists? In spite of reports of a broad dietary spectrum (Battaglia, 1970) there are some indications in favor of the latter possibility. Lwoff (1927) and Rieper (1978) found that some *Tisbe* can thrive on a diet of pure bacteria, whereas Betouhim-El and Kahan (1972) reported that *T. pori* can subsist on any of 9 algae, but none of 6 bacterial strains. Strangely enough, controlled choice experiments involving *Tisbe* have never been carried out. In this paper we investigate the possibility of (differential) food selection in three sympatric, well-identified (Bergmans, 1979) species. Our preference experiments involved bacteria and ^{14}C-labelled *Dunaliella*, offered in different relative concentrations.

MATERIAL AND METHODS

C o p e p o d s . *Tisbe holothuriae* Humes, 1957, *T. battagliai* Volkmann-Rocco, 1972 and *T. furcata* (Baird, 1837) were obtained from the Spuikom, a sluice dock near the Ostend harbor (Flemish Coast). Mass cultures (2,000 ml vessels containing macroalgae and detritus, receiving 50 ml of dense *Dunaliella* culture every

Table 1. Known food sources for *Tisbe* species. (1) Barnard and Reish (1960): *T. gracilis*', probably a mixture of *T. holothuriae* and *T* sp. (cf. Volkmann-Rocco, 1973). (2) Standard culture methods used by Bocquet (1951), Battaglia (1970) and co-workers, and ourselves for over 20 species. (3) Betouhim-El and Kahan (1972): *T. pori*. (4) Brown and Sibert (1977): *T. furcata*'. (5) Garstang (1900): *T. furcata*' (6) Guérin and Gaudy (1977): *T. holothuriae*. (7) Hoppenheit (1975): *T. holothuriae*. (8) Johnson and Olson (1948): *T. furcata*' (cf. Volkmann-Rocco, 1971; Bergmans, unpubl.). (9) Lwoff (1927): *T. furcata*', probably *T. holothuriae* (cf. Bergmans, 1979, unpubl.). (10) McClelland in Marcotte (1977): *T. furcata*' (11) Rieper (1978): *T. holothuriae*. (12) Kahan (1979): *T. holothuriae*. (13) Personal observation on several species (*T. furcata, T. bulbisetosa, T. holothuriae, T. dattagliai, T. gracilis*) feeding on starch granules from wheat grain albumen

Condition	Bacteria	Microalgae	Plant detritus	Animal detritus	Living animals
Controlled*	4, 9, 11	3, 4	13		5,10
Not controlled		2, 6	1, 2, 6, 8, 9, 12	6, 7, 8, 9	

* Studies which have unequivocally demonstrated that *Tisbe* fed on the food source mentioned rather than on the associated microflora

3rd d) were set up in September 1976 for *T. holothuriae* and *T. battagliai*, and in October 1977 for *T. furcata*. The experiments were carried out between April and July, 1978. To ensure the availability of animals, single families were subcultured by letting gravid ♀♀ deposit 1 egg sac per 10-ml Petri dish. Food at this stage was 1 ml of non-axenic *Dunaliella* added every 2nd or 3rd d. Before each experiment, some 400 adult males were collected from the different dishes and rinsed twice in filtered seawater to remove contaminant ciliates and flagellates.

As a result of our subculturing procedure, the *Tisbe* males in each experiment constituted a single age group rather than a random sample with respect to age. This circumstance may have affected the absolute quantity of food assimilated (which varied rather much between, though not within, different experiments). It did not influence the selective uptake of algae and bacteria — the object of our investigation — which turned out to be quite reproducible.

A l g a e . Axenic *Dunaliella tertiolecta* Butcher, strain 19/6b (9.5 μm) of the Cambridge Culture Centre of Algae and Protozoa, was grown on Medium ASP$_2$ (Provasoli et al., 1957). Two d before a feeding experiment took place, 10 μCie of NaH^{14}CO$_3$ was added to 250 ml of an exponentially growing culture. Immediately before the experiment, the algae were killed by a temperature shock (10 min at 50 °C), washed twice by centrifugation (1,500 rpm) and resuspended in filtered seawater to remove all traces of dissolved radioactivity. (A control experiment had shown that dead algae do not lose any significant amount of radioactivity over 24 h). The approximate carbon content was then estimated spectrophotometrically at 660 nm, using a previously established calibration curve. Two 1 ml samples were taken for subsequent determination of total organic carbon (T.O.C. analyser) and specific radioactivity (scintillation counter).

B a c t e r i a . We used an unidentified rod-shaped bacterium (4 μm) isolated from the Spuikom sediment and grown on liquid medium 'Marine Broth' (Difco). As with the algae, we preferred to use a monoclonal stock to improve reproducibility. Treatment was the same as for the algae, except that here no radioactive marker was added; the washing was done to remove undesirable dissolved organic matter.

F e e d i n g   e x p e r i m e n t s . On the basis of the estimated carbon content, bacteria and algae were diluted to a concentration of 50 μg C ml^{-1}. The two cultures were then mixed in different approximate a:b ratios, usually 1:3, 1:1 and 3:1. Using a micropipette, 1 ml of a particular mixture was gently deposited at the bottom of a Petri dish containing 8 ml of filtered (0.8 μm) and sterilized seawater. Food was thus offered in excess, as preference is only expressed when density of preferred food is not limiting (Sih, 1979). Other dishes were prepared with bacteria or algae alone. Of each dish type several replicates (usually 4) were made; to each dish were added 20 adult *Tisbe* males. Two 1:1 dishes received 20 copepods killed previously by means of a temperature shock (5 to 10 min at 40 °C).

All dishes were left to stand for 24 h at 18 °C. At the end of the experiment, they were emptied over a 50 μm mesh width gauze. After rinsing with 20 ml of seawater, the gauze was reimmersed and the *Tisbe* transferred onto a cellulose acetate filter. Individuals that had died in the course of the experiment were not used. Overall mortality in the course of our experiments was low (4.5 %) so that stress due to manipulations appears to have been limited. Once dry, each filter was dissolved in 1 ml of 'Lumasolve', with 0.1 ml of H$_2$O$_2$ to discolor the whole. The scintillation vials were left to stand for 12 h; 10 ml of 'Lumagel', a standard scintillation liquid, and 40 μl 15 % ascorbic acid were then added. Scintillation counting was done after 1 week. A preparatory experiment had shown that the efficiency of the scintillation count was higher when the

copepods were transferred to the lumasolve on filters rather than in water. The experiment was repeated twice for *T. battagliai* and *T. holothuriae,* three times for *T. furcata.*

The use of dead bacteria and algae in the preference experiments had a three-fold advantage. First, it excluded colonisation of the copepod cuticles by bacteria and algae. (To use living food and a control with dead *Tisbe* would have been no solution, as the cuticle of a dead organism appears to be colonised much more quickly than that of a living one). Second, this procedure ruled out the occurrence of changes in specific radioactivity as a consequence of algal and bacterial metabolism during the experiment. Third, the difference in attainability between algae and bacteria was minimized. *Tisbe* is a raptorial bottom dweller (Mar-

cotte, 1977). The bacterial strain used in the experiments showed the tendency to settle to the bottom, while living *Dunaliella* remain in suspension. The use of freshly killed rather than living food organisms is hardly likely to affect the significance of our conclusions for the natural situation; in particular, if *Tisbe* feeds on phytoplankton at all *in situ*, it will almost certainly be on senescent and dead cells settled to the bottom. Also, Lwoff (1927) and Rieper (1978) successfully used dead bacteria as a food source for *Tisbe.*

C a l c u l a t i o n s . Quenching corrections were made according to the external standard method. In each experiment, the mean CPM (counts-per-minute) value of the series without radioactivity (i.e. the series where only bacteria were added) served as a blank to be subtracted from the other measurements. Next, all

Table 2. Algal carbon consumption by *Tisbe holothuriae, T. battagliai* and *T. furcata:* amount assimilated and estimated proportion in the diet of adult males fed various mixtures of dead bacteria and *Dunaliella tertiolecta*

| Species	Carbon added			Carbon assimilated					Average algal	Estimated % algal
	Algal (μg)	Total (μg)	% algal	Algal ($\mu g \ ind.^{-1} \ d^{-1}$)						
T. holothuriae,	31	105	30	.089	.139	137	.122		.122	31
1st experiment	62	111	56	.284	.275	.270	.303		.283	72
	93	118	79	.316	.340	.315	.344		.329	83
	123	123	100	.400	.424	.344	.407		.394	100
T. holothuriae,	22	88	25	.041	.048	.032	.037		.040	22
2nd experiment	44	88	50	.098	.092				.095	54
	66	88	75	.114	.115	.126	130		121	68
	88	88	100	.176	.195	.172	.167		.178	100
T. battagliai,	22	58	38	.082	.110	.097	.116		.101	49
1st experiment	44	68	65	.117	.139	.068*			.128	62
	67	79	85	.206	.221	.199	.188		.204	99
	89	89	100	.207	.187	.236	.233	.165	.206	100
T. battagliai,	22	88	25	.058	.052	.067	.081		.064	34
2nd experiment	44	88	50	.124	.124				.124	65
	66	88	75	.152	.172	.164	.174		.166	87
	88	88	100	.195	.187	.174	.205		.190	100
T. furcata,	11.0	27.0	41	.003	.002				.003	5
1st experiment	22.0	32.7	67	.004	.009				.007	13
	32.9	37.3	88	.006	.043				.024	47
	38.4	41.1	93	.045	.039				.042	81
	43.9	43.9	100	.052					.052	100
T. furcata,	13.6	30.1	45	.005					.005	8
2nd experiment	20.4	28.7	71	.020					.020	33
	23.8	26.6	89	.037	.038				.038	63
	23.8	25.5	93	.052	.049	.044			.049	81
	27.2	27.2	100	.057	.063	.060			.060	100
T. furcata,	8.6	57.6	15	.009	.008	.012	.012		.010	8
3rd experiment	17.2	49.9	34	.015	.015	.024			.018	15
	25.8	42.1	61	.035	.024	.029	.039	.031	.032	26
	34.4	34.4	100	.126	.142	.111	.107		.121	100

* Value excluded from calculations
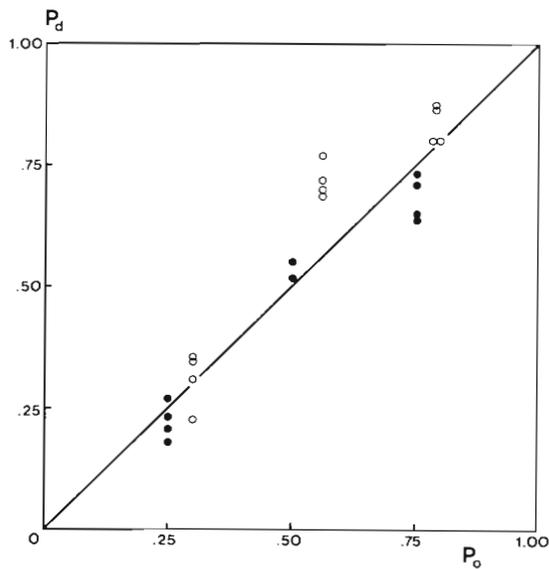
Fig. 1. *Tisbe holothuriae*. Proportion of algal carbon in the diet (P_d) as a function of proportion of algal carbon offered (P_o). Different symbols refer to different replicate experiments

values were converted to 24 h and 1 individual. All uptake of radioactivity not resulting from ingestion will be measured in dead animals also. A preliminary experiment had shown this uptake to be approximately proportional to the amount of radioactivity added and to the number of animals in the dish. Therefore the mean CPM value of the dishes with killed animals was weighted by the different concentrations of radioactive algae offered and subtracted from the respective measurements. Mean uptake (in CPM) in the 'pure algae' replicates was then calculated.

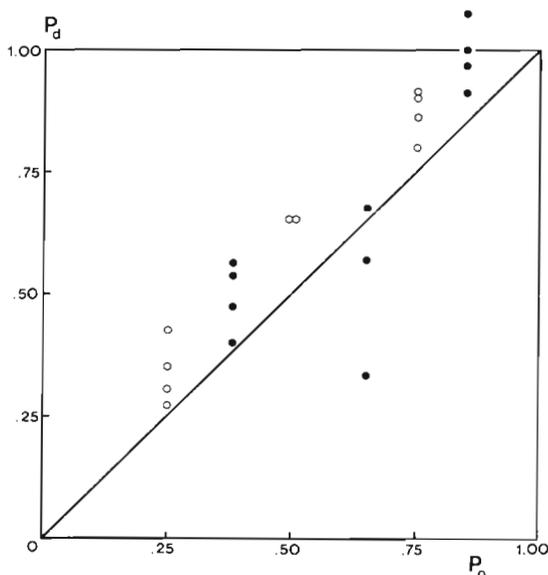The CPM value for each dish was divided by the mean uptake of algae in the series where only algae were offered to obtain a measure of the proportion in which algae and bacteria had been assimilated. In doing so, we assumed that the total amount of carbon ingested was the same for all animals in one experiment, i.e. we assumed the uptake of unlabeled (bacterial) carbon to make up for the difference between measured uptake in the 'pure algae' and 'mixed food' treatments. The exact proportion in which the two food sources were offered was calculated from the total organic carbon contents as measured with the T.O.C. analyser.

In an approach inspired by Emlen (1966), we plotted percentage algal carbon coffered along the abscissa and percentage algal carbon assimilated along the ordinate. Experimental points near the bisector of this graph indicate no selection, i.e. the proportion in which algal carbon was ingested equals the proportion in which it was offered. Points below or above the bisector indicate preferential uptake of bacteria and algae, respectively.

Finally, using the T.O.C. and scintillation data for the algal culture, the amount of algal carbon ingested was calculated.

RESULTS

Results are presented in Figures 1–3 and Table 2. We observed a range of assimilation values of 0.18–0.39 μg C copepod^{-1} d^{-1} for *Tisbe holothuriae* and *T. battagliai*, 0.05–0.12 μg C copepod^{-1} d^{-1} for *T. furcata*. This range narrowly overlaps that measured by Rieper (1978) on *T. holothuriae* (both sexes) in a
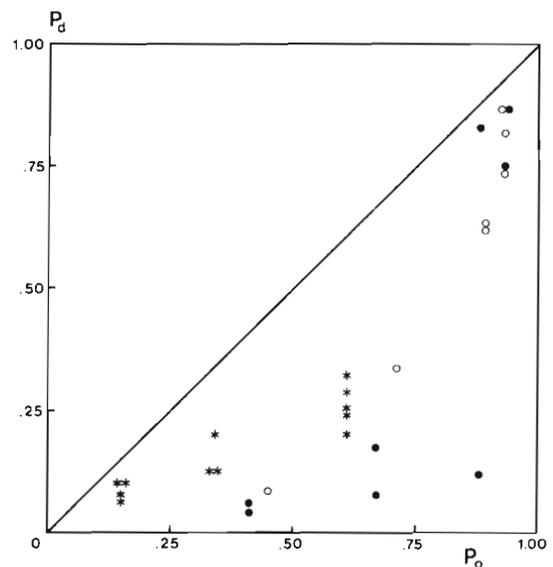

Fig. 2. *Tisbe battagliai*. Symbols as in Figure 1

Fig. 3. *Tisbe furcata*. Symbols as in Figure 1

similar short-term radiolabeling experiment, as she observed a maximum of 0.07 μg C copepod^{-1} d^{-1}.

Whereas the sibling species *Tisbe holothuriae* and *T. battagliai* behaved as indiscriminate feeders under our experimental conditions, we found *T. furcata* to show a clear preference for bacteria. This is evident from the strongly nonlinear relationship between the proportion of algae offered and assimilated, respectively (compare Emlen, 1966). *Tisbe* is able to actively discriminate between food items, as shown by the 'rejection reaction' observed by Marcotte (1977).

DISCUSSION

F o o d   p r e f e r e n c e s . Preferential uptake of heterotrophic carbon was mentioned by Brown and Sibert (1977) for mixtures of harpacticoids, including 'Tisbe furcata'. Our results indicate that it would be unwise to extrapolate this to all *Tisbe*, let alone to all harpacticoids. Apart from our own study, however, there exists but a single hint at species-specific food preferences pertaining to harpacticoids: the beautiful food-patch choice experiment of Lee et al. (1977) on *Nitocra typica* and *Leptocaris brevicornis*, offered 8 species of algae. Different food preferences are probably related to different nutritional values, a topic on which some more information is available (Provasoli et al., 1959; Shiraishi and Provasoli, 1959; Betouhim-El and Kahan, 1972; Lee et al., 1976; Sellner, 1976; Rieper, 1978), though some of the evidence is open to serious criticism. (Provasoli et al.'s experiment entailed massive inbreeding and sampling drift. Lee et al. do not state the number of replicates per food source, which seems to have been unity: so the observed differences could very well not reflect nutritional phenomena but extreme sampling error, especially with regard to age-dependent reproductive value (*sensu* Fisher, 1958) of the females used to start each culture).

Our findings constitute the first evidence for intrageneric dietary differentiation in harpacticoids. The possibility of such differentiation was adumbrated by Provasoli et al.'s (1959) observation that the same axenic strain of *Platymonas* could support 8 generations of *Tigriopus japonicus*, but only 2 of *T. californicus*. Analysing gut contents, Fryer (1957) had demonstrated dietary differentiation among closely related freshwater cyclopoids. In his study, as in ours, similarity in diet was correlated with phylogenetic affinity (albeit at a different level of relatedness).

M a n d i b l e   s t r u c t u r e . Differences in the structure of mouthparts, especially concerning form and number of teeth on the mandibles, have often been linked to dietary differences in the Copepoda (Anraku

and Omori, 1963; Maly and Maly, 1974; Sullivan et al., 1975; Ivester and Coull, 1977; Turner, 1978). Marcotte (1977), studying the functional morphology of the oral appendages of *T. furcata* by means of slow-motion videotape, concluded that the mandibles serve to crush the food between them and against the labrum.

One of us (W.V.) studied mandible morphology by light and scanning electron microscopy. Adult males were dissected in glycerine under a stereomicroscope. For SEM, mandibles were transferred to alcohol which was left to evaporate, and coated with a gold-palladium alloy. Light microscopic measurements of the Md cutting edge yielded lengths (tip of distal tooth to base of proximal one) of 21.7 μm (s.d. = 1.4; n = 6) for *Tisbe battagliai*, 20.3 μm (s.d. = 1.2; n = 6) for *T. holothuriae* and 27.2 μm (s.d. = 1.7; n = 16) for *T. furcata*. It is interesting to note that the ratio of these lengths is about 1.3 for *T. furcata* against the other two species, conforming to the Hutchinsonian minimal difference of feeding structure dimensions in related sympatric species (Hutchinson, 1959, 1967). The SEM study indicated that in all 3 species, the cutting edge bears three successive ridges of teeth, about 3 μm high in *T. holothuriae* and *T. battagliai*, about 4 μm in *T. furcata*. Apparently these do not closely correspond to the 'ventral' and 'central' teeth in Beklemishev's classification of calanoid mandible dentition (Sullivan et al., 1975). Dorsally comes an additional row of small teeth (1.5 μm) in the former 2 species, and 2 sizable teeth of about 2.5 μm in the latter. It seems, therefore, that gross mandible morphology parallels the food preferences we observed, though we cannot at present account for this hypothetical relationship in terms of functional anatomy.

E c o l o g y   o f   *T i s b e*   s p p . Six species of *Tisbe* occur in the Spuikom (Bergmans, 1979) including 1 recently discovered and as yet unidentified species. *T. bulbisetosa* and *T. gracilis* appear to be rare residents. Our preliminary food selection investigations with these species have not yielded unequivocal results. Though it is premature to draw conclusions from this, it may be that our test system is inappropriate for them. Lang (1948) considers that *T. gracilis* may be a preferential carrion-feeder, a view supported also by the more recent observation that it eats dead *Sepia* eggs (Richard, 1976). Both species may nevertheless be mass-cultured using the same methods as for the other *Tisbe*.

One of us (M.B.) has studied the phenology of *Tisbe* spp. in the Sluice dock during 3 consecutive years, 1975–77. With minor year-to-year variations, *T. furcata* was observed from December through July, with a March-May spring bloom. This bloom possibly relates to the fact that the sluices connecting the Dock to the Ostend harbor remain closed from March to

October. Planktonic marine bacteria introduced with the last charge of harbor water suffer heavy mortality in the Dock (Podamo, 1972). In the light of our findings, this may provide a rich food source for *T. furcata*, to which also remains of larger planktonic organisms may contribute (either directly or as a substrate for bacteria). Warwick (unpubl.) has recently observed a similar relationship between the bloom of certain harpacticoid species and mass mortality of specific phytoplanktonic populations.

The sibling species *Tisbe holothuriae* and *T. battagliai* attain their greatest population densities in fall (August – November) and can be observed through February. Data collected so far indicate some measure of spatial segregation over the Sluice Dock as a whole; nevertheless the temporal and spatial niche dimensions of these two species appear exceedingly similar. The situation is certainly reminiscent of the *Enhydrosoma propinquum – E. baruchi* coexistence observed by Ivester and Coull (1977) and that of the *Eucyclops* spp. observed by Fryer (1957). *T. holothuriae* and *T. battagliai* in the Sluice Dock are often encountered in the same small-surface sample, a point also made by Fava and Volkmann (1975) working on the lagoon of Venice. With respect to these sibling species, our present findings regarding food preference and mandible morphology raise more problems than they resolve.

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