International Council for the Exploration of the Sea

C.M. 1975/ K:14
Shellfish and Benthos Committee

Experiments with infrared light on the motion and efficiency of food search of the shrimp Crangon crangon (Linnaeus 1758)

by
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INTRODUCTION

In studies concerning the feeding habits of the shrimp *Crangon crangon*, not only is the natural food spectrum of importance but also the efficiency of the search by Crangon. Continuing the work of DAHM (1973) in which the preying behaviour, the effect of tidal currents on preying and the efficiency of the food search was studied, the present study, using methods of direct observation, proceeds with the latter field of study.

MATERIAL AND METHODS

The shrimp were kept in aquaria with a weak current at 15$\pm$ 0.5°C in seawater of 32$\pm$ 0.5°/oo. A 12-hour light/dark period was imposed. The shrimp were fed regularly with largeflaked dry food used for pet fish. After a maximum of 4 weeks the shrimp were replaced by newly caught ones.

The locomotive behaviour of Crangon is controlled by light (HAGERMAN 1970), the animals normally becoming active in the dark. The observations, therefore, had to be carried out in the dark. This was accomplished by use of infra-red spot lights (bulb: 25 W, filter: Wrattenfilter Kodak, wave length: 800 nm and above) and special infra-red glasses (Elektrooptik Düsseldorf).

The floor of the observation container was covered with 2 cm of sea sand, as lack of substrate has a great influence on the behaviour of the shrimp (HAGERMAN 1970). The water had an effective depth of 3 cm; a greater depth would have caused a too great an absorption of the IR-light. Over the dark substrate a grid of white quarz sand was laid with squares of 10 cm. The areas were identifiable by means of letters and numbers, so that besides the various other observations, the exact path of the shrimp could be recorded on tape. The length of the observations was 10 min. Before the begin of the observed time the animals were kept in the observation container for 10 min to allow for adaptation to the new surroundings. Each animal was observed only once a day.

RESULTS

Size and Shape of Container

The effect of various sizes and shapes of containers on the activity of fed shrimp was examined. Figure I shows the paths of such shrimp (3-6 cm in length, both sexes) in rectangular containers of 1, 0.5, 0.25 m^2 and in circular containers of various size. It can be seen that the length of the paths diminishes with size of the container. Fed shrimp change their direction only slightly (Fig. 2 a). They prefer to swim along the edges of the containers in the rectangular and in the circular forms. The increase in inhibition of movement in the smaller rectangular containers is caused by the more frequent contact with the walls. The continual changing of direction in the circular tank has the same effect.

In the 1 m^2-tanks the fed shrimp travelled on the average 593 cm/min or 360 m/h. In still larger tanks the maximum would probably be approximately 400 m/h.

Feeding Condition

Table 1 shows the results of observations in 1 m^2 and 0.5 m^2 containers with animals that were hungered for 2.9 and 10 days (♂♂ and ♀♀, 4-5 cm in length). The average path travelled by fed shrimp is listed as a comparison.

Table 1: Distance moved by 4-5 cm Crangon of both sexes starved for several days in containers of various sizes

Container size m^2	Days of starvation	Distance moved cm/min	Numbers of tests
0.5	0	429.0 ∓ 47.0	16
0.5	2	268.0 ∓ 66.0	6
0.5	9	249.6 ∓ 52.8	9
1.0	0	593.7 ∓ 43.4	29
1.0	10	178.4 ∓ 42.8	14

The path is definitely shorter. The container size is no longer a factor. In contrast to the fed animals, the hungry ones only rarely swim. The direction is changed constantly and the animals no longer show a preference for the tank edges (Fig. 2 b). Using a pendulum motion, the area covered by the second antennae is increased by 5 cm. The antennae thereby search independently from one another semicircular areas. Fed shrimp maintain their antennae in an angle of approx. 45^{o} from the length axis.

An intensive search of the surrounding area coincided only with the movement of hungry animals. Only such locomotion, in contrast to the spontaneous movement of fed Crangon, can be considered as appetenz-behaviour in connection with forageing.

In order to compute the area searched, the average speed of approximately 140 m/h and the width of the area covered by the second antennae, 15 cm, were used. The size of the area searched is thus 21 m^2/h.

The more than twice as great locomotory activity by fed shrimp seems to be of biological significance. In another context LORENZ (1963) maintains: "The danger, that in an area of the available biotop a large population density of a species could exhaust the food supply and lead to malnutrition, whereby another area remains unexploited, is alleviated in that the animals of the same species are mutually repulsive." This repulsion is ensured in the shrimp by means of a simple dispersion, intraspecific aggression thus being unnecessary.

Tests of the forageing efficiency

Dead Corophia

As experimental prey the amphipod *Corophium volutator* was used, this sympatric species being one of the main food animals of *Crangon crangon*.

In order to eliminate independent movement by Corophia and at the same time to injure them as little as possible, the animals were frozen and thawed out at the beginning of the tests. The shrimp were fed 24 to 30 hours before testing.

The locomotory behaviour of all test animals was the same as that of hungry animals that had no food in their containers. The point of fullness was easily determined: directional changes became less frequent, the path travelled more straight. Soon the shrimp would begin to swim and a preference for the tank edges was again observed (Fig. 3).

At a concentration of one Corophium per 100 cm^2 (50 Corophia evenly distributed in a 0.5 m^2 container) on the average 10.6 Corophia would be found and eaten within 10 minutes, the majority of these (8.4 Corophia) being consumed within the first five minutes. The degree of fullness was usually reached after 6 minutes ($\bar{x}$ = 9.4 Corophia).

In order to test whether or not a purposeful search takes place, 17 Corophia were arranged in a square meter tank in the shape of an X and in a half square meter tank 9 Corophia in the shape of a V (Fig. 3 and 4). A detailed observation of the movements shows that besides random finding a purposeful component in the search for Corophia is at work.

The tests with the 9 Corophia showed an increase in time between two positive findings with decreasing Corophia density. To better clarify this aspect, a single shrimp was placed in each of the following tanks: 1 m^2, 0.5 m^2 and 0.25 m^2. At a point distant from the shrimp a freshly killed Corophium was placed and the time necessary for the shrimp to find it measured. This was repeated so long until the shrimp showed signs of satiety. The results are summarized in Table 2. Freshly killed Corophia thus are highly attractive to the shrimp.

Table 2: Time needed to find one dead Corophium in containers of different size

Container size m^2	Time needed to find one Corophium in sec	Numbers of tests
1.0	132.8 ∓ 17.4	39
0.5	93.6 ∓ 10.5	73
0.25	62.6 ∓ 8.1	65

Live Corophia

In the previous experiments the success in locating the Corophia by the shrimp was dependent on the density of the prey and on the search capacity of the shrimp. In experiments with live Corophia the success is made more difficult for the shrimp by the independent movement of the prey.

30 Corophia were placed in a square meter tank. Since Corophia cannot build their tubes in pure, coarse sand (MEADOWS and REID 1966), they were to be found swimming or moving along the substrate.

In comparison to dead Corophia these free-swimming live ones were difficult to find. The average time between two successive findings was, at this density, 65.9 seconds and 13.0 Corophia in 10 minutes. The comparable figures for dead Corophia were 32.9 seconds and 13.0 Corophia in 10 minutes.

In a further experiment the Corophia were given the possibility to build their tubes by mixing mud from their natural waters with the sand. In each of two 0.25 m^2 tanks were placed 50 Corophia. After 24 hours, at the beginning of the experiment, tubes were more or less equally distributed along the tank floor. No Corophia were mobile.

In these experiments the shrimp dug very intensely for the prey. They created by means of heavy beating with their pleopods, a strong current which transported the substrate behind them. Such digging was not always successful. The Corophia are usually located in the incoming mouth of the tube. The shrimp, however, dig preferably at the outgoing end of the tube. It was frequently observed that the shrimp continued to dig long after the Corophium had escaped from the tube's mouth. Often the shrimp would dig at places which the Corophium had already left for some time.

For location of the Corophia by the shrimp, the respiratory current produced by the Corophia in their U-shaped tubes is only of minor importance. More important, however, are faecal and other substances that are carried out by these currents and which make a sensory location possible.

Influence of Current on Preying Efficiency

In a round container (outer radius 50 cm, inner radius 20.5 cm) a circular current was produced. One half of the container was partitioned off by a screen. (Water level and substrate as in previous tests). The following currents were produced (measured at the outer edge of the tank): 0; 0.8; 2.1 and 3.4 cm/sec. Observations were at first carried out without prey. The shrimp showed no reactions to the currents tested. Sometimes by sudden changes in the speed of the current, for example, from o cm/sec to 3.4 cm/sec, the animals became suddenly very lively. Therefore the currents were only gradually increased. The forageing duplicated the typical picture of hungry shrimp as previously seen.

LUTHER and MAIER (1961) observed a positive rheotaxis. These experiments as those of DAHM could not confirm this. LUTHER and MAIER, however, worked with much stronger currents (5 cm/sec), light and without substrate.

In a series of tests with prey animals in the tank,the paths were measured at each of the three current speeds. They did not differ essentially from each other or from the previously tested results.

To test the catch success in currents, a freshly killed Corophia was placed on the sand as far away as possible from the Crangon, either near the inlet screen or the outflow screen. The time required to catch the prey was measured.

In table 3 is a list of the times divided into inlet and outflow screen placements. This shows that the catch success is better at the tested current speeds than in non-moving water. The food stimuli are carried with the current, building a gradient which the shrimp can follow.

Table 3: Time needed to find one dead Corophium at inlet and outflow screens

Current cm/sec	Time needed to find the prey in seconds			
	Corophia at the inlet screen	N	Corophia at the outflow screen	N
0.8	71.0 ∓ 18.5	6	83.4 ∓ 22.0	8
2.1	59.6 ∓ 21.6	5	80.3 ∓ 18.8	7
3.4	28.9 ∓ 3.7	26	68.1 ∓ 12.2	27
0	117.3 ∓ 23.0 N = 41			

The Corophia at the inlet screen were captured substantially faster than those at the other screen. The conclusions of DAHM (1973) that currents disrupt the reception of food stimuli, so that the catch efficiency is reduced or feeding completely stopped, could not be confirmed.

Amazing still is the short time needed for the shrimp with Corophia at the outflow screen as compared to those without current. When current is absent, the shrimp search small areas very intensively. With increasing current it was observed, that the shrimp changed their area more quickly thus increasing the chances of a random location. This behaviour was only observed when prey animals were in the tank (see Fig. 5).

SUMMARY

The movement of well-fed *Crangon crangon* decreases with the size of the experimental container. In a container with one square meter of surface area, the animals moved with a mean velocity of 593 cm/min. In small round containers the distance the animals moved was correspondingly reduced.

In contrast to well-fed shrimp, hungry ones seldom swim. They move along an irregular course, constantly changing direction, rather than swminning in a long straight path, which is the usual behaviour of individuals after a full meal. Oscillations of the forward part of the body increase the surface area in which the shrimp searches by about 15 cm.

This searching activity averaged about 230 cm/min, indeoendent of the container size.

Freshly killed Corophia are readily eaten by shrimp. It takes them an average of 132 seconds to find a Corophium in an area of one square meter. A 5 to 6 cm shrimp will eat ten to thirteen 7 mm Corophia before it is satisfied. The feeding time is five to ten minutes when the container is well supplied with food organisms. After feeding, the animals display the typical swimming behaviour of well-fed shrimp. In comparison with dead Corophia, free-swimming living ones are hard for the shrimp to find. The shrimp are capable of finding and digging the Corophium out of their natural burrows. Shrimp display no rheotaxis in currents up to 3.4 cm/sec. The searching behaviour was not affected by the flow. The results of the search, however, were affected. With increasing current it was observed, that the shrimp changed their area more quickly thus increasing the probability of a food particle being encountered. When the Corophium were placed in a position from which the current carried their scent to the shrimp, the navigation of the shrimp to their food was greatly simplified. Thus, at the inlet of the 3.4 cm/sec water current a Corophium was found within 29 seconds, while at the outlet it took 68 seconds. A water current, for the most part, simplified the search for food.

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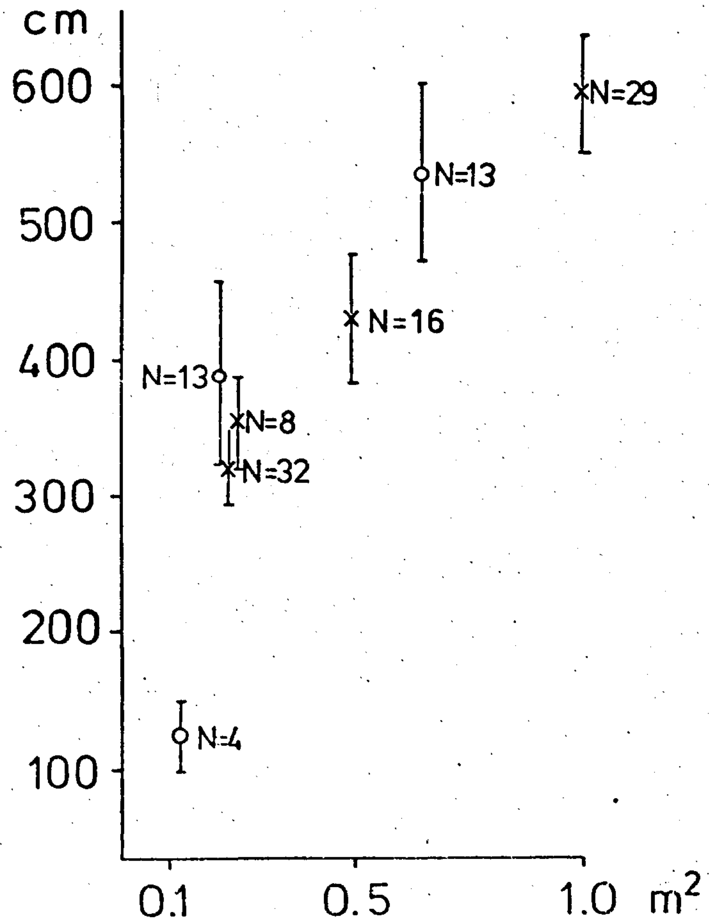
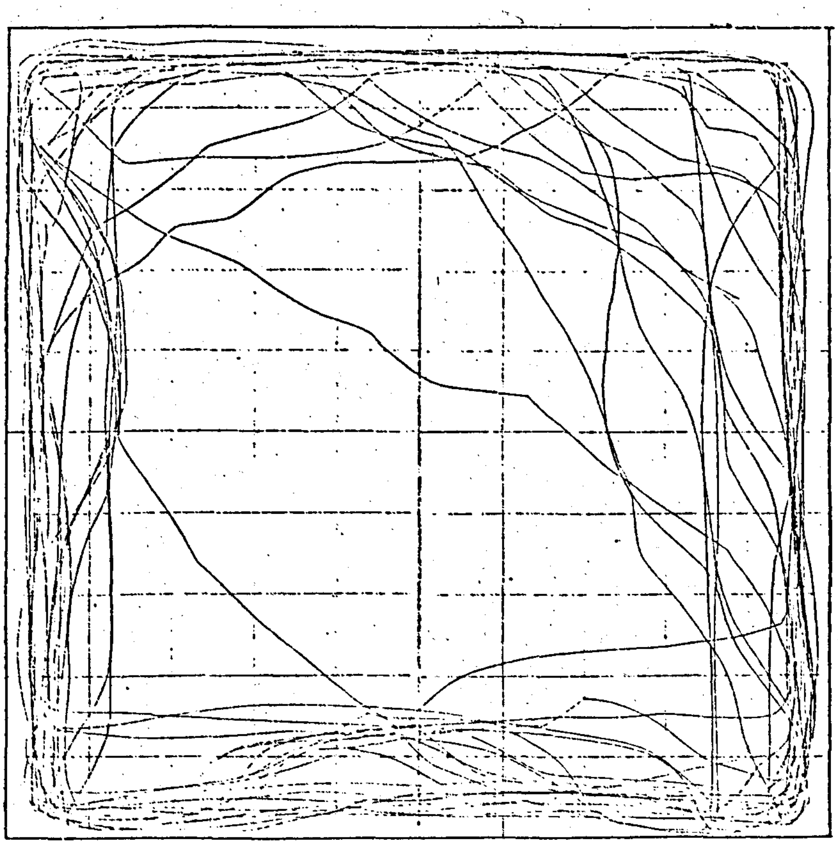


Figure 1

Distance covered per minute by well fed *Crangon crangon* in rectangular and round tanks of different size

X : rectangular tanks
O : round tanks



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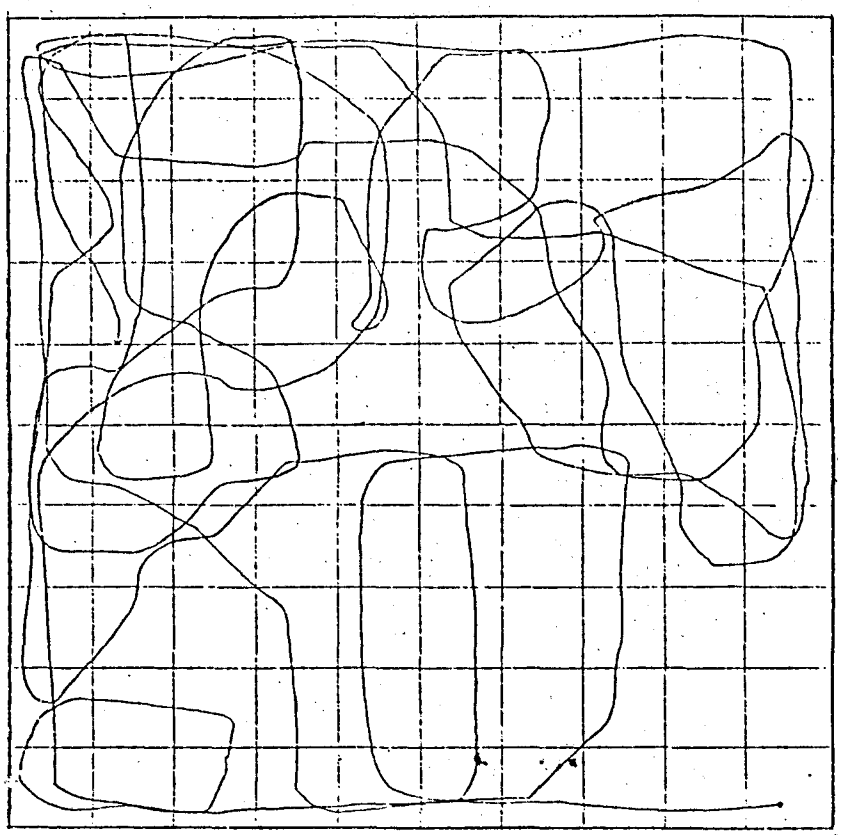

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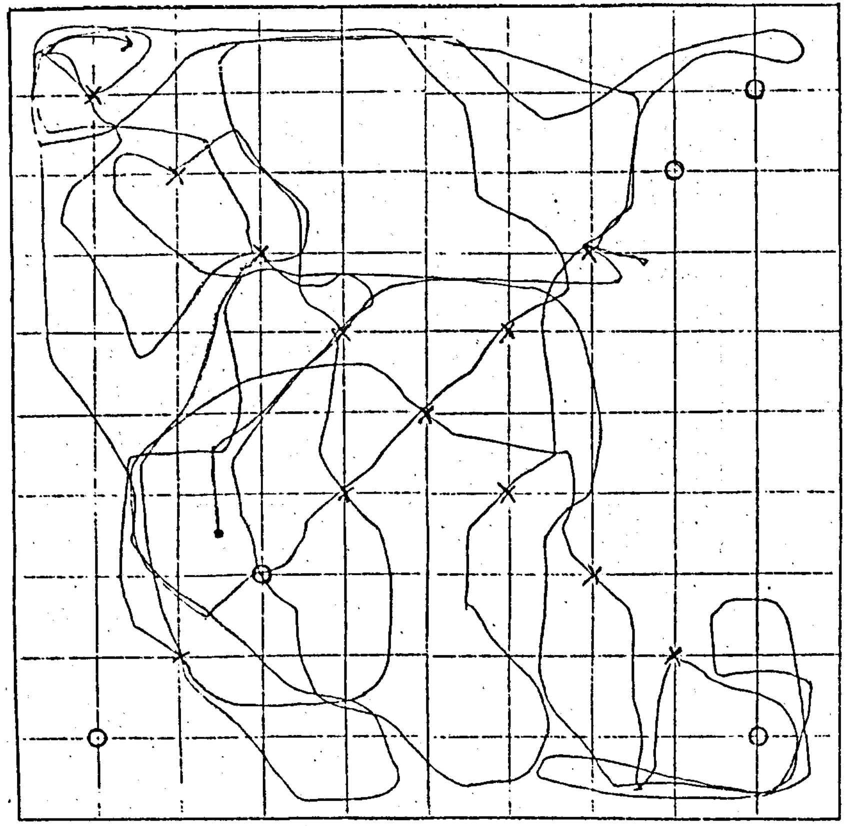
Figure 2

Path diagram of Crangon in a square meter tank without prey

a) well fed shrimp (5.5 cm, ♀ , 7715 cm/1o min)

b) hungry shrimp (4,5 - 5 cm, ♀ , 11 days without food, 1385 cm/10 min)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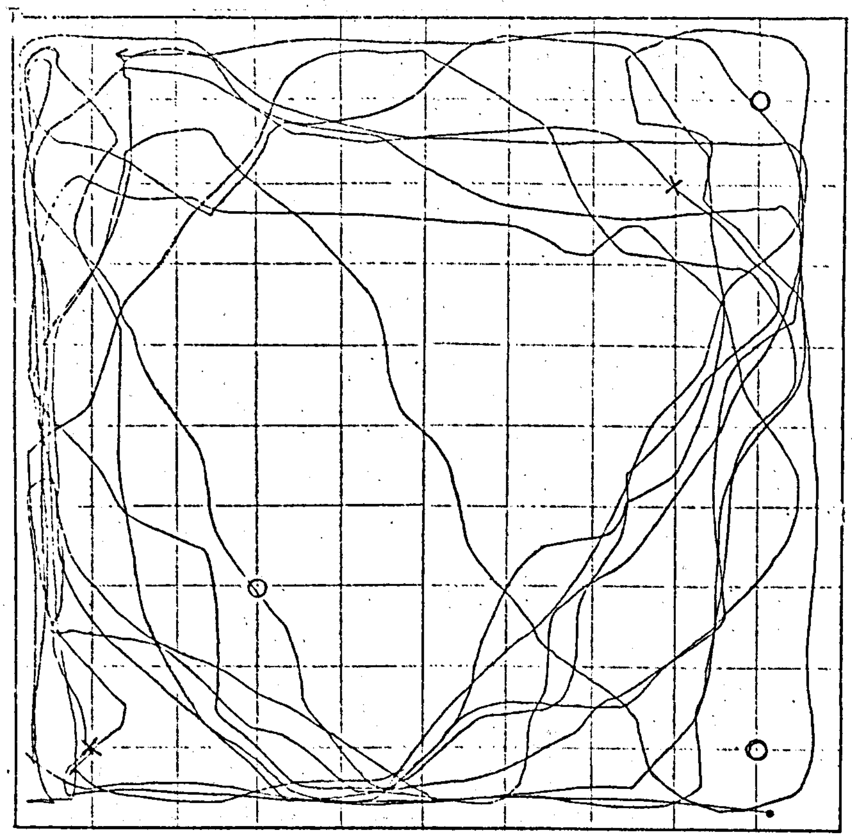
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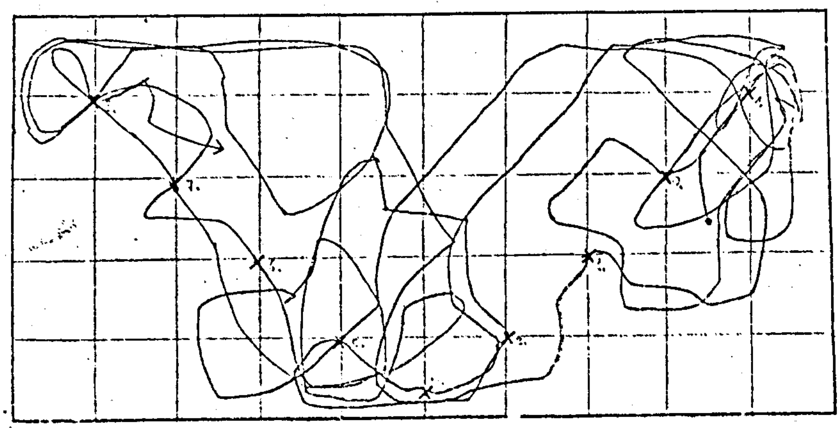
Figure 3

Path diagram of a Crangon (5.5 cm, ♀ , fed 24 h before testing) in a 1 m² container with 17 dead Corophia

x : eaten Corophia
o : not eaten Corophia

a) first to fifth minute
covered distance : 1660 cm

b) sixth to tenth minute
covered distance : 2880 cm



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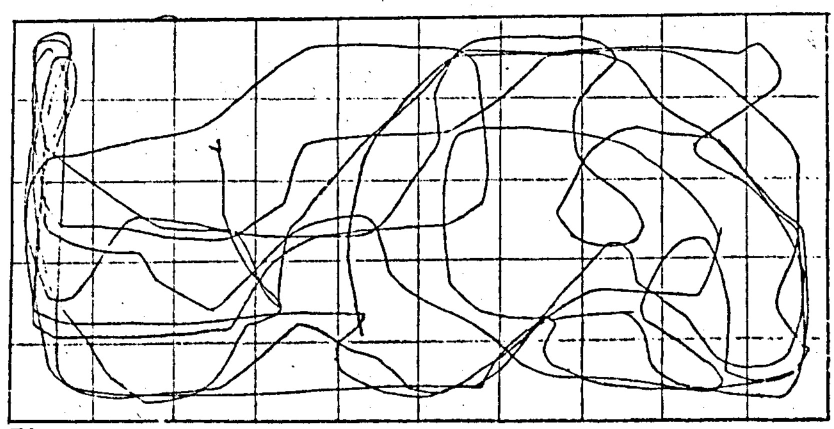

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Figure 4

Path diagram of a Crangon (5 - 5.4 cm, ♀ ,fed 24 h before testing) in a 0.5 m^2 container with 9 dead Corophia

x : eaten Corophia
o : not eaten Corophia

a) first to fifth minute
covered distance: 1200 cm

b) sixth to tenth minute
covered distance: 1230 cm

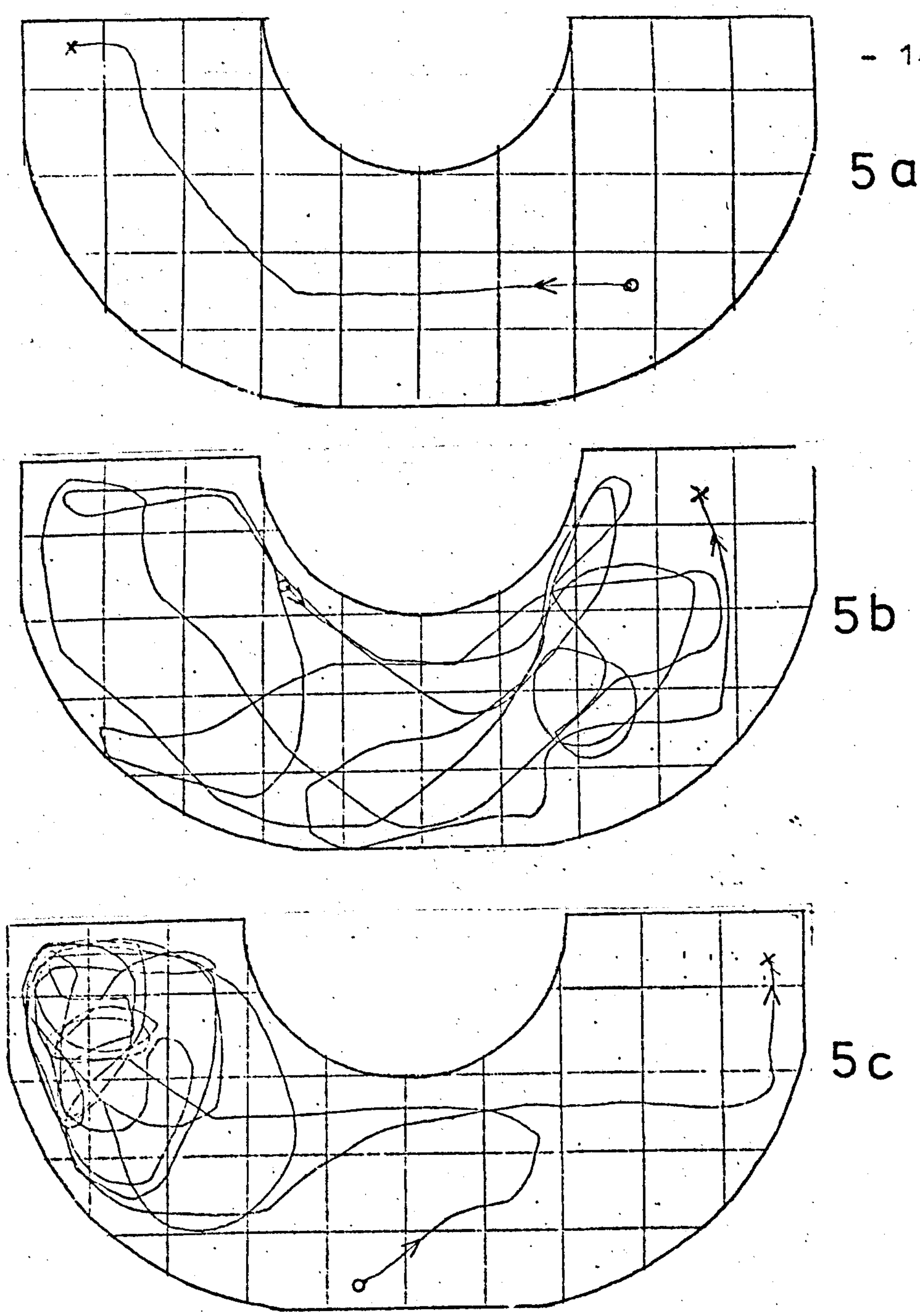

Figure 5

Path diagram of Crangon in different currents

Path diagram of Crangon (4.5-4.9 cm, ♀♀ , fed 24 h before testing) in different currents

a) Search against a current of 0.8 cm / sec
covered distance : 90 cm in 28 sec

b) Search with a current of 2.1 cm / sec
covered distance 840 cm in 107 sec

c) Search without current
covered distance : 860 cm in 105 sec

x : Position of the Corophium
o : Position of the Crangon at the beginning of the test