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Dietary Differences between Two Co-Occurring Calanoid Copepod Species

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Summary. Two co-occurring high altitude calanoid copepods, *Diaptomus shoshone* Marsh and *D. coloradensis* Forbes are of different size: the former is approximately twice as long as the latter. There are also temporal differences in development: the former matures 2–3 weeks before the latter in most ponds. Gut analyses of copepodids and adults of both species indicate that *D. shoshone* eats larger food particles but that *D. shoshone* early copepodids eat particles similar in size to *D. coloradensis* adults. Morphology of feeding appendages partially explains the dietary differences. These data are discussed from the viewpoint of competition between the species; it is concluded that either temporal differences or size differences of copepodids and adults would allow coexistence and that extreme size differences are probably unimportant compared to morphological differences of feeding appendages and perhaps behavioral differences.

Introduction

It is well established that calanoid copepods feed selectively in many situations (Lowndes, 1935; Fryer, 1954; Anderson, 1970; McQueen, 1970). It is also well established that temporal, size, or spatial differences among co-occurring calanoids are common (Hutchinson, 1959; Cole, 1961; Sandercock, 1967; Hammer and Sawchyn, 1968). Investigators often assume that competition for food or another resource in limited supply necessitates differences between co-occurring species or the exclusion of one species by another: Hutchinson (1967) suggests that non-overlapping food niches are possible if two copepod species differ in size by a factor of 1.35, Hammer and Sawchyn (1968) suggest that an 0.5 mm difference is necessary, and Sandercock (1967) suggests that coexistence depends upon the additive effects of two factors or mechanisms (two of temporal, size, or spatial differences). In those studies mentioned which stress the importance of size differences, it is implied that size differences are indicative of diet differences. Fryer (1954) is one of a few who has shown both size and diet differences among adults of co-occurring calanoids.

In this study we compare gut contents of late copepodid and adult stages of *Diaptomus coloradensis* Forbes and early copepodid to adult stages of *D. shoshone* Marsh, and in addition we compare feeding appendages of both species to produce data bearing on the following issue: It is well established that there are temporal

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differences in development and size differences between these species (Dodson, 1970; Sprules, 1972; Fig. 1). *Diaptomus shoshone* is univoltine and matures approximately 2–3 weeks before the first *D. coloradensis* generation. *Diaptomus coloradensis* produces at least two generations yearly. How do these differences contribute to their ability to coexist, and are the size differences that Hutchinson (1967) and Hammer and Sawchyn (1968) discuss essential for coexistence in small pond environments where spatial differences are unlikely?

Materials and Methods

We would like to thank the Nature Conservency for setting aside Mexican Cut as a research area. We thank L. Livingston for his help in identification of diatoms and S. I. Dodson for his helpful criticism of the manuscript.

Descriptions of the study area can be found in Dodson (1970) and Sprules (1972). Six high altitude ponds (Sprules' D5, S6–11) located at Mexican Cut in Gunnison County, Colorado, were sampled in late June and July of 1971 and 1972. Copepodid II through adult stages of *D. shoshone* were sampled; adult females contained eggs in mid July samples. Copepodid I through adult stages of *D. coloradensis* were sampled although adults did not carry eggs. Other samples and observations were taken in June, July, and August of 1968 and 1970. Copepods were sampled with a #20 mesh, silk bolting plankton net. Open water and mud bottom samples were taken with 300 ml DO bottles. The latter were taken by stirring up a small area of the bottom with wire screen. All samples were fixed in 5% formaldehyde solution.

Copepodid and adult guts were examined by dissecting the gut from the animal, squashing it on a microscope slide, and recording the numbers of all identifiable particles at 320× magnification under a Zeiss microscope. We did not analyze guts of nauplii, nor did we analyze guts of *D. shoshone* copepodid I individuals because we arrived at the study site too late in 1972. To obtain relative numbers of diatoms, desmids, fir pollen, protozoans, and spores in the ponds, the water samples were filtered through a 0.45 μ membrane filter. The filter was cleared using immersion oil, and 15–20 fields were counted from each sample at 320× magnification except one set which was scored at 600× magnification. Since all data analysis utilizes percentages and no extremely small particles such as bacteria were scored, different magnifications do not affect results. Size estimates of food particles were made using an ocular grid and an ocular micrometer; also references (Smith, 1933; Livingston, pers. comm.) were consulted for some details about cell shapes. Approximate volumes of particles were obtained by using a formula for the appropriate geometric shape.

Selectivity of the copepods for these particles was determined using the following index, taken from Ivlev (1961):

$$E = (p_i - p_a)/(p_i + p_a)$$

where p_i is the proportion of particles of a particular size found in guts, and p_a is the proportion of the same size class available in the water or on the bottom. This formula gives a scale of -1 for total avoidance or inability to ingest to nearly $+1$ if the particle size is preferred. (The scale would read $+1$ only if a particle was found in guts but not at all in the water.)

We did not obtain estimates of relative abundance and selectivity of some larger food particles such as copepods, rotifers, and palmelloid colonies of green algae. Compared to algae and pollen, the former two are rare in both guts and in the water, and many more samples would be necessary to obtain the degree of preference for these. We had no way of estimating the size of algal colonies in open water or on the bottom since most clumps were broken in preparation for examination.

Dissection of copepods to learn morphology of mouth parts was done under a dissecting microscope at 30–60× magnification using fine wire and a scalpal. Specimens were examined under the Zeiss microscope between 800× magnification (oil immersion, phase contrast) and 80× magnification.

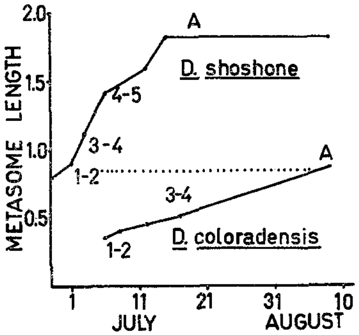

Fig. 1

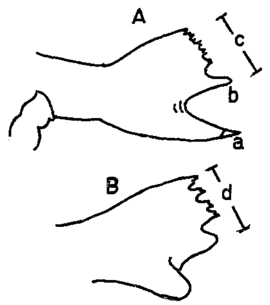

Fig. 2

Fig. 1. Mean metasome length of copepodid and adult copepods by day from Pond 8, 1971. Only individuals from the first *D. coloradensis* generation was measured. Each point represents the mean of either a sub-sample of 20 individuals chosen at random or the entire sample from that day

Fig. 2. Schematic representation of denticular cutting edges of the mandibles of adult and copepodid II *D. shoshone*

Results

Structure of Feeding Appendages

The following observations are based upon examination of between 3 and 10 individuals of each stage or species mentioned. Individuals are taken from pond 9 where possible.

The denticular cutting edges of the mandibles of both *D. shoshone* and *D. coloradensis* adults are similar. They are toothed structures with two large marginal teeth (Fig. 2A). The tooth labelled "*a*" may be proportionally larger in *D. shoshone*; the tooth labelled "*b*" is clearly sharper in *D. shoshone* than in *D. coloradensis*. The cutting edge of *D. shoshone* is proportionately larger thant hat of *D. coloradensis*; the length "*c*" is approximately 120 μ in *D. shoshone*, approximately four times the same length in *D. coloradensis*, but the metasome length of the former species is only twice that of the latter.

The teeth labelled "*a*" and "*b*" do not become fully developed until copepodid III *D. shoshone*; Fig. 2B shows the cutting edge of a copepodid II individual. The length "*d*" is approximately 40 μ, already larger than the similar measure in adult *D. coloradensis*, and these individuals are approximately equal in size (Fig. 1).

The second maxillae, those appendages used primarily for trapping particles, are similar in both species, but the spacing of the hairs on chosen at random the setae differs by stage and by species. Fig. 3 shows the regression lines of hair separation on copepodid stage. The distance between hairs is clearly greater in *D. shoshone*, although the distance between hairs of adult *D. coloradensis* and early copepodid *D. shoshone* is similar.

The maxillipeds of the two species exhibit greater differences than either the mandibles or the second maxillae. Although the maxilliped of each species is in approximately the same proportion to the size of the animal, spines on the distal

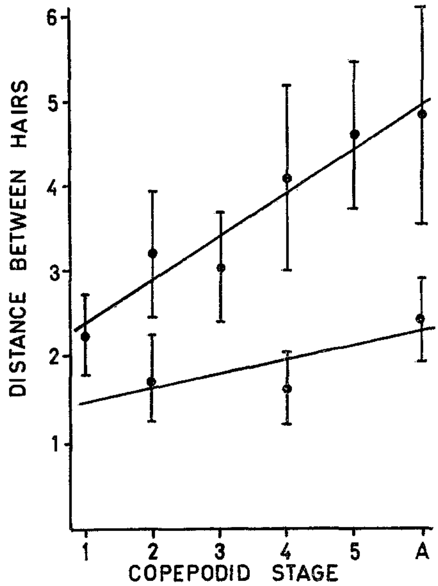

Fig. 3. Distance between hairs on setae of the second maxillae of both species. The top regression line represents *D. shoshone*; the bottom, *D. coloradensis*. The vertical bars are standard deviations; distance is in microns

segments (2–6) of *D. shoshone* maxillipeds are massive compared to those on *D. coloradensis* (also see Anderson, 1967). Each of these segments on *D. shoshone* contains a spine over 225 μ in length and the length of the inner margin of segments 2–7 is slightly over 200 μ in two adult males and two adult females examined. In *D. coloradensis*, on the other hand, the corresponding spines are less than 75 μ, and the length of the inner margin of segments 2–7 is approximately 90 μ in four adults. In addition, the inner margin of segment 2 in *D. shoshone* contains stiff hairs or teeth while the corresponding inner margin in *D. coloradensis* contains hairs.

All other appendages are similar, although there may be small differences in proportion or setation.

Gut Analyses

Particles that appeared in the guts of one or both species are summarized in Table 1. The numbers and percentages of particles found in the water are shown in Table 2; the numbers and percentages of particles of different sizes found in copepod guts are shown in Table 3. Only guts of *D. shoshone* contained the two rotifer genera found in these ponds (*Conochilus* and *Keratella*), long filaments, and palmelloid clumps of green algae. The only major differences between open water and bottom samples are that the latter contained more algal colonies and less pollen. These differences do not alter any conclusions. To describe overall diet differences, all ponds are combined in the following analysis since all ponds are similar [Dodson's (1970) type B community]. On any one day, water samples were taken from all ponds, and guts were analyzed from

Table 1. Food particles found in the guts of one or both copepod species. Length of cells is in microns, and bulk is a scale based upon volume: 1, represents particles less than 260 μ^3; 2, represents particles up to 3000 μ^3; 3, up to 11000 μ^3; 4, up to 75000 μ^3; and 5, over 75000 μ^3

Particle description	Approximate particle length	volume	Bulk
Small diatoms (*Achnanthes, Cymbella, Fragilaria, Nitzschia*)	5–20	140	1
Medium diatoms (*Gomphonema, Neidium, Nitzschia, Synedra, Hannaea, Anomoeneis, Pinnularia, Navicula, Cymbella, Diatoma, Eunotia*)	20–60	2590	2
Large diatoms (*Frustulia, Pinnularia, Tabellaria*)	60–120	10780	3
Small desmids (*Staurastrum, Cosmarium, Arthrodesmus*)	5–20	260	1
Medium desmids (*Cosmarium, Euastrum, Staurastrum, Euastridium*)	20–40	2740	2
Large desmids (*Micrasterias, Euastrum*)	150[a]	400000[a]	5
Testate protozoan	6	113	1
Fir pollen (*Abies lasiocarpa*)	75	80000	5
Miscellaneous spores (of green algae and fungi)	5–10	250	1
Filaments (green algae such as *Spirogyra*, a diatom, and fungi)	Variable	2–100000	4
Miscellaneous green colonies (palmelloid colonies of algae and unidentified clusters of cells)	—	—	—
Other (copepod parts, rotifers, protozoans)	—	—	—

[a] Most individuals were broken.

Table 2. Numbers of particles and fraction of total sample size represented by particles of different bulk (Table 1) found in the water on single days or groups of days. Column A is June 22, B is June 26 and July 5, C is July 7, July 14 and July 19, and D is July 19, 1972

Bulk	A		B		C		D	
1	159	0.60	446	0.40	1335	0.55	317	0.46
2	78	0.29	595	0.53	775	0.31	236	0.34
3	22	0.08	33	0.03	223	0.09	123	0.18
4	0	0.00	24	0.02	78	0.03	12	0.02
5	7	0.03	18	0.02	25	0.01	5	0.01

all ponds. Guts of early copepodid *D. coloradensis* yielded few identifiable particles. Guts of all individuals of all stages of both species contained large amounts of detritus.

On the basis of gut analysis and some laboratory observations, several diet differences between species and among stages of the same species are apparent. It should be emphasized, however, that gut analyses alone do not reveal considerable information about total diet, because not only visible particles are a source of nourishment. The differences and similarities observed are these:

Table 3. Number of particles of fraction of total sample size represented by particles of different bulk found in copepod guts on individual days. Columns E–I are *D. shoshone* totals; J and K are *D. coloradensis* totals. Roman numerals refer to copepodid stages, and numbers in parentheses are the numbers of guts analyzed

Bulk	E II (6) 22 Jun		F III, IV (15) 22 Jun		G V (25) 30 Jun		H Adult (10) 30 Jun		I Adult (28) 13 Jul		J V (9) 18 Jul		K Adult (7) 18 Jul	
1	4	0.05	133	0.27	280	0.25	27	0.11	172	0.18	4	0.14	15	0.37
2	70	0.91	149	0.30	290	0.25	25	0.10	138	0.14	24	0.86	25	0.61
3	3	0.04	86	0.17	261	0.23	40	0.17	249	0.26	0	0.00	1	0.02
4	0	0.00	126	0.26	214	0.19	81	0.34	187	0.19	0	0.00	0	0.00
5	0	0.00	0	0.00	93	0.08	67	0.28	230	0.24	0	0.00	0	0.00

1. Guts of late copepodid and adult *D. coloradensis* do not contain as many varieties of identifiable particles as similar stage *D. shoshone*. Guts of the former contain no filaments, no fir pollen, and no zooplankton.

2. Guts of late copepodid and adult *D. coloradensis* contain fewer particles than similar stage *D. shoshone*. The "average" gut of the former contained 4 identifiable particles, while the average gut of the latter contained over 30 identifiable particles.

3. Late copepodid and adult *D. shoshone* obviously eat particles too large to filter. In cultures containing both species, we often observed dead *D. coloradensis* and *D. shoshone* that had been partially consumed, but we found no evidence of damage to any living *D. coloradensis* or *D. shoshone*. S. I. Dodson (pers. comm.) has observed *Daphnia pulex* that have been bitten into by *D. shoshone*, and Anderson (1970) reports rotifer loricas that have been "sucked out" by predatory calanoids, including *D. shoshone*.

4. Early copepodid guts of *D. shoshone* contained particles similar in size to adult *D. coloradensis* guts. Neither contained large particles (Table 3). The youngest *D. shoshone* gut that contained a copepod part was a copepodid IV individual, and the youngest that contained a palmelloid colony of green algae was a copepodid V individual.

Diet Overlap

Since *D. shoshone* adults and late copepodids can eat large particles while *D. coloradensis* apparently cannot, we attempted to determine if the former prefer large particles, and if so, can the morphological differences described explain this preference. We calculated electivity coefficients which compare proportions of particles ingested with proportions in the water. Results are shown in Table 4. Adult *D. shoshone* ingest proportionately low and high amounts of small and large particles respectively. Even early stages eat disproportionately little of the smallest particles. Copepodid V and adult *D. coloradensis* eat disproportionately little of the larger particles (Table 4). We were unable to analyze early copepodid stages of *D. coloradensis* because few identifiable particles were found in guts. However, in eight copepodid IV and V guts analyzed on July 11, 1972, there appears to be a slight preference for the smallest particles ($E = 0.17$)

Table 4. Electivity coefficients for various copepod stages. The letters in parentheses indicate the column (A–D) in Table 2 which is being compared with the column (E–K) in Table 3

Bulk	*Diaptomus shoshone*					*D. coloradensis*	
	II (A–E)	III, IV (A–F)	V (B–G)	Adult (B–H)	Adult (C–I)	V (D–J)	Adult (D–K)
1	−0.85	−0.38	−0.27	−0.57	−0.51	−0.53	−0.11
2	+0.52	+0.02	−0.36	−0.68	−0.38	+0.43	+0.28
3	−0.33	+0.36	+0.77	+0.70	+0.49	−1.00	−0.80
4	0.00[a]	+1.00	+0.81	+0.89	+0.73	−1.00	−1.00
5	−1.00	−1.00	+0.60	+0.87	+0.92	−1.00	−1.00

[a] None found in water samples or in copepodid guts.

and a slight "avoidance" of particles in the second size category ($E = -0.15$) although the data are not significant.

There is some morphological basis for the observed diet differences. The maxillipeds of late copepodid and adult *D. shoshone* contain massive spines (Anderson, 1967) and there are teeth along the inner margin of segment 2. These structures may serve to trap particles too massive to be caught in the second maxillae. The maxillipeds of adult *D. coloradensis* and early copepodid *D. shoshone* are similar in size, and guts of these individuals contained particles of similar size.

The hairs on the second maxillae are spaced according to both stage and species although the overall morphology of the appendages are similar in both species (Fig. 2). *Diaptomus shoshone* hairs are separated by distances up to 7.5 μ, and the mean separation is approximately 5 μ. *Diaptomus coloradensis* hairs are separated by distances up to 3.5 μ, and the mean is approximately 2.5 μ. The spacing of copepodid I and II *D. shoshone* hairs is similar to the spacing of adult *D. coloradensis* hairs. Thus, minimum size of particles trapped is a function of both species and stage. All distances between hairs appear to be sufficient to trap the smallest particles, however, but *D. coloradensis* would be more efficient, and flexible hairs might require that the particle be trapped by several hairs.

According to the criteria set forth by Anraku and Omori (1963), both species have characteristics of both filter feeders and predators. The second antennae, mandibular palps, and the 1st maxillae have large surface areas, thus can efficiently maintain feeding currents. But the mandibular cutting edges of both are toothed and contain no processes, similar to Anrakua and Omori's (1963) predatory copepods. The maxillipeds of *D. coloradensis* are similar to those of filter feeders while the maxillipeds of *D. shoshone* differ from all six species examined by these authors.

Discussion

The diets of the two species examined appear to be substantially different, although there is considerable overlap in food ingested. *Diaptomus shoshone* adults eat larger particles than *D. coloradensis* adults. The difference in particle size ingested can be partially explained by size differences and consequent morphological differences in feeding appendages of the two species, since size of particles ingested by early copepodids of *D. shoshone* is similar to the size ingested by adults of *D. coloradensis*, and these individuals are approximately the same size—maxillipeds are not massive, and the distance between hairs on the 2nd maxillae is similar. The difference in particle size ingested can be partially explained by the difference in maxilliped structure—maxillipeds of adult *D. shoshone* contain massive spines and teeth that can trap large particles. Anderson (1970) has photographed *D. shoshone* holding large prey, and Lowndes (1935) has observed another calanoid, *Diaptomus castor*, which also contains "stout" setae on the maxillipeds, grasping a leaf and scraping it with its maxillae.

Sandercock's (1967) suggestion that coexistence depends upon the additive effects of two different isolating mechanisms appears to be incorrect in the present situation, at least for copepodid and adult stages. Even if temporal differences did not exist, *i.e.*, equivalent copepodid and adult stages always coexisted, the diets insofar as we have determined from gut analyses would differ because of the substantial size and morphological differences and perhaps because of behavioral differences (Anderson, 1967).

Several investigators stress the importance of size differences between similar species as a necessity for coexistence. Hammer and Sawchyn (1968) suggest that an 0.5 mm difference is necessary, and Hutchinson (1967) suggests that a size ratio of 1.35 would allow non-over-lapping food niches. Both statements seem to be oversimplifications on the basis of the present study and similar studies (Anraku and Omori, 1963; Sandercock, 1967; Anderson, 1967). Perhaps size is often indicative of morphological differences in feeding appendages, but the morphology of feeding appendages and probably behavior are probably the major determinants allowing coexistence, just as beak size and behavior of Darwin's finches are thought to be more important than actual bird size in situations where several coexist (Lack, 1954). Size becomes increasingly important as the above differences decrease, and perhaps a minimum size difference or ratio is of primary importance for coexistence of nauplii, not adults.

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