FEEDING ORIENTED MOVEMENTS OF THE ATHERINID FISH *PRANESUS PINGUIS* AT MAJURO ATOLL, MARSHALL ISLANDS

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ABSTRACT

The feeding behavior of the atherinid *Pranesus pinguis* was studied in the lagoon at Majuro Atoll, Marshall Islands, during March 1972.

During the day, individuals larger than about 35 mm (standard length) assemble in relatively inactive schools along the shore. Shortly after sunset the schools migrate offshore to feeding grounds in the lagoon, following the same route night after night. Once out in the lagoon the schools disperse, and individuals 2 to 4 m apart feed on plankton at the water's surface throughout the night. Their prey include hyperiid amphipods, caridean shrimp larvae, myodocopid ostracods, the tretomphalus stage of foraminiferans, and calanoid copepods. Most of their prey are at the surface at night, but at greater depths in daylight. At first morning light the silverside begin to concentrate in the shoreward part of their feeding ground. Then about 45 min before sunrise, having reached daytime proportions, the school moves inshore over the same route it had taken outward the night before and at about 20 min before sunrise arrives at its diurnal schooling site to take up its relatively inactive daytime mode.

In contrast, limited evidence indicates that individuals smaller than about 30-mm standard length feed by day but not at night.

The silverside *Pranesus pinguis* (Lacépède) is widespread in the western Pacific and Indian Oceans (Schultz, 1953) and is a potential baitfish for tuna fishermen (Hida, 1971). Because biological information of the species does not exist, we studied its feeding activity in the lagoon at Majuro Atoll, in the southeastern Marshall Islands, from 16 to 25 March 1972.

Majuro Atoll is a ring of shallow coral reefs and low islands encircling a lagoon about 40 km east to west and 10 km north to south (Figure 1). Around the perimeter of the lagoon a narrow shelf of sand and isolated coral heads extend offshore under 1 to 6 m of water. At the outer edge of this shelf, several hundred meters from shore, the sea floor falls abruptly to a depth of 40 m, which is the approximate water depth over most of the lagoon.

The study was centered on silverside that schooled during the day (Figure 2) along the shore of Arniel Island (Figure 3). The behavior of fish in this school was judged typical of that seen in other members of the species during a limited survey along the shores of other islands bordering the lagoon.

Movements and other behavior of this fish were observed directly using a face plate and snorkel at all hours of day and night over the 10 days we spent at Majuro. Specimens were collected for analysis of gut contents, and plankton samples were taken in the lagoon during both day and night. Sampling methods and procedures are described below where pertinent. All lengths given for the silverside are standard length. Because the horizon frequently was obscured by clouds, times of sunrise and sunset were calculated using the Nautical Almanac, U.S. Naval Observatory.

ACTIVITY PATTERN

The Diurnal School

During each day, individuals about 35 to 65 mm long hovered in a quiet school that was strung out along the shore. Here, where it is 1 to 2 m deep, the school occupied most of the water

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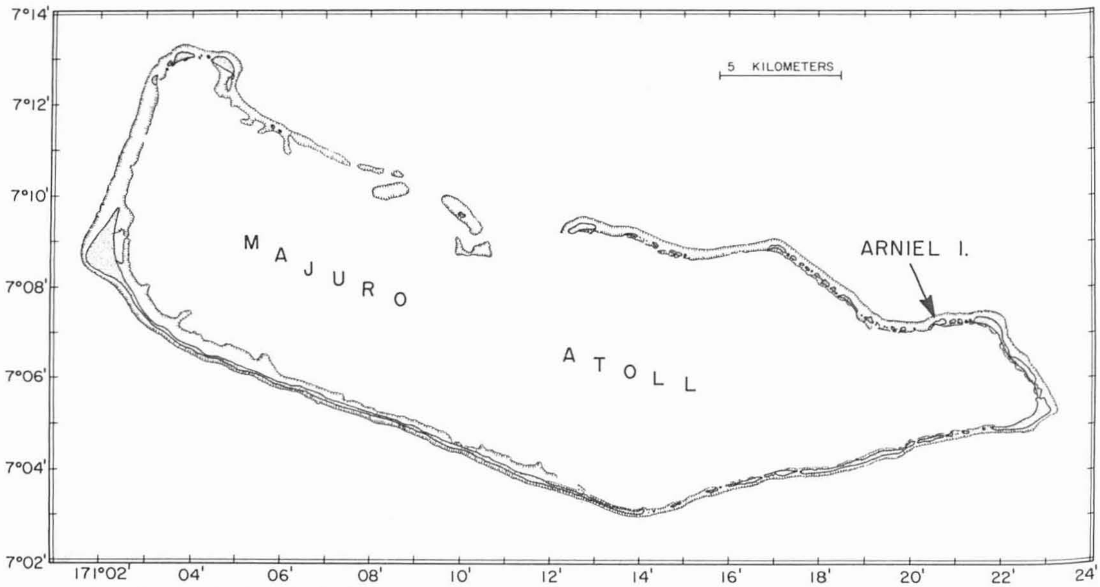

FIGURE 1.—Majuro Atoll, Marshall Islands, showing Arniel Island. Adapted from U.S. Hydrographic Office chart 6087.

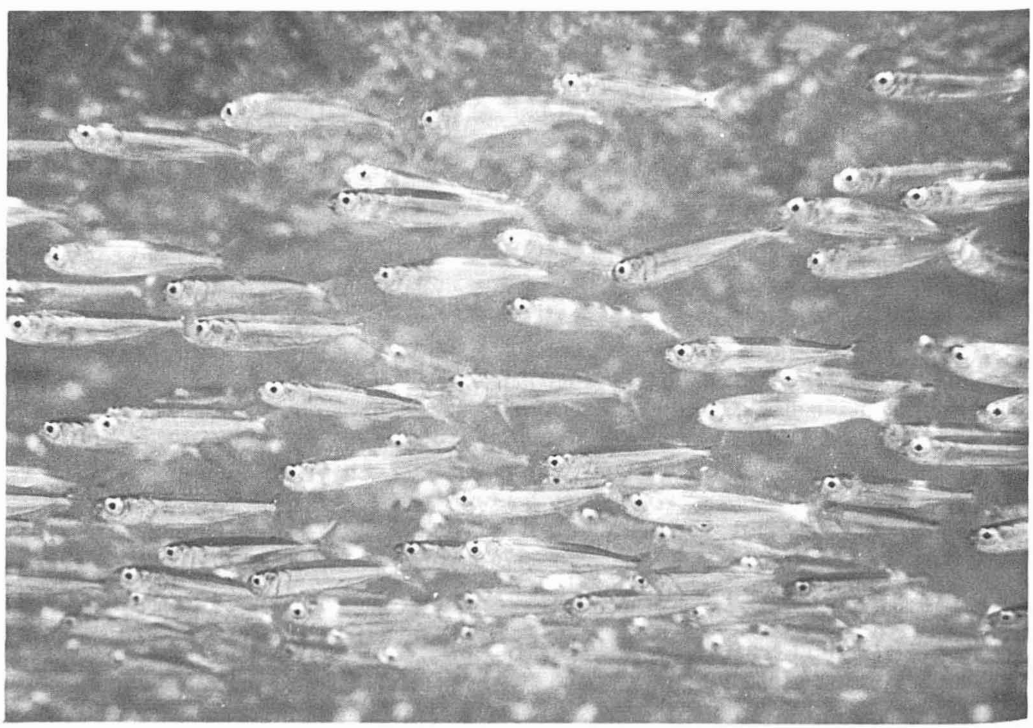

FIGURE 2.—*Pranesus pinguis* schooling during the day along the lagoon beach of Arniel Island.

FIGURE 3.—The lagoon shore of Arniel Island, viewed from the point at the western end of the bay in which this study was centered.

column. Perhaps the outstanding characteristic of the school at this time was the inactivity of its members.

The situation began to change late in the afternoon, when fish in the school gradually drew together at a point in the center of the bay. By sunset the school was a compact unit, concentrated just beneath the surface of the water.

As evening approached, the fish became increasingly restless, and often the school was briefly in motion, only to return to its original position. The fish were highly responsive to disturbances at this time. Repeatedly a segment of the school exploded from a point within, so that a void suddenly appeared. Sometimes this maneuver could be traced to a predator—usually a carangid or a belonid—but more often no basis for the action was noted.

The Offshore Migration

Shortly after sunset the silverside migrated away from their daytime schooling site. We recorded this phenomenon on all three occasions when observations were made at this time of day.

The school could not be seen effectively from out of water at this time of day, owing to the fading light and wind-waves on the water's surface. Consequently, we watched from underwater: once (21 March) from the center of the school, when the fish around us began to migrate 14 min after sunset; once (22 March) at the eastern edge of the school, when the fish in view began moving out at 9 min after sunset; and once (24 March) at the western edge, when the observed fish got underway at 4 min after sunset. Because we made observations from three widely separated parts of the school, these times are not directly comparable. Nevertheless, on each occasion the last of the silverside had left the schooling site about 10 min after the first individuals moved out.

When the migration was recognized to be underway, one of us remained at the schooling site to follow developments there, while the other accompanied the migration. The major segment of the school did not move directly offshore; rather, each evening it headed westward along the beach. It continued in this direction until reaching the point of land at the western end of the bay (Figure 4) and then veered offshore over the deeper water of the lagoon, where contact with it was lost.

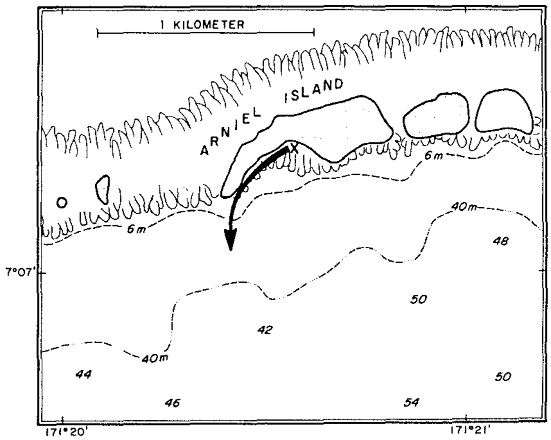

FIGURE 4.—Route taken by the silverside when migrating offshore from Arniel Island. The diurnal schooling site of this fish is marked by "X." Soundings are in meters. Adapted from U.S. Hydrographic Office chart 6087.

Nocturnal Activity

Later during the night the silverside were found offshore in the lagoon, spread out just below the surface of the water, with 2 to 4 m between each fish. They remained there throughout the night, feeding on plankton (discussed below); although some of them ranged as much as 2 km out into the lagoon, most occurred within 1 km of the beach. Their distribution at 0400 h on 24 March, more than 2 h and 30 min before sunrise, is illustrated in Figure 5. The method used to obtain the distribution of silversides in Figure 5 is as follows: Running a skiff along Arniel Island, we established a speed that took us the length of the Island in precisely 4 min. Maintaining this speed, we then headed out into the lagoon from the center of the bay, using a light on the opposite side of the atoll to stay on course. Upon passing over the dropoff

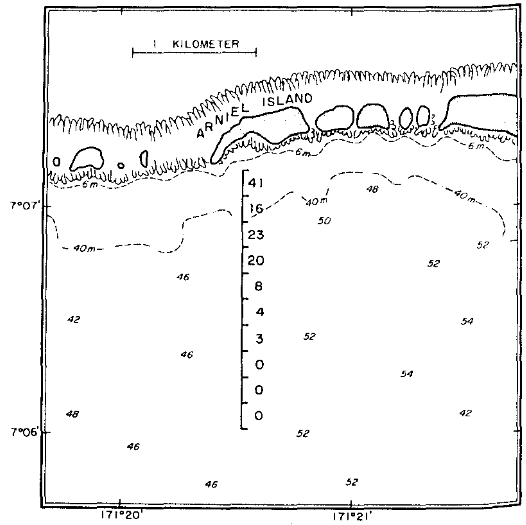

FIGURE 5.—Distribution of silverside at the surface along a transect running offshore from Arniel Island at 0400 h on 24 March 1972 (see text for method used). Adapted from U.S. Hydrographic Office chart 6087.

into deeper water, we used a hand light to count the number of silversides in our path during each minute of a 10-min run. These fish are readily seen using this method owing to the characteristic reflections from their silvery bodies when struck by the light.

At first morning light, about 1 h and 15 min before sunrise, the silverside began to concentrate in the shoreward part of their feeding ground. Soon it was apparent that the silverside were regrouping directly offshore from where they had departed the island the previous evening.

The fish continued to regroup until about 30 min before sunrise, by which time the school had attained daytime proportions and was ready to return to its diurnal location.

The Inshore Migration

The lagoon was glassy-calm on each of the three consecutive mornings that we witnessed the inshore migration (23-25 March) so that observations could be made from above the surface of the water near the daytime schooling site. By noting agitation on the water's surface, the school was seen arriving each morning off the point at the western end of the bay, and then progressing steadily eastward along the shore. Thus, in the morning the silverside reversed the route they had taken offshore the night before. The vanguard of the school arrived at the diurnal schooling site on each of the three mornings at 20, 18, and 16 min before sunrise, respectively. Because these observations, unlike those of the evening, were made from the same vantage point, they are directly comparable.

For a while after arriving inshore, the silverside remained in a compact school but progressively strung themselves out along the beach until the midday situation prevailed.

P. pinguis is another example of a fish that assembles in relatively inactive schools in shallow water during the day and then migrates to feed elsewhere at night. This phenomenon is known in certain clupeids, pomadasyids, carangids, sciaenids, and lutjanids in the Gulf of California (Hobson, 1965, 1968), and has also been reported for many species in the tropical Atlantic (Starck and Davis, 1966). Obviously it is a widespread activity pattern among shore fishes in tropical seas.

FEEDING HABITS

The inactivity of silverside (>35 mm long) that hover in their inshore schools during the day indicates that they do not feed at this time. To obtain more data on this question, specimens were collected for gut-content analysis three times during the day (19 March). The first collection was made early in the day (0700 h); the second collection, during midday (1030 h); and the third collection, late in the day (1600 h). Ten specimens from each collection were examined.

All 10 specimens (61 to 73 mm long) examined from the early collection had material in their guts, which on the average were about 20% full. Composition of these gut contents, ranked as the mean percent (by volume) of each item in all silverside specimens, were as follows: hyperiid amphipods, 49.6%; caridean shrimp larvae, 6.7%; calanoid copepods, 6.2%; ostracods, 5.5%; crab megalops, 2.3%; mollusk veliger larvae, 1.0%; polychaetes, 0.5%; foraminiferans (tretomphalus stage), 0.4%; and unidentified, well-digested material 27.8%. Digestion had damaged all of this material so that identifications could be made only to major groups.

Of the 10 specimens (61 to 70 mm long) examined from the midday collection, three were empty; the guts of the remaining seven were on the average about 15% full, but digestion had reduced this material to a soup of unidentifiable fragments.

Finally, the guts of all 10 specimens (58 to 64 mm long) from the collection made late in the day were empty.

The data clearly demonstrate that the silverside in these inshore schools do not feed during the day. But even in those individuals taken during early morning, digestion had damaged the gut contents beyond the point where a precise analysis could be made. Being small themselves, the silverside take tiny prey, mostly under 2 mm long, whose identifying features do not resist digestion well.

To obtain material for a detailed analysis of food habits, we went 200 to 800 m offshore from Arniel Island between 0400 and 0500 h on 23 and 24 March. Here, using a dip net and flashlight from a moving skiff, we collected 64 specimens between 35 and 69 mm long, which were immediately placed into a 10% Formalin[2] solution. With this procedure, we obtained fish that were actively feeding, and whose gut contents (Table 1) included fresh material. In Table 1, the items are ranked by a "ranking index," which is computed by multiplying the mean percent (by volume) of each item in the gut contents of all silverside specimens by the ratio of silverside containing that item to total silverside sampled. Thus, for *Hyperia bengalensis* found in silverside collected on 23 March, the ranking index is 46.71 × 30/31 = 45.20. To increase the precision of the ranking index, the mean percent of each item in the gut contents is carried to two decimal places. The actual observed values for individual fish were estimated to the nearest percent, except where the estimate was <1.00, in which case the estimate was to > or <0.50%. For purpose of calculating the mean percent,

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Gut contents of 64 silversides collected on 23 and 24 March 1972.

Rank	Item	Size (mm) Mean	Size (mm) Range	Number of silverside with this item	Mean percent (vol.) of each item in all silverside specimens	Ranking index
	Gut contents of 31 silversides 35 to 67 mm long, collected on 23 March 1972					
1	*Hyperia bengalensis* (hyperiid amphipod)	1.6	(1.0-2.0)	30	46.71	45.20
2	Tretomphalus stage of foraminiferan(s)	0.3	(0.2-0.7)	14	18.43	8.32
3	Caridean shrimp larvae	1.7	(0.5-6.0)	18	7.84	4.55
4	Myodocopid ostracods	1.3	(0.5-2.0)	18	6.61	3.83
5	*Undinula vulgaris* (calanoid copepod)	1.5	(1.0-2.0)	11	1.94	0.69
6	Crab megalops	2.0	(1.0-3.0)	4	3.70	0.48
7	*Lucifer* (sergestid shrimp)	7.0	(4.0-16.0)	3	4.03	0.39
8	*Candacia discaudata* (calanoid copepod)	1.6	(1.0-2.0)	8	1.19	0.31
9	Insects	3.0	(2.0-5.0)	3	1.77	0.17
10	Mysids	5.0		2	1.77	0.11
11	Veliger larvae (mollusks)	0.9	(0.5-1.5)	5	0.22	0.04
12	Zoea larvae (crabs)	1.5	(1.0-2.0)	2	0.32	0.02
13	"Other" calanoid copepods	1.0		2	0.13	0.008
14	Polychaetes	—		1	0.13	>0.004
15	*Saphirella* sp. (cyclopoid copepod)	0.9	(0.7-1.0)	2	0.06	<0.004
16	*Oncaea* sp. (cyclopoid copepod)	0.3		1	0.03	<0.001
17	Larvaceans	1.0		1	0.03	<0.001
	Also, unid. amorphous material	—		8	5.09	1.27
	Gut contents of 33 silversides 35 to 69 mm long, collected on 24 March 1972					
1	*Hyperia bengalensis* ((hyperiid amphipod)	1.9	(1.0-3.0)	24	28.28	20.57
2	Myodocopid ostracods	1.5	(0.5-2.0)	21	14.75	9.39
3	Tretomphalus stage of foraminiferan(s)	0.3	(0.1-0.8)	20	12.00	7.27
4	*Candacia discaudata* (calanoid copepod)	1.5	(0.5-2.0)	15	4.46	2.02
5	Caridean shrimp larvae	2.2	(1.0-4.0)	12	4.88	1.77
6	*Undinula vulgaris* (calanoid copepod)	1.6	(1.0-2.5)	12	2.73	0.99
7	Mysids	5.5	(2.0-7.0)	5	5.60	0.85
8	"Other" calanoid copepods	0.9	(0.8-1.0)	8	2.25	0.54
9	Insects	2.5	(1.5-3.0)	7	1.89	0.40
10	Veliger larvae (mollusks)	0.7	(0.3-1.0)	9	1.45	0.39
11	Polychaetes	—		4	0.88	0.11
12	*Labidocera acuta* (calanoid copepod)	2.0	(1.5-2.5)	3	0.64	0.06
13	*Lucifer* (sergestid shrimp)	3.0	(1.0-5.0)	2	0.60	0.04
14	Crab megalops	5.0		1	1.20	0.04
15	*Oncaea* sp. (cyclopoid copepod)	0.7	(0.5-1.0)	3	0.36	0.03
16	*Saphirella* sp. (cyclopoid copepod)	0.8	(0.5-1.0)	4	0.17	>0.02
17	Stomatopod larvae	5.0		1	0.60	<0.02
18	Alphaeid shrimp	4.0		1	0.30	0.009
19	Zoea larvae (crabs)	3.0		1	0.30	0.009
20	Gammarid amphipods	1.0		1	0.20	0.006
21	*Globigerina* sp. (foraminiferan)	1.0		1	0.03	<0.001
	Also, unid. amorphous material	—		10	12.57	3.81
	unid. crustacean fragments	—		5	3.86	0.59

>0.50 was considered to be 0.75, and <0.50 was considered to be 0.25.

A few forms predominated in the silverside diet when these observations were made. The hyperiid amphipod *Hyperia bengalensis* was especially important, with other major prey including: the tretomphalus stage of a foraminiferan(s); myodocopid ostracods; caridean shrimp larvae; and two calanoid copepods: *Candacia discaudata* and *Undinula vulgaris*. These forms constituted over 90% of the food in the guts of the silverside that were sampled.

PLANKTON AS PREY FOR THE SILVERSIDE

To determine whether these forms were selected by the silverside or were taken only in numbers relative to their abundance in the plankton, net hauls were made concurrently with the fish collections. The plankton sampled were from the lagoon between 22 and 24 March 1972. Additional plankton collections were made in the same location during daylight, thus providing a comparison of the plankton between day and night. These data (Table 2) demonstrate the importance of sampling the plankton right along with the fish. The methods of collecting were as follows: Seven tows were made over one 500-m course (duration approximately 15 min), about 600 m offshore from Arniel Island using a 1-m net with a 0.333-mm mesh. Night tows were made on 23 and 24 March at the same time that the fish were collected for gut-content analysis (Table 1). Day tows were made at 1600 h on 22 March and at 1200 h on 24 March. Six of the tows were paired: on both nights and during the day of 24 March one tow at 4 to 5 m deep was immediately followed by a second tow with the net breaking the water's surface. On the day of 22 March only the 4- to 5-m depth was sampled. The analysis is of 10% subsamples, one taken from each collection. Significantly, except for a lone alphaeid shrimp in one gut, every prey species found in the silverside occurred in the night plankton samples.

Clearly there was a great difference in the composition of the plankton between day and night, and a lesser though significant difference from one day or night to the next. Furthermore, these differences are reflected in the feeding habits of the silverside.

The daytime samples had greater volume (measurements by displacement: day volume—mean 16 ml, range 11-26 ml; night volume — mean 13 ml, range 10-15 ml), but this was due mostly to there being more chaetognaths in those collections. As shown in Table 2, there were many more species in the plankton samples taken at night, and most of the species present in both day and night collections were more numerous in the night collections. This is especially true of forms taken as prey by the silverside. Nevertheless, although many forms taken by silverside were relatively numerous, they contributed relatively little to the total volume of the plankton samples, even at night.

Major Prey Organisms

The habits of the silverside are better understood after a closer look at some of its major prey.

Hyperia bengalensis

This amphipod was the major prey of the silverside at the time of this study. Our collections indicate that it is present at the surface in greater numbers at night. This widespread species has been found elsewhere to move toward the surface after dark, and retreat to deeper water in daylight (G. J. Brusca, Humboldt State College, Calif., pers. comm.). It was equally numerous at the surface and at the 4- to 5-m depth in all night collections, but occurred in only 1 day collection, here in lesser numbers (Table 2).

Although *H. bengalensis* was the top-ranked prey on both nights, it was considerably more numerous in the gut samples on 23 March than on 24 March. Significantly, it was also more numerous in the plankton samples taken on the 23d (Table 2).

Tretomphalus Stage of Foraminiferans

Perhaps several species are represented here, but all are characterized by a calcareous, gas-filled float that buoys them at the surface (Myers, 1943). Undoubtedly, this habit accounts for this form's high incidence among prey of the surface-feeding silverside. One would not expect the tretomphalus to migrate vertically between day and night, and the data indicate they do not (Table 2).

Although the tretomphalus were well represented in the plankton collections on both nights, they were more numerous on 24 March; nevertheless, although their importance as prey on the two nights was similar, they were the third-ranked prey on the 24th and second-ranked prey on the 23d.

Myodocopid Ostracods

Being relatively numerous in the night plankton collections, but absent from the day plankton collections, these forms, like the hyperiid, apparently rise toward the surface in darkness, and descend to deeper water in daylight. Myodocopids were prominent among the gut contents on both nights, but whereas they ranked only fourth on the 23d, they ranked second on

TABLE 2.—Plankton samples 22, 23 and 24 March 1972.

Organism	Size (mm)	Number of individuals							Rank in silversides gut contents	
		Night				Day				
		Surface		4-5 m depth		Surface	4-5 m depth			
		23 Mar.	24 Mar.	23 Mar.	24 Mar.	24 Mar.	22 Mar.	24 Mar.	23 Mar.	24 Mar.
Foraminiferans										
Globigerinids	0.2- 1.0	130	130	68	160	48	5	147	—	21st
Tretomphalus	0.2- 0.6	18	58	0	2	10	12	2	2d	3d
"Other" forams	0.6- 2.0	18	6	0	41	2	1	8	—	—
Coelenterates										
Siphonophores	3.0-10.0	9	3	16	0	7	37	14	—	—
Flatworms										
Turbellarians	1.0	0	1	0	0	0	0	0	—	—
Annelids										
Polychaete larvae	0.5- 4.0	35	6	12	18	0	16	2	14th	11th
Polychaete post larvae	4.0	3	0	0	0	0	0	0	—	—
Brachiopod larvae	0.5- 2.0	8	0	4	3	0	20	0	—	—
Mollusks										
Veligers	0.2- 0.5	36	47	25	70	15	84	40	11th	10th
Heteropods (1 sp.)	0.5- 3.0	12	2	6	1	1	21	8	—	—
Pteropods (2 sp.)	1.0- 8.0	6	6	3	5	1	17	0	—	—
Crustaceans										
Myodocopid ostracods	0.4- 2.0	50	150	160	190	0	0	0	4th	2d
"Other" ostracods	—	4	18	35	20	24	27	0	—	—
Cladocerans	0.5	0	1	0	0	0	0	0	—	—
Calanoid copepods										
Candacia discaudata	1.5- 3.0	19	370	16	330	0	0	0	8th	4th
Undinula vulgaris	1.0- 3.0	173	90	200	180	11	192	191	5th	6th
Labidocera acuta	1.0- 3.0	24	2	15	1	1	0	8	—	12th
"Other" calanoids	0.5- 2.0	54	1,304	90	390	34	130	60	13th	8th
Cyclopoid copepods										
Oncaea sp.	0.5	3	4	1	2	2	3	1	16th	15th
Corycaeus sp.	0.5	0	1	0	1	0	0	0	—	—
Sapphirina sp.	0.5	0	1	0	1	0	0	0	—	—
Saphirella	0.5	1	1	0	0	0	0	0	15th	16th
Caligoid copepods	3.0	0	1	0	0	0	0	0	—	—
Hyperiid amphipods										
Hyperia bengalensis	0.2- 2.5	282	24	238	29	0	10	0	1st	1st
Gammarid amphipods	1.0	1	1	1	0	0	0	1	—	20th
Isopod larvae	—	0	2	0	0	0	0	0	—	—
Mysids	2.0- 7.0	2	15	15	16	0	0	0	10th	7th
Stomatopod larvae	3.0- 8.0	3	1	1	0	0	0	0	—	17th
Caridean shrimp larvae	0.5-10.0	243	630	330	130	70	214	35	3d	5th
Panaeid shrimps										
Lucifer	3.0-12.0	8	4	10	10	0	0	0	7th	13th
Crab zoea	0.2- 3.0	26	162	55	280	55	65	0	12th	19th
Crab megalops	0.3- 2.0	3	12	0	3	0	0	0	6th	14th
Lobster puerulus	4.0	0	1	0	0	0	0	0	—	—
Lobster phyllosome	—	0	1	0	0	0	0	0	—	—
Insects	1.0	0	0	0	1	0	0	0	9th	9th
Echinoderms										
Echinopluteus larvae	0.2- 1.0	>4,000	>1,000	>2,000	>3,000	—	>100	>1,000	—	—
Holothurian larvae	0.2- 1.5	3	0	2	1	0	0	1	—	—
Ophiuroid larvae	—	3	0	2	0	0	0	0	—	—
Chaetognaths										
Sagitta enflata	4.0-12.0	~120	~180	~150	~350	~900	~440	~600	—	—
S. neglecta	4.0- 8.0	4	30	~100	~40	~80	~100	~100	—	—
S. regularis	3.0- 6.0	0	6	50	10	28	10	30	—	—
Chordates										
Larvaceans	0.5- 3.0	30	36	50	100	35	9	682	17th	—
Fish eggs	0.2- 1.0	26	80	40	55	200	14	60	—	—
Fish larvae	1.0- 5.0	20	22	25	9	—	4	22	—	—

the 24th. Significantly, they were three times more numerous in the surface plankton samples on the 24th (Table 2).

Caridean Shrimp Larvae

Our data suggest an increase in caridean shrimp larvae at the surface after dark, even though many are present in daylight (Table 2). Based on the collections, caridean larvae were more numerous in the plankton than were the forms discussed above, but many were too large to be taken as prey by the silverside (see below). It remains undetermined how many of those individuals in the plankton were, in fact, suitably sized prey, so that numbers in the gut samples cannot be related to numbers in the plankton, as is done above.

Candacia discaudata

The greater numbers of this copepod in the diet of the silverside on 24 March, when it ranked fourth, compared to 23 March, when it ranked eighth, is consistent with its relative numbers in the plankton on these two dates (Table 2). As with other prey of the silverside, the presence of *C. discaudata* in the night collections, and its absence from the day collections (Table 2), probably can be attributed to a diel vertical migration.

Undinula vulgaris

In the samples from 4 to 5 m deep, *U. vulgaris* was equally abundant day and night; however, it was numerous in the surface collections only at night (Table 2). Thus, although this copepod swims at the surface after dark, it seems to be at least a few meters deeper during the day. This conclusion is in agreement with Johnson (1949), who found *U. vulgaris* abundant at or above 2 m only at night and concluded that it descends to deeper water in daylight.

Based on the plankton hauls, *U. vulgaris* was present in similar numbers on both nights—with perhaps more at the surface on 23 March. Consistent with this, it was ranked fifth in the gut contents on the 23d, and sixth on the 24th.

Other Prey

The silverside preyed on many other forms at the time of this study, but in fewer numbers than the above (Table 1). Probably various of these lesser prey, though of secondary importance here, assume major status under appropriate conditions. In general, these other prey have many of the characteristics of the major prey: most are crustaceans or larval forms of other groups, and generally they seem to rise into the surface waters at night, then descend to deeper water during the day (Table 2).

Prey Size

Undoubtedly size is important in determining whether or not a given organism is suitable prey for the silverside. Based on the gut-content analysis, most prey are between 0.5 and 3 mm in their greatest dimension. Nevertheless, other factors are also important. For example, the size range of the abundant larvaceans in the plankton samples was precisely the size range of most prey—0.5 to 3 mm—and yet only a single larvacean was found among the gut contents. Obviously some characteristic of the larvaceans, apart from size, excluded them as prey for the silverside.

BEHAVIOR OF SMALL SILVERSIDE

Limited observations indicate that individuals smaller than about 30 mm behave differently than the larger fish, discussed above. During the day the smaller fish do not school with the larger individuals along the beach; instead, they occur in small schools 1 m or so in diameter that swim in the upper part of the water column 20 m or more away from shore. The fish in these schools appear to be actively feeding, as individuals are continually breaking away from the school, snapping at objects in the water that were too small to be seen by us, and then immediately dashing back to the school—all in one rapid, continuous movement. None of these small active individuals were collected during the day for gut-content analysis; however in the collections offshore at night, in which the 64 larger individuals were collected for the gut-content analysis (Table 1), 5 individuals less than 30 mm long also were taken (3 on 23 March; 2 on 24 March). Significantly, although the guts of all 64 larger individuals contained food, the guts of all 5 small individuals were empty.

These limited data suggest that the small silverside may feed during the day but not at night.

CONCLUSIONS

1. During the day in the Majuro Atoll lagoon silverside larger than 35 mm long assemble in relatively inactive schools along the beaches. These fish do not feed at this time.

2. Shortly after sunset these schools migrate away from shore, following the same route day after day.

3. Once out into the lagoon the schools disperse, and the fish spread out just under the water's surface. They feed throughout the night,

operating as individuals 2 to 4 m apart. Some occur as far as 2 km off the beach.

4. The prey of the silverside are zooplankton, mostly crustaceans between 0.5 and 3 mm in greatest dimension, that occur right at the water's surface after dark. Generally they are species that rise to the surface at night, and descend to deeper waters during the day, and are selected by the silverside from among other organisms of similar size that are not taken.

5. Major prey include a hyperiid amphipod, myodocopid ostracods, the tretomphalus stage of foraminiferans, caridean shrimp larvae, and calanoid copepods.

6. At first morning light, about 1 h and 15 min before sunrise, the silverside begin to concentrate in the shoreward part of their feeding ground. The school continues to develop for about 45 min, then having attained daytime proportions, it moves inshore over the same route it had taken when moving outward the night before. About 20 min before sunrise it arrives at its diurnal schooling site, and the daytime period of inactivity begins.

7. The behavior of silverside less than 30 mm long is in contrast to that of large individuals. Limited evidence indicates that these small fish feed by day and not at night.

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