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ON THE DIET AND FORAGING STRATEGY OF TUNDRA WADERS AT SIVASH

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On the Diet and Foraging Strategy of Tundra Waders at Sivash. Kirikova, T. A. The feeding on aquatic invertebrates, intensity and efficiency of forage intake were studied at the Sivash lagoons in 1995–2002 by the example of 6 wader species (217 birds). The diet composition significantly varied from seeds of plants to different species of aquatic and soil organisms. The diet at Eastern Sivash was based on Polychaeta, at Central Sivash — on Crustacea and chironomid larvae (Insecta). Foraging intensity depended on the abundance of main prey and the size of prey items taken. We distinguished the studied wader species as "probers" and "gatherers" of forage. The highest foraging intensity among "probers" and "gatherers" were observed at the Sivash lagoons in feeding sites with a high number of chironomid larvae, and the lowest one — in feeding sites with a polychaeta worm *Hediste diversicolor*. The wader foraging intensity was associated with high density and availability of prey items: at Central Sivash — chironomid larvae and brine shrimps (*Artemia salina*), at Eastern Sivash — chironomid larvae and polychaetes. Results of the stomach analysis and obtained correlations indicate a determinative role of polychaetes, molluscs, brine shrimps and chironomids in the foraging behaviour and distribution of the studied species of waders at migratory stopovers of the Azov-Black Sea Region.
Key words: prey items, foraging intensity and efficiency, tundra waders, Sivash, Azov-Black Sea Region.

Introduction

The distribution of waders during seasonal migrations is determined by a variety of factors, some of them playing a special role, for example, availability of forage resources, their accessibility, absence of disturbance and low predator pressure.

The studied group of waders is represented by transcontinental (long-distance) migrants, except for some European populations of Dunlins *Calidris alpina* classified as short-distance migrants. Distant migrations of these bird species sometimes (Ruff *Philomachus pugnax*, Little Stint *Calidris minuta*) exceed 10,000–12,000 km (Lebedeva, 1974).

Forage resources at stopovers are critically important, since they give the migrants a possibility to accumulate enough energy for a long-distance flight. In the majority of important stopovers, benthic resources make up essential part of the wader diet (Zwarts et al., 1990; Alerstam et al., 1992).

Numerous studies on the foraging of tundra waders during the migration have mainly described and assessed foraging habitats of birds along the East Atlantic Flyway (Recher, 1966; Zwarts et al., 1990; Meltofte et al., 1994; Le Drean-Quenec'hdu, 1995; Ntiamoa-Baidu et al., 1998). Data on the wader diet at inland bodies of water (Andrusenko, 1980; Shubin, 1999; Shubin, Ivanov, 2005; Sukharev, 2015), including those in the Azov-Black Sea region (Verkuil et al., 1993; Verkuil et al., 2003; Khomenko et al., 1999) have been scanty.

Results of these studies have shown that during migrations the waders are capable to find the areas with the highest density of prey items (Colwell & Landrum, 1993; Piersma, Ntiamoa-Baidu, 1995).

Some researchers emphasized that a weak correlation between the distribution of waders and abundance of prey indicates that birds prefer areas with surplus forage resources (Recher, 1966; Goss-Custard et al., 1991).

Information on a trophic ecology of migrants along transcontinental migration routes has been controversial with nothing known about the role of a foraging factor in the intensity and efficiency of foraging at migratory stopovers in the Azov-Black Sea region.

Material and methods

Prey items were studied basing on the analysis of 172 stomachs from accidentally died birds belonged to five species of tundra waders (Dunlin, Curlew Sandpiper *Calidris ferruginea*, Broad-billed Sandpiper *Limicola falcinellus*, Ruff, and Little Stint), being the most abundant at migratory stopovers in the Azov-Black Sea region and 375 benthos samples taken from 51 stations according to the method of Zhadin (1960). The stomach contents, namely species composition of the bird's food lumps, was studied according to the method of G. A. Novikov (1949) using identification guides of fauna of the Black Sea and the Sea of Azov under the geeral editorship of F. D. Mordukhay-Boltovsky (1968, 1969, 1972). For those species of waders, which stomachs were absent in the study material, the probable diet was determined by means of correlation analysis (the obtained dependences were statistically significant).

The foraging intensity and efficiency of waders were studied at the Sivash lagoons during 1995–2002 by the example of 6 species (217 birds). We distinguished them as "probers" and "gatherers" of forage, taking the

Fig. 1. Map of monitoring areas (shown in circles) where the observations of the wader foraging behaviour were taken.

N o t e . Central Sivash: 1 — near the Sivashivka village; 2 — southern discharge near the Tselynne village; 3 — near Zmiini Islands. Eastern Sivash: 4 — at the lagoon of Chonhar Peninsula; 5 — in the southern part of Lake Yasnopolianske; 6 — at Solonoozerna Bay; 7 — at the Pobedna River Mouth; 8 — at the Stalna River Mouth.

prey by pecking. Four of the species predominantly belonged to "probers": Dunlin, Curlew Sandpiper, Broad-billed Sandpiper and Bar-tailed Godwit *Limosa lapponica*. Other two species, Little Stint and Grey Plover *Pluvialis squatarola*, were referred as "gatherers".

The observations of foraging behaviour were carried out in 8 monitoring areas: in coastal marshes of Central Sivash (near the village of Sivashivka); in bays at local freshwater discharges of Central Sivash (southern discharge near the Tselynne village); in open bays of Central Sivash (near Zmiini Islands); at the lagoon of Chonhar Peninsula (Eastern Sivash); in bays at local freshwater discharges of Eastern Sivash (in the southern part of Lake Yasnopolianske, at the Pobedna River Mouth, and at the Stalna River Mouth); in open bays of Eastern Sivash (Solonoozerna Bay) (fig.1).

The wader foraging intensity was calculated as the number of pecks per minute, while the average daily foraging efficiency was expressed as the percentage between successful pecks and their total number.

Results and discussion

The diet structure of waders significantly varied from seeds of plants to different species of aquatic and soil organisms. The stomach contents were mainly represented by polychaetes, mollusks, crustaceans, and also larvae and imagoes of Diptera. All species of tundra waders in the studied foraging sites mainly fed on aquatic invertebrates and plant seeds, pecking prey from the water column, surface of mud, or probing the mud to the assessible depth.

The wader stomachs usually contained from several dozens to several hundreds of prey items.

According to the analysis of collected samples, the forage zoobenthos included 22 species of aquatic invertebrates (Kirikova, Antonovskiy, 2010), namely Polychaeta — 2 species, Crustacea — 7 species (Anostraca — 1, Isopoda — 3, Amphipoda — 3 species), Gastropoda — 11 species and insect larvae (Insecta) — 2 species.

According to the analysis of stomachs, the prey items included 8 species of aquatic and 4 species of soil invertebrates, namely Polychaeta — 1 species, Crustacea — 3 species (Anostraca — 1, Ostracoda — 1, Amphipoda — 1), Gastropoda — 2 species and Insecta — 6 species (Diptera — 2 species, Coleoptera — 4 species).

The diet of the investigated wader species at Eastern Sivash and the limans mainly consisted of polychaetes (except for Ruffs, which autumn aspect of foraging shows a weak correlation with macrozoobenthos). The occurrence of polychaetes in the wader diet varied: at Eastern Sivash — from 50 to 70 % in Dunlins, 65 to 93 % in Curlew Sandpipers, 27 to 75 % — in Broad-billed Sandpipers; at the limans — from 92 to 100 % in Dunlins and Curlew Sandpipers.

The wader diet at Eastern Sivash was supplemented by small crustaceans (Ostracoda sp.) and chironomid larvae (Chironomidae). Occurrence of crustaceans ranged from 1 % (in Dunlins) to 65 % (in Broad-billed Sandpipers), and that of chironomid larvae — from 1 % (in Dunlins) to 45 % (in Little Stints).

The basis of the wader diet at Central Sivash included small crustaceans (brine shrimp *Artemia salina* and ostracods Ostracoda sp.) as well chironomids (larvae and imagoes). Occurrence of small crustaceans at Central Sivash ranged from 36 to 44 % in Dunlins, and that of chironomid larvae — from 89 % (in Curlew Sandpipers) to 96 % (in Ruffs).

Soil organisms (beetles Coleoptera and their larvae) served as secondary prey items, ranging from 1 to 22 % at Eastern Sivash and from 1 to 40 % at Central Sivash.

At Eastern Sivash, polychaetes *Hediste diversicolor* served as the main prey items for Curlew Sandpipers and Dunlins in both migration seasons, and for Broad-billed Sandpipers — only during the spring migration. Ostracods and chironomid larvae formed the basis of the diet for Broad-billed Sandpipers and Little Stints during the autumn migration season at Eastern Sivash.

At Central Sivash, crustaceans served as the main prey items for Dunlins, feeding on *Artemia salina* mainly during spring migrations, on ostracods (Ostracoda sp.) — during autumn migrations.

Dipteran larvae (Chironomidae sp. and Diptera sp.) formed the basis of the diet of Curlew Sandpipers, Little Stints and Ruffs at Central Sivash and Molochnyi Liman. Thus, the dipteran larvae, not identified as a species (Diptera sp.), were the main forage for Curlew Sandpipers and Ruffs in the spring migration season, and chironomid larvae (Chironomidae sp.) — in the autumn season.

Special attention was paid to the study of foraging behavior of the Broad-billed Sandpiper at Eastern Sivash as a species with a limited breeding range (Piersma, 1986; van der Winden et al., 1993 a) and unknown areas of migratory stopovers. According to the results of the previous studies, the Broad-billed Sandpiper was known as a species feeding mainly on *Hediste diversicolor* at Eastern Sivash and, in small numbers, on plankton organisms (*Artemia salina*) at Central Sivash (Verkuil et al., 1993; van der Winden et al., 1993 b).

Our studies confirmed the importance of *Hediste diversicolor*, as the main prey species for the Broad-billed Sandpiper during the spring migration at Eastern Sivash and established the importance of ostracods in the autumn diet of the species. Mass use of small crustaceans Ostracoda sp. in the diet of young Broad-billed Sandpipers in the autumn season at Eastern Sivash (Dyadicheva et al., 1999; de Nobel et al., 2001; Kirikova, 2002) was shown for the first time.

Average daily intensity and efficiency of foraging in the studied wader species

Among the "probers", the highest foraging intensity was recorded in Dunlins. During spring migrations, it made up 50.4 (S.E. = 3.5, n = 13) pecks/min at Eastern Sivash (in the lagoon of Chonhar Peninsula on 19.05.2001), and during autumn migrations — 43.5 (S.E. = 6.5, n = 3) pecks/min at Central Sivash (in coastal marches near the Sivashivka village on 07.09.2000). A high foraging intensity of Dunlins at Eastern Sivash was associated with the density of two types of prey: chironomid larvae and mollusks *Hydrobia* sp. (average number reached 1668 (S.E. = 101.8, n = 3) spec./m^2), and at Central Sivash — with the density of chironomids in coastal marches near the Sivashivka village on 07.09.2000 (average number — 3113 (S.E. = 588.2, n = 3) spec./m^2).

Both high and low foraging efficiencies of Dunlins at Eastern Sivash in the spring season were recorded within the same control plot during wind-driven tides in the bay near the freshwater discharge (at the Pobedna River Mouth): on 22.05.2001 — 77.4 (S.E. = 6.9, n = 6), and on 20.05.2001 — 7.7 (S.E. = 3.7, n = 7) pecks/min.

During strong onshore winds, the areas with a higher density and biomass of prey items were periodically inaccessible. The highest foraging efficiency of Dunlins in autumn was recorded at the Pobedna River Mouth (29.08.2001) — 53.9 (S.E. = 16.7, n = 8) pecks/min.

Correlation analysis confirmed that the intensity of Dunlin foraging in the period of spring migration at Eastern Sivash was associated with the distribution density of the smallest prey item — the mollusc of *Hydrobia* sp. — (r = 0.94), and the foraging efficiency — with the density and availability of the polychaete *Hediste diversicolor* (r = 0.89) (table 1).

No positive correlations between the foraging intensity and prey items density were found for Dunlins in the autumn period at Eastern Sivash. It can be due to the fact that when choosing the stopovers at this time of the year the Dunlins were focused not on the forage reserves at Sivash, but on large areas of feeding sites convenient to preserve a social structure of their flocks during a post-nuptial moult.

At Central Sivash, the average daily foraging efficiency of Dunlins was also high and amounted in spring to 70.5 % (S.E. = 17.9, n = 6) in shallows near Zmiini Islands (17.05.2001), and in autumn — to 100 % (n = 14) in coastal marches near the Sivashivka village (14.09.2001). These values of efficiency were associated with a very high density of chironomid larvae, the average number of which in spring constituted up to 2334.5 (S.E. = 333.5, n = 3) spec./m^2 in the open bay near Zmiini Islands (on 17.05.2001), and in au-

Table 1. Correlation coefficients between the density of prey items and the foraging intensity / efficiency of tundra waders at the Pobedna River Mouth (Eastern Sivash) during the period of seasonal migrations

Species	Season	*C.alpina*		*C.ferruginea*		*C.minuta*		*Pluvialis squatarola*	
		K^i	K^e	K^i	K^e	K^i	K^e	K^i	K^e
Hediste diversicolor	spring	0.12	0.89	–0.64	0.26	–	–	0.73	0.08
	autumn	–0.49	–	–0.75	0.71	–	–	–	–
Gammarus insensibilis	spring	–0.97	–0.20	0.54	0.16	–	–	0.94	–0.47
	autumn	–	–	–	–	–	–	–	–
Hydrobia acuta	spring	0.94	–0.12	0.16	–0.55	–	–	–	–
	autumn	–0.30	–0.69	–0.75	0.49	–0.97	0.96	–	–
Chironomus sp.	spring	–	–	–	–	–	–	–	–
	autumn	–0.24	–	–	–	–	–	–	–
Total number of prey items	spring	0.89	–0.03	0.22	–0.59	–	–	0.96	0.90
	autumn	–0.19	0.43	0.14	–0.53	–0.20	0.26	–	–

Note. K^i — the correlation coefficient between the density of a prey item (spec./m^2) and foraging intensity (pecks per minute) of waders; K^e — the correlation coefficient between the density of a prey item (spec./m^2) and foraging efficiency (successful pecks per minute); «–» data is not available.

tumn — up to 800.4 (S.E. = 277.7, n = 3) spec./m^2 in coastal marches near the Sivashivka village (14.09.2001).

The lowest foraging intensity among "probers" was recorded for Dunlins in the bays near local freshwater discharges at Eastern Sivash: in spring — 7.0 (S.E. = 2.2, n = 6) in the southern part of Yasnopolianski Lakes on 05.05.1995, and in autumn — 18.0 (S.E. = 3.0, n = 3) at the Pobedna River Mouth on 02.09.2000. Probably, this was due to the feeding on polychaetes, the size and energy value of which considerably exceeds that of chironomid larvae. The average number of polychaetes in the southern part of Yasnopolianski Lakes on 05.05.1995 constituted 66.7 (S.E. = 18.5, n = 3) spec./m^2, and in the Pobedna River Mouth on 02.09.2000 — 466.9 (S.E. = 77.0, n = 3) spec./m^2.

High values of foraging intensity of Curlew Sandpipers in spring were recorded at Eastern Sivash at Chonhar Bay on 19.05.2001. — 46.6 (S.E. = 4.1, n = 3), and at Central Sivash — in the open bay near Zmiini Islands on 17.05.2001 — 43.9 (S.E = 2.9, n = 15). In autumn, high values were observed in the bay near freshwater discharges at Eastern Sivash (at the Pobedna River Mouth on 26.08.2002) — 47.8 (S.E. = 1.5, n = 4), and the lowest ones — in the open bay (in shallows of Solonoozerska Bay on 10.09.2001) — 28.0 (S.E. = 4.2, n = 4).

High foraging intensity of Curlew Sandpipers in the Sivash lagoons was associated with a high density of the prey item — chironomid larvae, the average number of which in spring was from 1668 (S.E. = 101.8, n = 3) spec./m^2 in the lagoon of Chonhar Peninsula on 19.05.2001 and up to 2334.5 (S.E. = 333.5, n = 3) spec./m^2 in the open bay at Central Sivash (near Zmiini Islands on 17.05.2001). In autumn this prey item was the most numerous in the bay near the freshwater discharge at Eastern Sivash (the Pobedna River Mouth on 26.08.2002) — 1845.4 (S.E. = 422.4, n = 3) spec./m^2. The lowest foraging intensity of Curlew Sandpipers at Eastern Sivash (in shallows of Solonoozerna Bay on 10.09.2001) was apparently determined by their preference to polychaetes, which density equalled to 444.6 (S.E. = 145.8, n = 3) spec./m^2.

High foraging efficiency of Curlew Sandpipers was recorded in open bays of Central Sivash: in shallows of Zmiini Islands in spring it was 95.5 (S.E. = 3.4, n = 15), and in autumn — 100 % (n = 4). In autumn, high foraging efficiency was also recorded in coastal marches near the Sivashivka village — 79.6 % (S.E. = 12.5, n = 5), which was associated with a high density of chironomid larvae.

Foraging efficiency of Curlew Sandpipers in bays of Eastern Sivash (the Pobedna River Mouth) was much lower, ranging in spring from 10.7 (S.E. = 1.7, n = 11) to 42.1 % (S.E. =

10.8, n = 5), and in autumn — 22.2 (S.E. = 1.1, n = 4) and 13.9 (S.E. = 4.9, n = 4) — in the open bay of Eastern Sivash (Solonoozerna Bay).

Thus, the highest foraging intensity among the "probers" (Dunlin and Curlew Sandpiper) was observed in the Sivash lagoons in feeding sites with chironomid larvae, and the lowest one- in the feeding sites with polychaete *Hediste diversicolor*.

The foraging efficiency analysis shows that the foraging success of Dunlins and Curlew Sandpipers in spring is higher than that in autumn. At this, the foraging efficiency of Dunlins is higher at Eastern Sivash, and that of Curlew Sandpipers — at Central Sivash.

The foraging intensity of the Broad-billed Sandpiper at Eastern Sivash in the bay near the local freshwater discharges (at the Pobedna River Mouth) differed from that of other species of tundra waders by almost equal peck frequency between seasons — from 32.5 (S.E. = 2.6, n = 4) to 34.0 (S.E. = 3.8, n = 10) in spring, and — 33.7 (S.E. = 5.4, n = 3) pecks/min in autumn. Probably, this is because the Broad-billed Sandpiper more preferred polychaetes, and less often — chironomids and hydrobia.

The foraging efficiency of Broad-billed Sandpipers during the spring migration period at Eastern Sivash ranged from 19.9 (S.E. = 0.8, n = 4) to 22.3 % (S.E. = 1.9, n = 10) at the Pobedna River Mouth and depended on *Hediste diversicolor* distribution density and availability.

The Bar-tailed Godwit during the spring migration at Eastern Sivash (the Pobedna River Mouth) had foraging efficiency of 37.2 % (S.E. = 3.9, n = 8).

Among the "gatherers" the highest foraging intensity was recorded for Little Stints. In spring it equalled to 45.3 (S.E. = 2.7, n = 7) pecks/min in the open bay of Central Sivash (near Zmiini Islands on 17.05.2001), and in autumn — 36.4 (S.E. = 3.7, n = 7) pecks/min — in the bay near the freshwater discharge of Eastern Sivash (the Pobedna River Mouth on 29.08.2001). Peck frequency was associated with a high density of chironomid larvae, the average number of which at Central Sivash on 17.05.2001 was up to 2334.5 (S.E. = 333.5, n = 3) spec./m^2, and at Eastern Sivash on 29.08.2001 — 1778.6 (S.E. = 222.3, n = 3) spec./m^2.

Foraging efficiency of Little Stints was the highest during the spring migration at Central Sivash in the open bay near Zmiini Islands (17.05.2001) during feeding on chironomid larvae and constituted 95.4 % (S.E. = 2.9, n = 7).

At Eastern Sivash, the foraging efficiency of Little Stints was significantly lower ranging from 6.8 % (S.E. = 0.3, n = 3) in autumn at the Pobedna River Mouth (29.08.2001) to 25.3 % (S.E. = 4.1, n = 3) at Lake Yasnopolianske (26.08.2001). The foraging intensity and efficiency of Little Stints at Eastern Sivash during the autumn migration were associated with the distribution density of the mollusk *Hydrobia acuta*.

The lowest intensity of foraging among the "gatherers" was observed in Grey Plovers in the bay near the freshwater discharge at Eastern Sivash (at the Pobedna River Mouth). In spring it was from 5.0 (S.E. = 0.6, n = 3) to 11.3 (S.E. = 0.6, n = 3) pecks/min, and in autumn — from 3.7 (S.E. = 0.9, n = 4) to 9.0 (S.E. = 2.0, n = 3) pecks/min. Perhaps, the low foraging intensity was associated with large sizes of taken polychaetes, reaching a length of 7–9 cm, but low density of this size group.

In Grey Plovers, the most effective foraging was recorded in spring at Eastern Sivash at the Pobedna River Mouth (up to 100 % of successful pecks).

The correlation analysis confirmed that the foraging intensity of Grey Plovers in the period of spring migrations at Eastern Sivash was determined by the density of the polychaete *Hediste diversicolor* (r = 0.73) and the crustacean *Gammarus insensibilis* (r = 0.94) (table 1).

Thus, for the "probers", a strong correlation was found during the autumn migration at Eastern Sivash between the foraging intensity of these species and density of chironomid larvae (r = 0.78), as well as between their foraging efficiency and density of polychaetes *Hediste diversicolor* (r = 0.74) (table 2). At Central Sivash (coastal marches near the Sivashivka village, shallows near Zmiini Islands), in the period of autumn migrations the "probers" showed a strong correlation between the foraging intensity and density of chironomid larvae: 0.93 (n = 3) for Dunlins, and 0.99 (n = 3) for Curlew Sandpipers.

Table 2. Correlation coefficients between the density of prey items and the foraging intensity/ efficiency of "probers" and "gatherers" at Eastern Sivash (the Pobedna River Mouth) during the period of seasonal migrations.

Species	Season	"Probers"		"Gatherers"	
		K^i	K^e	K^i	K^e
Hediste diversicolor	spring	0.17	0.55	–0.83	0.08
	autumn	–0.20	0.74	–	–
Gammarus insensibilis	spring	–0.02	–0.02	–0.94	–0.47
	autumn	–	–	–	–
Hydrobia acuta	spring	0.39	–0.14	0.96	0.90
	autumn	–0.56	–0.16	–0.63	0.96
Chironomus sp.	spring	–	–	–	–
	autumn	0.78	–0.65	–	–
Total number of prey items	spring	0.28	–0.09	–0.15	0.90
	autumn	0.19	–0.05	–0.22	0.26

Note. K^i — correlation coefficient between the density of a prey item (spec./m^2) and foraging intensity (pecks per minute) of waders; K^e — correlation coefficient between the density of a prey item (spec./m^2) and foraging efficiency (successful pecks per minute); «–» data is not available.

The "gatherers" during seasonal migrations demonstrated a strong correlation between their foraging intensity and efficiency and the distribution density of the mollusk *Hydrobia acuta* (table 2). The inverse relationship in the "gatherers" between the peck intensity and density of large prey items (*Hediste diversicolor* and *Gammarus insensibilis*) indicate their preference to smaller prey.

The results of the analysis of wader stomachs as well as the obtained correlations indicate a determinative role of polychaetes, mollusks, brine shrimps and chironomids in the foraging behavior and distribution of the studied wader species at the migratory stopovers of the Azov-Black Sea region.

Recent studies of biochemists confirm the importance of these invertebrate species for waders (Kharchenko and Lykov, 2014). It has been established that mollusks, polychaetes, brine shrimps and chironomids serve for waders as the main source of essential polyunsaturated fatty acids, not synthesized in birds, but critically important for the stimulation of physiological processes in their flight muscles (Kharchenko and Lykova, 2014).

Conclusions

The basis of the diet of tundra waders, making migratory stopovers at the limans and lagoons of the Azov-Black Sea region, consisted of polychaetes, small crustaceans and chironomid larvae. Polychaetes were the main prey items of waders at Eastern Sivash and limans, while at Central Sivash these were small crustaceans and chironomid larvae.

The correlation analysis has confirmed the importance of prey items and their role in foraging behavior of waders. Thus, distribution density and availability of the main prey determined the foraging intensity and efficiency of waders. The highest foraging intensity among the "probers" and "gatherers" was observed in the lagoons of Sivash in the feeding sites containing a high number of chironomid larvae, and the lowest one — in the feeding sites with the polychaete *Hediste diversicolor*.

Foraging efficiency of waders was associated with a high density and accessibility of prey items: at Eastern Sivash these were polychaetes and chironomid larvae, at Central Sivash — brine shrimps and chironomid larvae.

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