SENSORY BASIS OF ORIENTATION TO A HOME SITE IN THE RADIATED SHANNY, ULVARIA SUBBIFURCATA (STORER) 1839 (PISCES: STICHAEIDAE)

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By

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ABSTRACT

The roles of olfaction and vision in the homing and orientation to a home site of Ulvaria subbifurcata were investigated. These were examined by studying the home site fidelity and the homing performance of normal, blind and anosmic fish. The orientation to a home site at a distance of 33 m of normal, bilaterally blind, bilaterally anosmic and unilaterally blind and anosmic fish was also studied. The activity pattern of normal and sensory impaired fish was examined in the laboratory. The home site resighting of replaced normal and anosmic fish did not differ significantly while resightings of replaced blind fish were somewhat lower. However resightings in the home site following displacement did not differ for normal and blind fish while there was a significant decrease in the number of anosmic fish resighted. Significantly fewer anosmic fish were able to home following long distance compared to short distance displacements. When normal, anosmic and blind fish were held out of their home sites for 7+ weeks and then displaced, there was a significant decrease in the home site resighting of normal fish. Normal, bilaterally blind and unilaterally blind and anosmic fish were able to orient in the direction of the home site from 33 m away. Anosmic fish oriented in a direction significantly different from the home direction. From the orientation and homing experiments olfactory contact with the home site is considered to be the steering mechanism in homing. The home site fidelity and short distance homing of anosmic fish indicated vision may also be involved in recognition of the area around the home site.

ACKNOWLEDGEMENTS

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I especially thank my wife Gillian who encouraged me during this project and typed the manuscript.

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GENERAL INTRODUCTION

Homing has been defined by Gerking (1959) as the return of an animal to a place formerly occupied rather than to other equally probable places. It has been observed in a number of species of exclusively marine fish. Beebe (1931) noted that 5 of 6 Bathygobius soporator displaced from a tide pool were back in the pool the next day. Other marine fish known to home include Sebastes flavidus (Carlson and Haight, 1972), Enophrys bubalis (Gibson, 1967), Oligocottus maculosus (Green, 1971), Clinocottus globiceps (Green, 1973), Tautogolabrus adspersus (Green, 1975), Ulvaria subbifurcata (Green and Fisher, 1977), Clinocottus analis (Williams, 1957) and Scarus guacamia (Winn et al, 1964).

The purpose of this study was to further investigate homing behaviour in Ulvaria subbifurcata. From the work of Green and Fisher (1977) it is known that homing occurs in Ulvaria subbifurcata. Since this species is a common year around inhabitant of rocky inshore areas in Newfoundland (LeDrew and Green, 1975) and is relatively easy to capture and maintain in the laboratory, it is a useful species with which to pursue studies on the mechanism(s) of homing. The experiments reported here were conducted in an attempt to elucidate the roles of olfaction and vision in the homing behaviour of U. subbifurcata to its home site.

The thesis is organized into five sections, the first four deal with an aspect of the behaviour of orientation to a home site. They include: home range fidelity of normal and sensory impaired fish; homing of displaced fish; the orientation of displaced fish; and the daily activity pattern of normal and sensory impaired fish. In the fifth section the results of the four studies are discussed.

The data were obtained between April 1976 and August 1977 both in the field at Broad Cove, St. Phillip's, Conception Bay and in the Marine Sciences Research Laboratory (M.S.R.L.) at Logy Bay.

DESCRIPTION OF THE STUDY AREA

All field work was conducted in Broad Cove, Conception Bay. The study site encompassed the former location of the Lora I underwater habitat (Figure 1a). The water depth at the study site ranged between 9 and 12 m. The substratum consisted of shelving bedrock that sloped gradually away from shore. Irregular patches of large and small boulders covered most of the study area. Patches of sand occurred at the fringes of the study area and extended seaward.

Corraline algae were present on rocks over the entire site. Strongylocentrotus droebrachiensis (sea urchin) and Modiolus modiolus (horse mussels) were distributed throughout the study area.

Monthly bottom water temperatures ranged from -1.25°C in February to 13°C in August and September. A graph of bottom water temperatures is given in Figure 2.

Figure 1a. Map of Broad Cove including enlargement of roped-in Study Area.

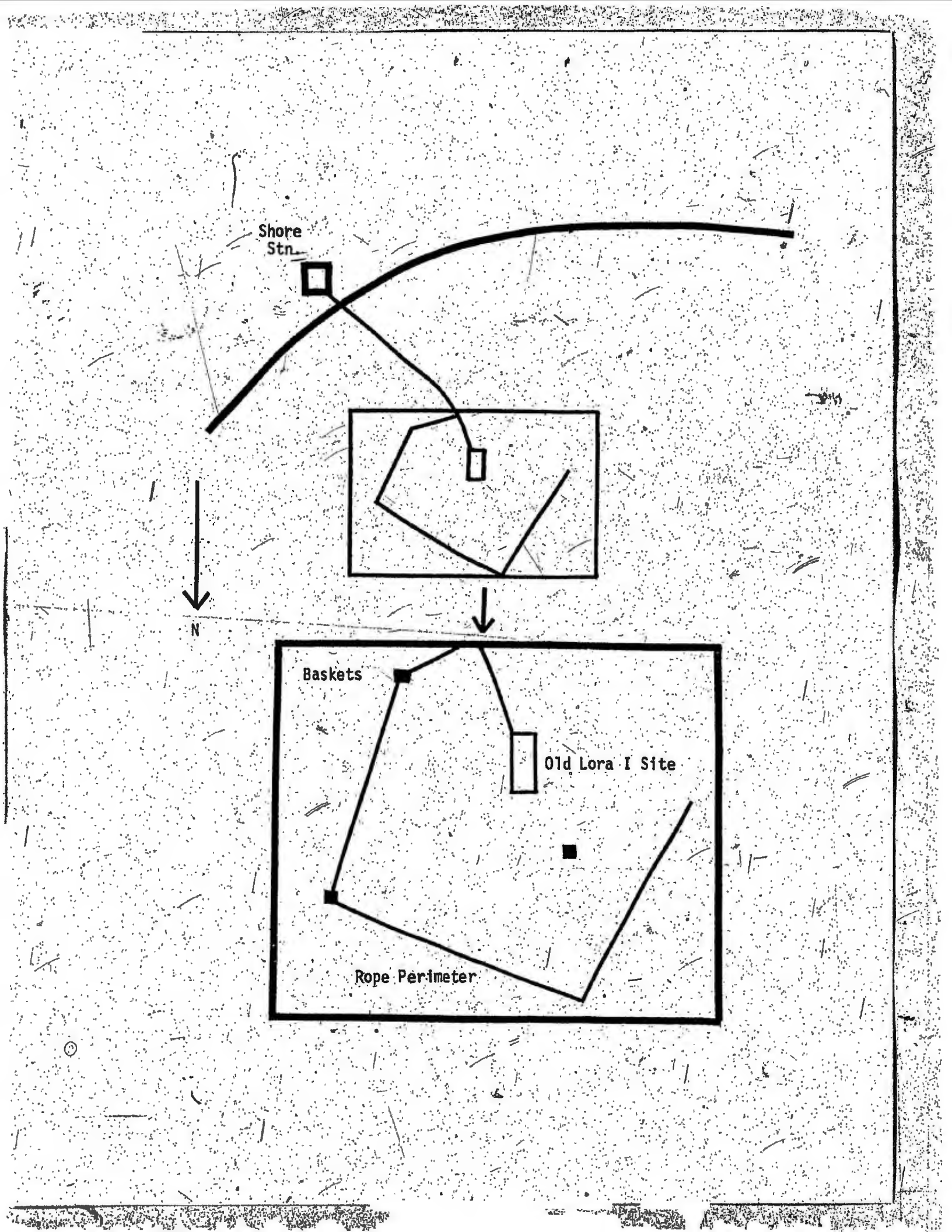
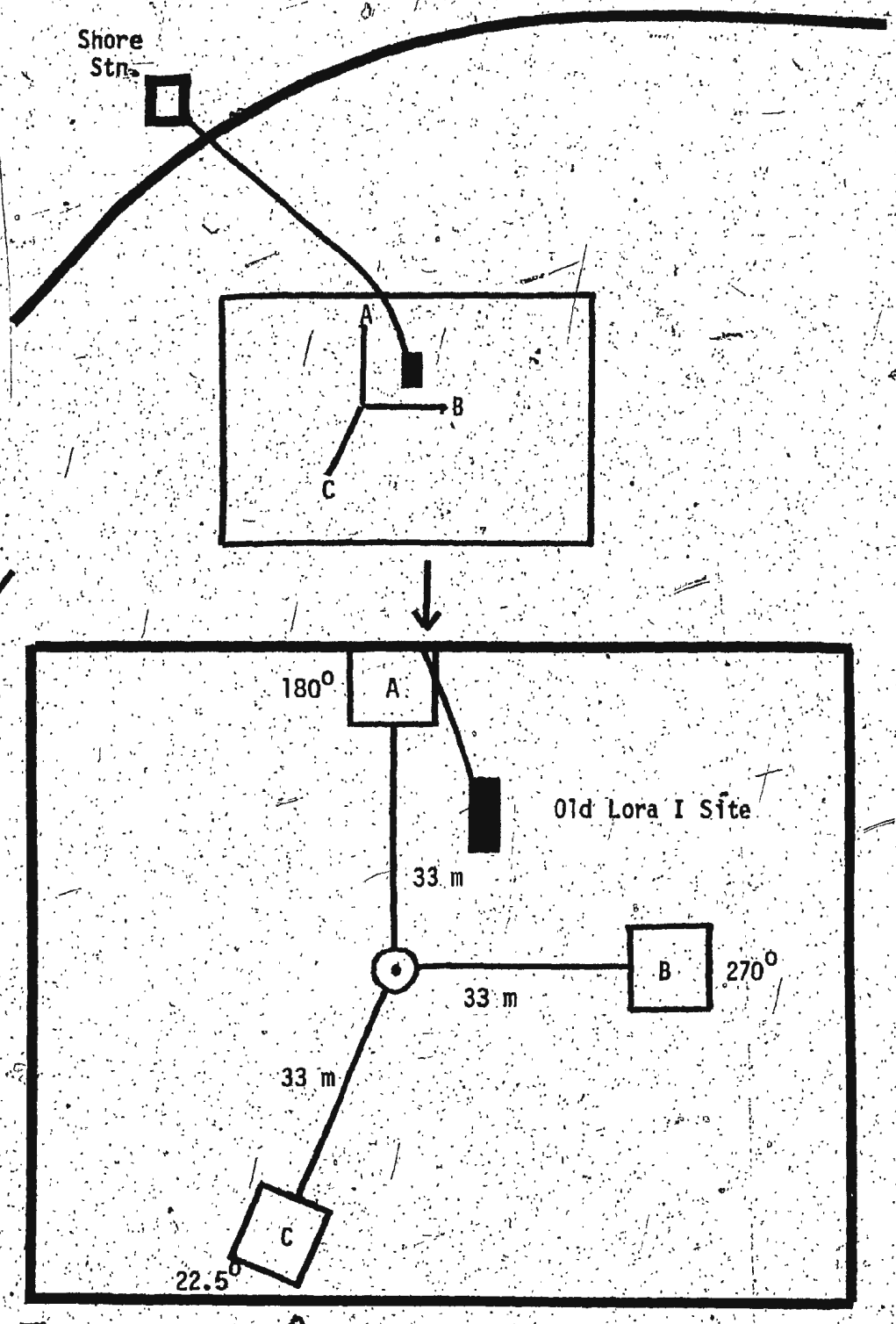

Shore
Stn.
N
Baskets
Old Lora I Site
Rope Perimeter

Figure 1b. Location of collection sites and orientation chamber site in Broad Cove (St. Phillip's).


Shore
Stn
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B
C
N
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A
Old Lora I Site
33 m
B
270°
33 m
33 m
C
22.5°

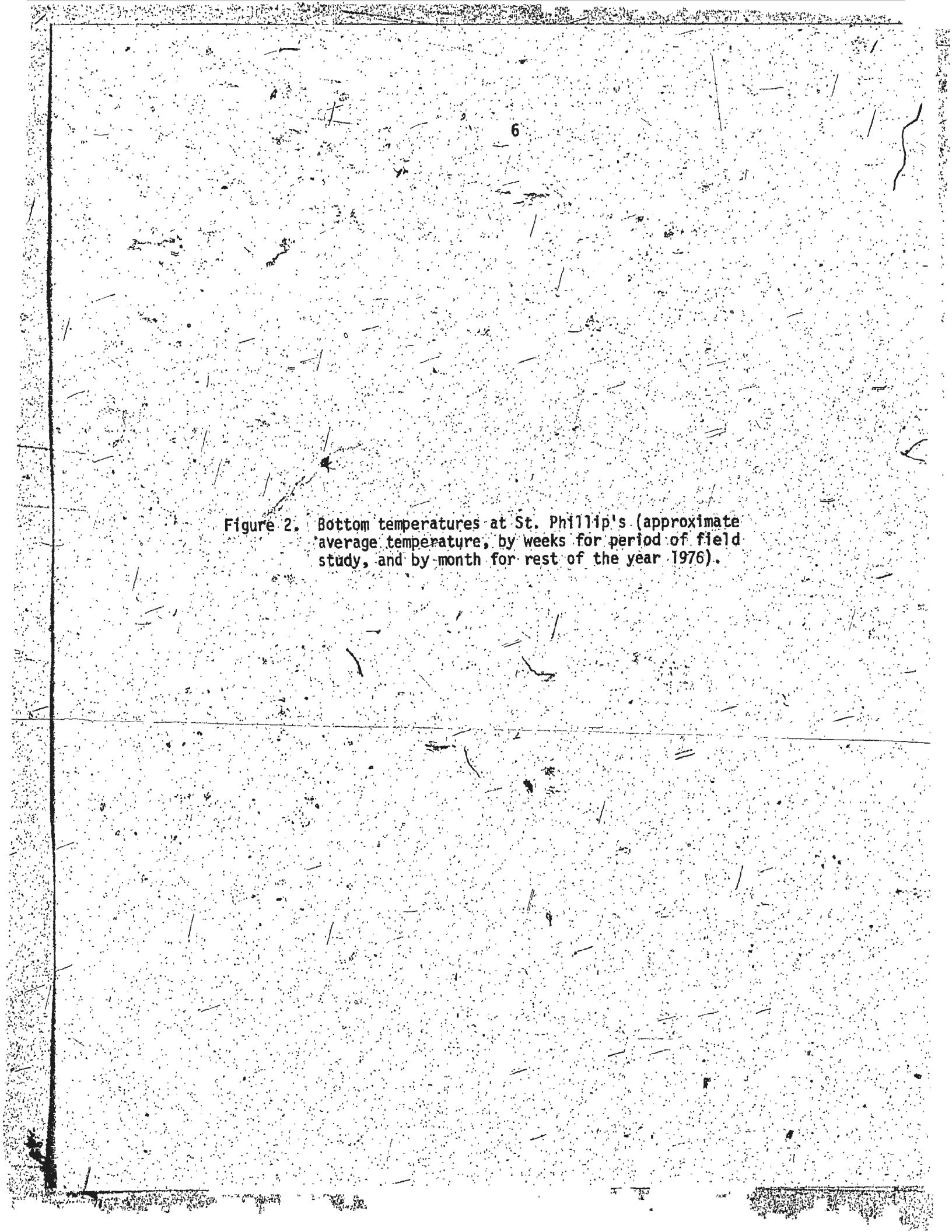
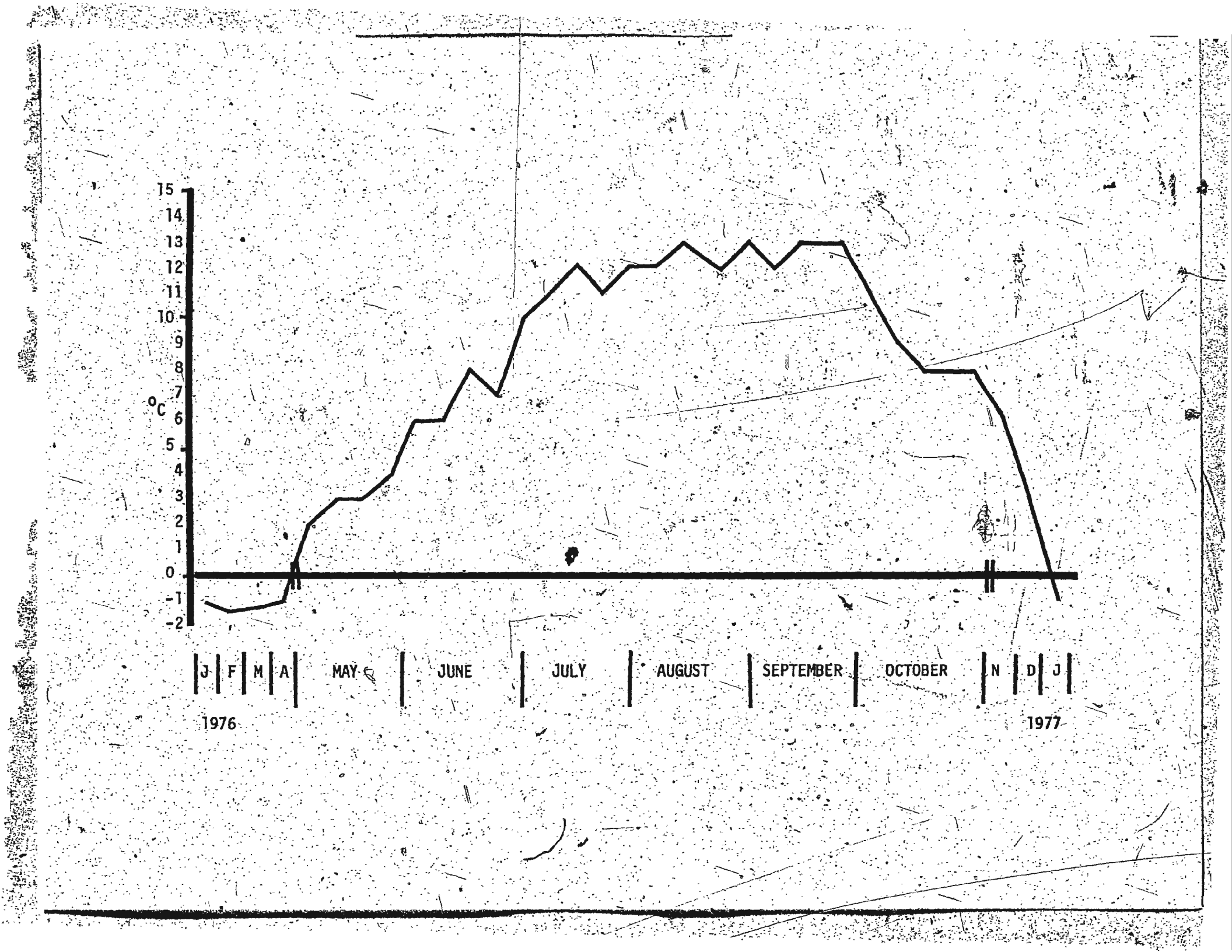


Figure 2. Bottom temperatures at St. Phillip's (approximate average temperature, by weeks for period of field study, and by month for rest of the year 1976).


15
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AUGUST
SEPTEMBER
OCTOBER
N
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J
1976
1977

HOME SITE FIDELITY

INTRODUCTION SECTION I

In attempting to study the roles of olfaction and vision in homing and orientation to a home site, it was necessary to obtain certain information. The experiment described in this section attempted to determine the likelihood of resighting tagged normal fish that had been released at their home site. This was possible because U. subbifurcata restrict their activity to a small area (2 - 3m^2) around a home site (Green and Fisher, 1977).

Providing normal fish were found at the home site, the next question was concerned with the effect of sensory impairment on the fidelity to the home site of treated fish. It is necessary to know the effect of sensory impairment on the fidelity of blind and anosmic fish to the home sites in order to assess the affect of sensory impairment on the ability of Ulvaria subbifurcata to return to the home site following displacement.

Observations of the decrease in resightings over time of fish that had been replaced in its home site was obtained as a rough approximation of predation mortality.

METHODS AND MATERIALS

Capture, Release and Resighting

All field work was performed with the use of SCUBA. Because *U. subbifurcata* is a nocturnal fish, dives were made between sunset and midnight, or later.

Fish were captured with a slurp gun and transferred to small individually marked bags made of nylon fly mesh and cotton cloth. Capture sites (home sites) were marked with 2.5 cm diameter, fluorescent-painted cork floats. These floats were attached with 50 to 70 cm of netting twine to 0.90 kg lead barrel weights.

Before each dive, the bags were prepared with cards and home site markers bearing the same code. When a fish was captured the marker was left to identify the home site. The fish was placed in the marked bag and carried with others to shore. The bags were transferred to a 20 liter container of sea water and transported to the M.S.R.L. for tagging and surgical impairment if required. Twenty-four hours following capture these fish were released at their home sites.

The home sites of the tagged fish were searched approximately forty-eight hours following capture. This was done with the aid of a 6V underwater hand lamp. When tagged fish were sighted they were held in the edge of the light beam and their colour code was recorded on an underwater slate. In the search for the fish care was taken not to

disturb or damage the home sites. The resighting of any tagged fish more than 3 m from its marked capture site was noted.

Tagging

The fish were first measured. Fish smaller than 85 mm were not tagged. This was done to conform with the minimum size fish used by Green and Fisher (1977). Tagging was carried out as described by Green (1971). Each fish was individually identifiable by a sequence of three coloured embroidery beads attached to the dorsal musculature by monofilament line (Figure 3). The beads were picked up with a needle and passed on to a line while the fish was anesthetized. Tagging was performed on a styrofoam tray covered with paper towels. The towels were kept wet with sea water the same temperature as the water the fish were held in.

Anaesthetic and Treatment

All fish were anaesthetized with MS-222 (Tricaine Methanosulfonate). The concentration of anaesthetic was approximately 0.1 g/l. The reaction of radiated shannies to this anaesthetic has been described by LeDrew (1972). Five to seven minutes in the anaesthetic were required to prepare the fish for tagging. After this period the fish turned on one side and/or would not react when their dorsal fin was raised from their body.

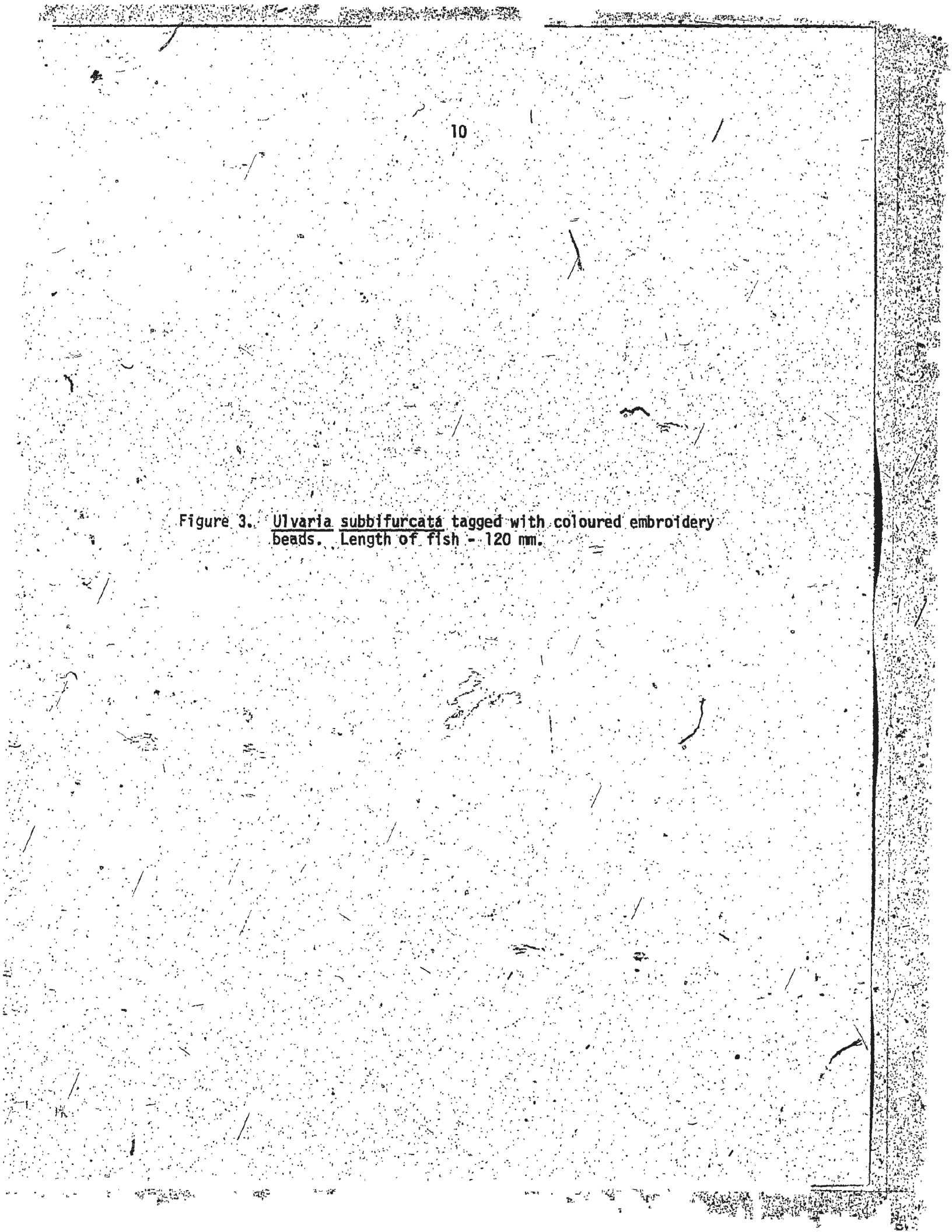
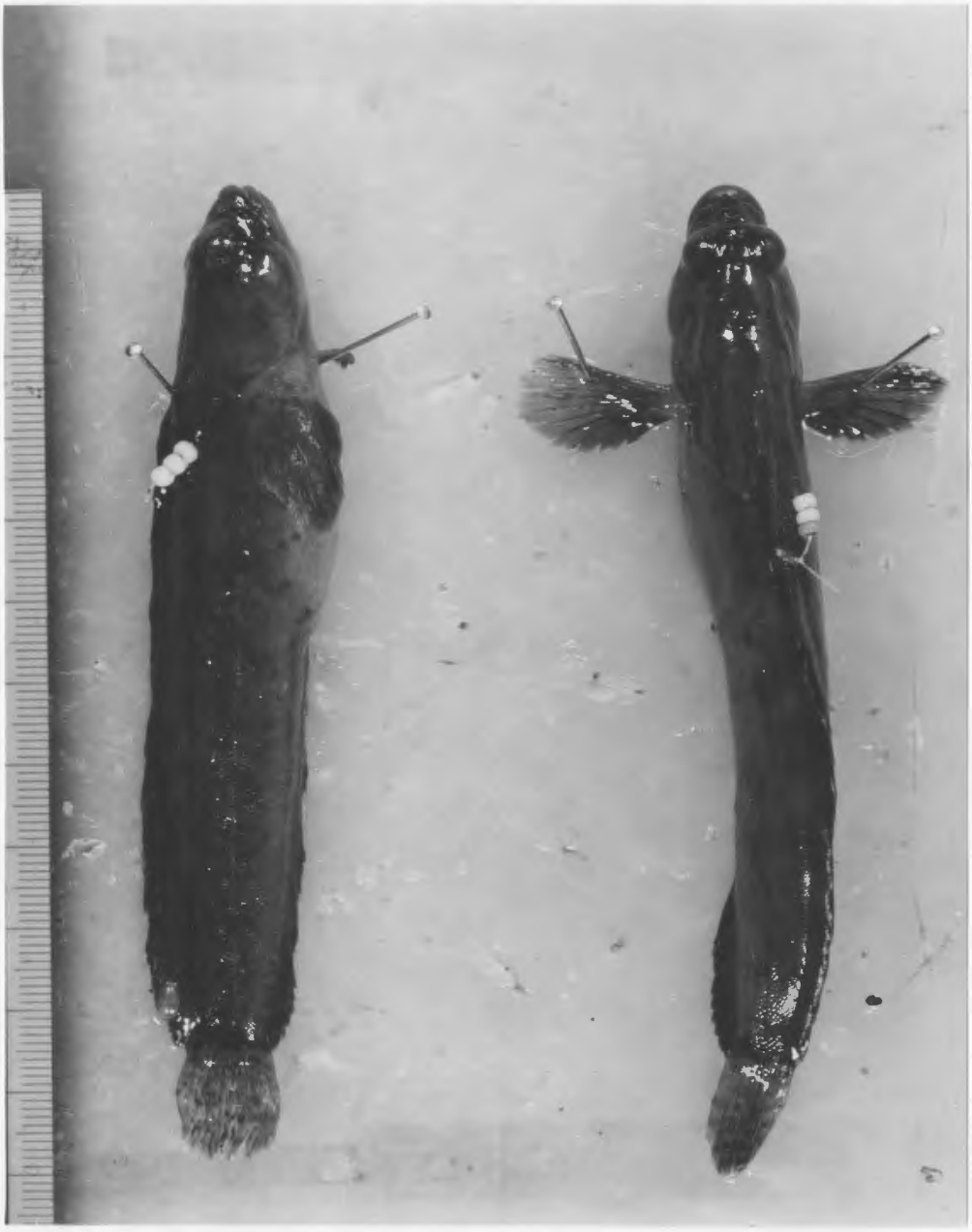


Figure 3. *Ulvaria subbifurcata* tagged with coloured embroidery beads. Length of fish - 120 mm.



Following tagging and sensory impairment where required, the fish were placed in a bucket of fresh sea water where they recovered in 5 - 10 min. The fish were held in a 183 cm x 61 cm tank containing shelters. While in the laboratory the fish were maintained under a natural photoperiod.

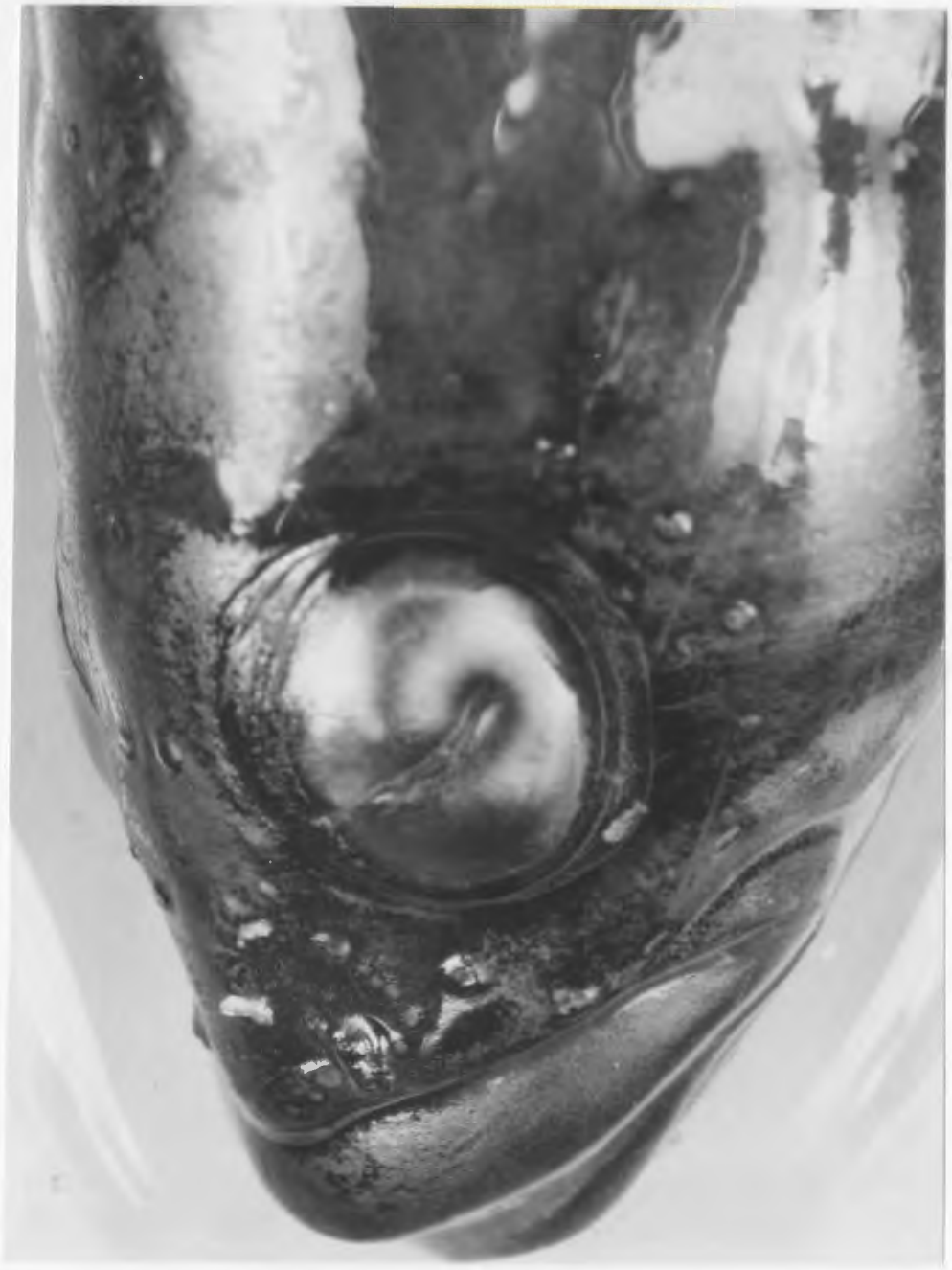
Sensory Impairment

Sensory impairment followed that of Khoo (1974) and Gunning (1959). Fish were blinded by removing their eye lenses and olfactory impairment was carried out by heat cauterization.

Lenses were removed by first making a slit with a sharp scalpel on the cornea. Pressure was then applied laterally with curved tweezers until the lenses 'popped' out. This was a rapid procedure requiring less than 30 sec. to do both eyes. During the surgery the fish was placed in a wet paper-covered depression on a styrofoam tray and covered to the operculum with sea water soaked paper towelling. Figure 4 shows the eyes following surgery and a two week period of recovery.

Olfactory impairment was carried out by heat cauterization of the olfactory rosettes. This was done by inserting the red hot point of a needle into the areas of both the raised olfactory siphons and manoeuvering the needle into the chamber of soft tissue where the rosettes are located. Figure 5 shows the olfactory siphon and Figure

Figure 4. Eye of Ulvaria subbifurcata two weeks following lens removal.



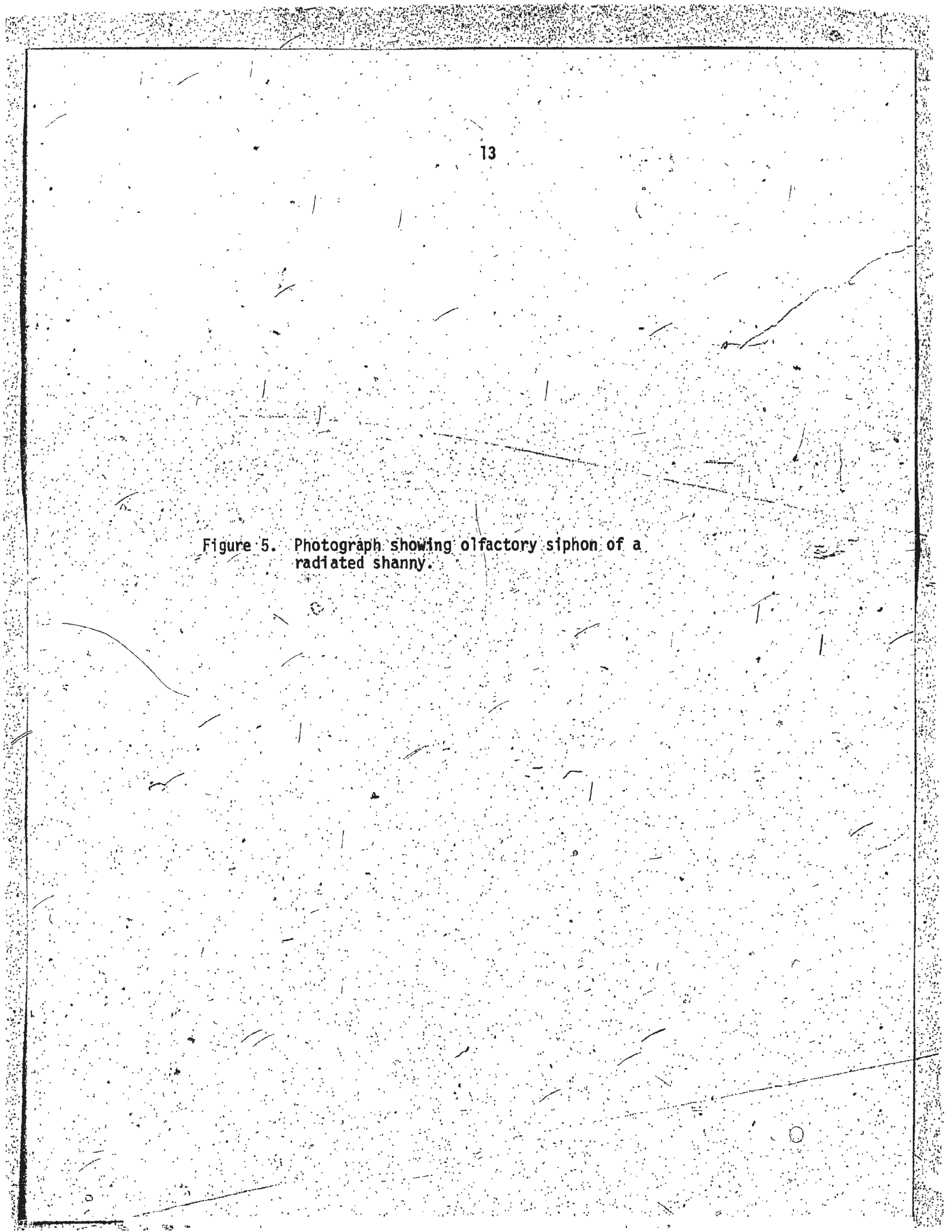


Figure 5. Photograph showing olfactory siphon of a radiated shanny.

6a shows through dissection an olfactory rosette in the olfactory chamber. Figure 6b indicates absence of the rosette in a similarly dissected fish that had been anosmicised by the above method two weeks previously.

Treatment Controls

Fifty-two fish were caught and held in the laboratory for 30 - 58 days to serve as controls. This group consisted of 15 normal, 19 blind and 18 anosmic fish. No mortalities attributable to surgical treatment occurred up until the end of this period.

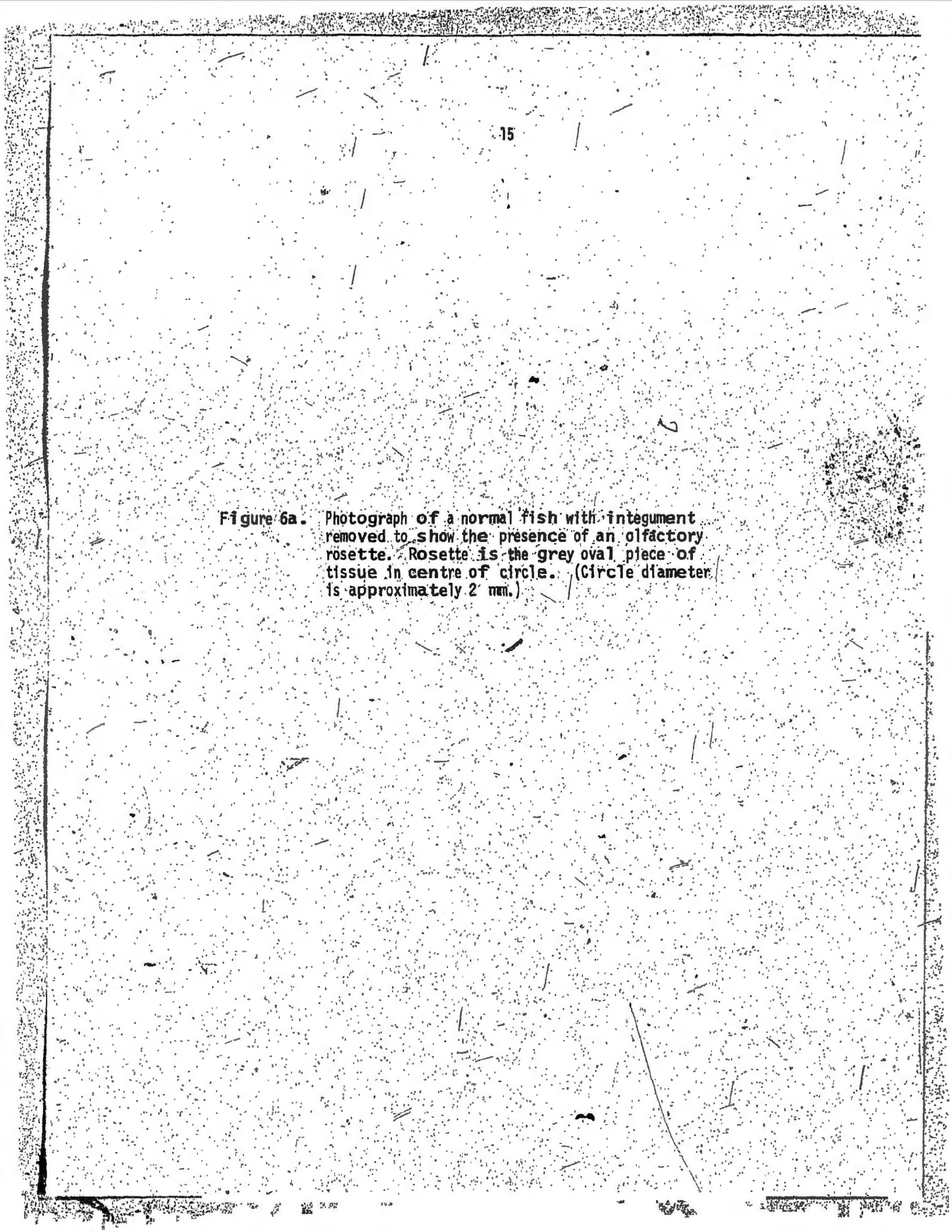
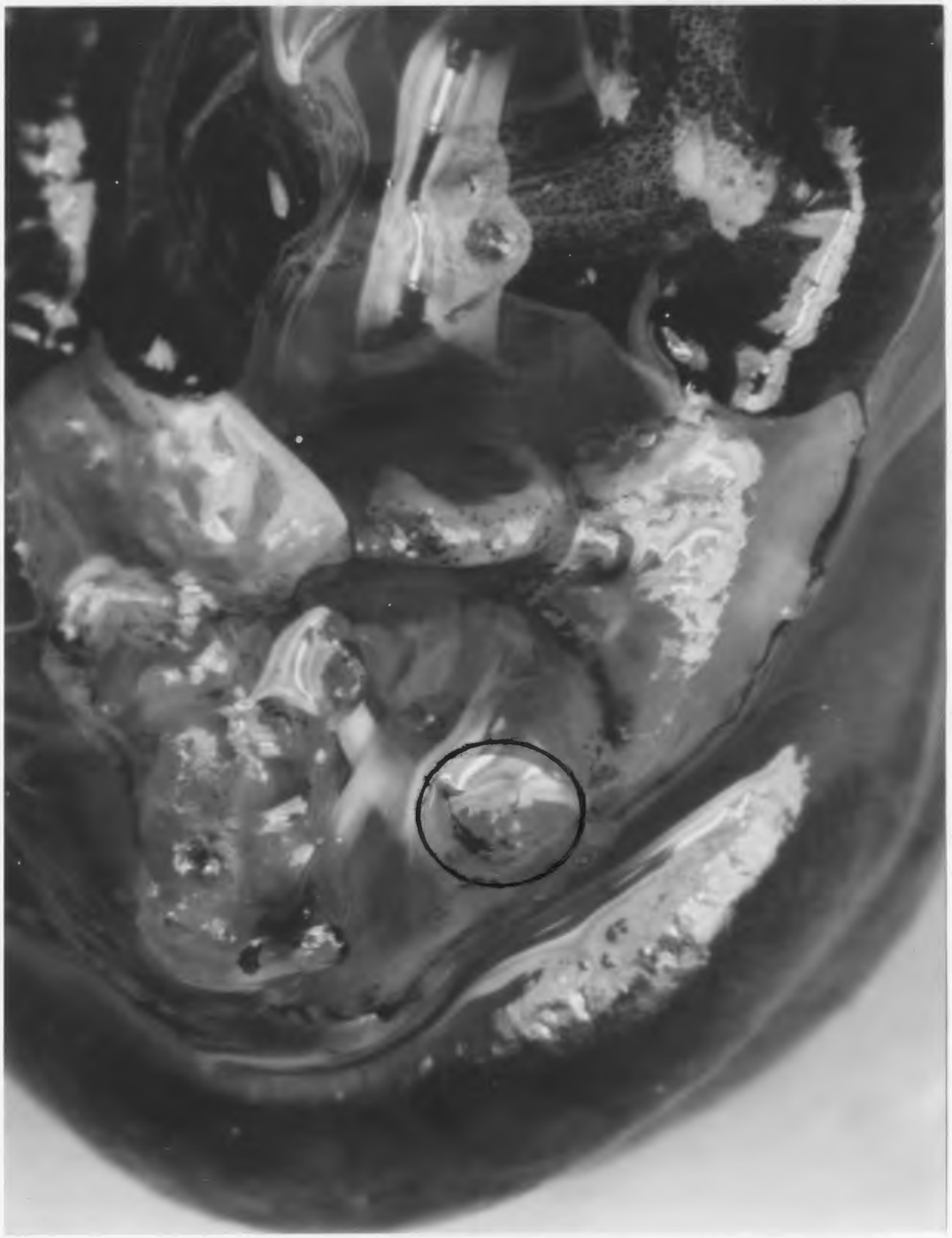


Figure 6a. Photograph of a normal fish with integument removed to show the presence of an olfactory rosette. Rosette is the grey oval piece of tissue in centre of circle. (Circle diameter is approximately 2 mm.)

Figure 6b. Photograph of a fish anosmicised two weeks previously with integument removed indicating the absence of an olfactory rosette. Stalk of tissue without rosette is in the olfactory chamber in centre of circle. (Circle diameter is approximately 2 mm.)



RESULTS

The occurrence of a restricted home area in Ulvaria subbifurcata was confirmed through resightings of tagged normal fish at their original capture sites. No fish was seen further than 3 m from their capture site. This agrees with the statement of Green and Fisher (1977) that U. subbifurcata restrict their activity to a small area (2 - 3 m^2) around a home site.

Table 1a shows the time in days following release that the fish were resighted. Eighteen of the nineteen tagged normal fish (94.7%) were resighted at least once.

The effects of the sensory impairments as previously described were to reduce the number of fish resighted at their home site. Tables 1b and 1c give the results for resighting of anosmic and blind fish respectively.

In Table 1b, fourteen of eighteen (77.7%) tagged anosmic fish were resighted at least once at their home site. The difference in the resightings of normal and anosmic fish was analyzed to determine if the difference was significant. A method of considering the independence of two proportions was used (Sokal and Rolfe, 1969). It is a method for testing the equality of two percentages and is based on the arcsin transformation. The test statistic t_s is given as:

Table 1a. Resightings of Normal fish replaced in home sites (N = 19).

Release Date	Total length of fish in mm.	Number Resightings	Time (in days) after release that resightings occurred
25/05	100	5	7,8,14,16,17
25/05	110	5	9,28,32,44,47
2/06	120	3	19,23,39
2/06	100	0	-
2/06	90	10	1,8,9,19,20,24,28,29,43,47
3/06	110	7	7,8,18,19,23,28,80
3/06	85	4	4,7,17,23
3/06	120	4	8,38,69,104
7/06	110	3	9,13,15
9/06	120	1	1,61
9/06	101	3	1,12
9/06	108	5	1,2,12,19,30
9/06	114	3	7,17,29
9/06	91	2	1,57
9/06	108	4	1,41,45,48
15/06	114	3	6,8,16
16/06	95	1	25
16/06	95	2	12,22
16/06	102	1	22
	Av. = 105 mm.		

Table 1b. Resightings of Anosmic fish replaced in home sites (N = 18).

Release Date	Total length of fish in mm.	Number Resightings	Time (in days) after release that resightings occurred
2/06	90	0	-
2/06	90	3	18,20,70
2/06	90	1	5
3/06	100	5	6,8,18,38,94
3/06	110	3	4,7,8
3/06	120	3	17,19,23
7/06	95	1	14
9/06	102	3	7,4,17
9/06	101	7	1,2,7,11,12,17,22
9/06	117	4	1,2,12,61
9/06	104	0	-
9/06	140	2	12,19
15/06	114	0	-
15/06	133	3	6,15,16
15/06	108	0	-
15/06	104	1	6
15/06	96	6	5,6,8,13,15,16
16/06	120	1	4

Av. = 107 mm.

Table 1c. Resightings of Blind fish replaced in home sites (N = 18).

Release Date	Total length of fish in mm.	Number Resightings	Time (in days) after release that resightings occurred
25/05	90	0	-
25/05	85	0	-
2/06	130	0	-
2/06	110	0	-
2/06	105	0	-
3/06	85	1	7
3/06	100	3	6,8,17
3/06	100	0	-
7/06	130	3	2,4,31
9/06	96	1	7
9/06	121	0	-
9/06	97	1	1
9/06	95	1	2
9/06	95	0	-
9/06	108	0	-
15/06	114	8	5,6,14,15,23,26,30
16/06	108	0	-
16/06	123	0	-

Av. = 105 mm.

$$t_s = \frac{\arcsin\sqrt{p_1} - \arcsin\sqrt{p_2}}{\sqrt{820.8\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where p_1 and p_2 are the resighted proportions of normal and anosmic fish n_1 and n_2 respectively. The value 820.8 is a constant representing the parametric variance of a distribution of arcsin transformations of proportions or percentages. The t_s obtained is compared with a normal deviate of the area under a normal curve in a two tailed test (Sokal and Rohlf, 1969).

The null hypothesis (H_o) with this test states that the proportions of resightings of the two samples of fish are not different. When applied to the differences in proportions of resightings of normal and anosmic fish a t_s of 1.581 is obtained. This indicates there is no significant difference ($p > .05$) in the proportions of normal and anosmic fish resighted at their home sites. Table 2 gives comparisons of resighted proportions of the samples of fish.

Only 7 of 18 tagged blind fish (38.9%) were resighted (Table 1c) in their home site. As shown in Table 2 this proportion of resightings was significantly lower ($p < .05$) than that of both normal and anosmic fish. t_s values of 4.089 and 2.481 were obtained in comparisons of blind fish with normals and anosmics respectively.

Table 2. Comparison of resighted proportions of treatment fish with normal fish and with each other.

Comparison	$\sum n_1 + n_2$	t_s (Calculated)	Significance level (p)
Normal X Anosmic	37	1.581	n.s.
Normal X Blind	37	4.085	<.001
Anosmic X Blind	36	2.461	<.05

Critical $t_{.05\ 30\ df} = 2.042$ *

$t_{.001\ 30\ df} = 3.646$ *

* from Table B
Siegel (1956)

Diving Observations on Released Fish

It was observed in the field that normal fish when released 0.5 to 1 m above their capture position descended directly and immediately entered a hole or crevice in the substrate. This was taken to be their home site.

Anosmic fish when released also moved quickly to the protection of the substrate. Their movements though quick were not direct. They did not descend vertically to the bottom but in many cases swam off to one side before reaching the bottom. Upon observation for a short period (~15 sec. to 120 sec.) the majority of anosmic fish that initially moved from their capture site were seen to return to a hole or crevice close to their original capture position. This was taken to be their home site.

Blind fish behaved slightly differently from the normal and anosmic fish. When released they did not move quickly. Some fish moved slowly in stops and starts around their original capture position. Of these fish, some entered a hole or crevice that was taken to be their home site. Others stopped in crevices that did not appear to offer the complete protection of a home site. Other blind fish did not move when released but remained fully exposed on the bottom longer than 2 and 3 minutes. These blind fish did not wander or stray upon release as did some anosmics. In contrast to blind fish recently released, blind fish later resighted in the field proceeded quickly to a home

site when startled by divers.

Likelihood of Decreased Sightings Over Time

To determine the decreased likelihood of resighting tagged fish over time, a period of 7 days was chosen. Over this time period starvation would not be a mortality factor. The data for normal, anosmic and blind fish released in their home sites between June 2 and June 16, 1976 was considered. Table 3 shows that of the total numbers of fish released 16 normal, 14 anosmic and 7 blind were resighted in their home sites. The number of resighted fish of each treatment that were not seen after 7 days in their home site were considered to be dead or moved. None of the 18 normal fish known to have been in their home site were absent after 7 days. Four of the seven blind fish (57%) were not in the home sites 7 days after release. Three of fourteen (21%) of anosmic fish disappeared in the same time.

Table 3. Decreased likelihood of resighting after 7 days of fish released to home sites between June 2 and June 16, 1976.

	Number Released	Total Number Resighted	Number resighted before day 7 but absent after day 7	Decreased likelihood of resighting a fish after 7 days
Normal	17	16	0	0%
Anosmic	18	14	3	21%
Blind	16	7	4	57%

HOMING

INTRODUCTION — SECTION II

It has been established from the first section that certain proportions of normal, anosmic and blind fish were able to remain in the home site when returned to that home site. The next important step was to determine the ability of normal and sensory impaired fish to return to the home site when displaced. Through the use of extirpation methods previously described, this portion of the project was performed to study the roles of olfaction and vision in homing.

Related to the actual homing of a displaced fish is the question of how long a fish may be kept out of its home area and still retain the ability to home. To obtain some information on this question, a homing experiment was performed with fish that were collected in the study area and held at the M.S.R.L. for slightly longer than 7 weeks.

METHODS AND MATERIALS

Capture, Tagging, Resighting, Treatment

The capture, tagging, sensory impairment treatment and searching for released fish were as described in Section I. The fish used in the homing experiments all ranged in size from 85 to 140 mm. The average size for all fish was 108 mm.

Groups of Fish Displaced

A. Fish released after 24 hours

The first group of fish used to study homing consisted of 18 normal, 18 blind and 17 anosmic fish. These fish were caught over 3 days (July 19 - July 21). They were tagged, treated and released within 24 hours following capture. These fish were released on a rocky substrate approximately 19 m from the majority of home sites. Minimum and maximum distances from home sites to the release site were 15 m and 22.5 m respectively. Upon release, care was taken not to disturb the substrate so as not to attract predators.

B. Fish released after 51 - 58 days

The second group of fish in the homing study consisted of 15 normal, 15 blind and 14 anosmic fish. These fish were caught on four nights between July 19 and July 26. The area where these fish were collected was adjacent and similar to the area where the previous group of fish had been collected. These fish were held at the M.S.R.L.

for 51 to 58 days and released on September 15. The release site consisted of a rocky substrate approximately 20 m from the majority of the home sites.

On two nights (September 12, 14) prior to the release of these fish, their home sites were searched. All fish found within 2 - 3 m^2 of the home sites were removed.

C. Tagged fish released immediately following capture

The third group of fish displaced consisted of tagged fish that had been replaced in their home sites between May 25 and June 16. These fish were recaught in their home sites with a slurp gun and displaced distances of 4.5 m to 13 m. Prior to recapture these fish had been in the ocean for a minimum of eight days.

D. Anosmic fish with short (12 m) and long (35 m) displacements

The last group of fish was displaced during July 1977. Nineteen anosmic fish were separated into two groups and displaced 12 m and 35 m from their home sites respectively. All fish were collected in the same restricted area. The direction of displacement was the same for both groups of fish.

Holding Facilities in Laboratory

The shannies collected July 19 - 26 were held in the laboratory in 2 tanks 183 cm x 61 cm x 15 cm. Rocks with scallop shells

leaning against or on top of them were provided as shelters. PVC tubing 15 - 20 cm long of 5 cm diameter and some short half cylinders of PVC tubing cut through the centre were also used.

Fresh sea water flowed through the tanks constantly. The tanks were in a room where the photoperiod was adjusted to approximate the natural photoperiod.

While this group of fish was being held at Logy Bay they were fed thin slices of caplin every day. Normal, anosmic and blind fish were all observed to feed on the caplin. At the time of release no emaciation was observed in any of the fish.

RESULTS

The homing performance of fish taken out of their home site for 24 hours and released approximately 19 m away are given in Tables 4a, 4b and 4c. Seventeen of eighteen normal fish were sighted at least once in their home site. Five of seventeen anosmic fish and 4 of 18 blind fish were also sighted at least once in their home sites.

The significance of the homing performances are considered in Table 5. Here the proportion of fish resighted when replaced in their home sites (0 m displacement) are compared with the proportion of fish resighted following 19 m displacement. This is given for normal, anosmic and blind fish. 't' values are calculated as described in the section on home site fidelity.

The differences in the proportion of resighted normal and blind fish were not significant ($p > .05$) for fish displaced 0 m or 19 m. Thus the homing ability of blinded fish did not seem to be impaired.

The proportion of anosmic shannies resighted decreased very significantly ($p < .01$) when displacement was 19 m as opposed to 0 m, indicating that olfaction plays an important role in the homing mechanism in U. subbifurcata.

Table 4a. Resightings of displaced Normal fish in their home sites (N. = 18).

Release Date	Total length of fish in mm.	Number Resightings	Time (in days) after release that resightings occurred
20/07	92	0	-
20/07	130	8	3,6,7,9,22,24
20/07	138	3	3,6,16
20/07	91	2	18,22
20/07	90	3	16,22,23
21/07	98	5	2,8,15,19,23
21/07	100	3	2,8,19
21/07	125	9	2,6,8,13,15,19,21,23
21/07	118	7	2,3,8,13,15,19,23
21/07	107	3	5,21,23
22/07	118	3	5,12,14
22/07	115	1	14
22/07	95	3	14,18,22
22/07	98	1	16
22/07	106	3	4,5,18
22/07	107	4	7,12,18,20
22/07	109	4	7,12,18,20
22/07	85	1	5

Av. = 107 mm.

Table 4b. Resightings of displaced Anosmic fish in their home sites (N = 17).

Release Date	Total length of fish in mm.	Number Resightings	Time (in days) after release that resightings occurred
20/07	121	0	-
20/07	90	0	-
20/07	105	2	20,22
20/07	108	0	-
20/07	100	1	14
21/07	95	0	-
21/07	105	0	-
21/07	100	4	2,15,23,57
21/07	90	0	-
22/07	134	0	-
22/07	130	0	-
22/07	109	0	-
22/07	112	0	-
22/07	114	0	-
22/07	110	1	5
22/07	108	0	-
22/07	87	1	18

Av. = 106 mm.

Table 4c. Resightings of displaced Blind fish in their home sites (N = 18).

Release Date	Total length of fish in mm.	Number Resightings	Time (in days) after release that resightings occurred
20/07	130	0	-
20/07	128	1	16
20/07	138	0	-
21/07	107	0	-
21/07	96	1	5
21/07	130	0	-
21/07	96	0	-
21/07	120	0	-
22/07	107	0	-
22/07	108	0	-
22/07	110	0	-
22/07	105	0	-
22/07	109	0	-
22/07	91	0	-
22/07	98	1	12
22/07	96	2	1,20
22/07	110	0	-
22/07	91	0	-
	Av. = 109 mm.		

Table 5. Comparison of differences in % of fish resighted following displacement of 0 m or 19 m.

	Displacement Distance 0 m	19 m	Calculated 't_s' of difference	Significance level p
Normal	94.7%	94.4%	.023	n.s.
Anosmic	77.7%	29.4%	3.035	<.01
Blind	38.8%	22.4%	1.064	n.s.

$t_{.05\ 30\ df}$ = 2.042 *

+ n.s. no significant difference at $p < .05$

* from Table B of Siegel (1956)

The homing performances of fish removed from their home sites and held 51 - 58 days in the laboratory are given in Table 6. These fish were released approximately 20 m from their home sites, in the same direction as those fish released after 24 hours. Only 3 of 15 normal fish were resighted in their home sites. One other normal fish was found by chance. It was occupying a new home site outside the study area. No anosmic or blind fish of this group were resighted.

The significance of the decreased proportion of normal fish homing following removal from their home sites for at least 51 days is given in Table 7. A calculated 't' value of 4.968 indicates a very significant decrease ($p < .001$) in the proportion of displaced fish resighted in their home sites. The search effort for these fish in their home sites was similar to the search effort for other groups of fish.

The third group of fish displaced to observe homing consisted of tagged fish that had been in their home sites at least 8 days prior to their recapture and displacement. Tables 8a and 8b list the individuals displaced, their time in the ocean before displacement and the displacement distance. Ten of eleven normal fish homed over distances of 9 to 24.4 m (average displacement 12.8 m). Five of eight anosmic fish homed over distances of 4.5 to 10.6 m (average displacement 7.6 m).

Table 6. Resightings of homed Normal fish held out of ocean 51 - 58 days before displacement and release (N = 15).

Release Date	Total length of fish in mm.	Number Resightings	Time (in days) after release that resightings occurred
15/09	105	5	1,5,7,28,43
15/09	100	0	-
15/09	132	0	-
15/09	105	0	-
15/09	90	0	-
15/09	133	2	28,43
16/09	128	1	7
15/09	106	0	-
15/09	138	0	-
15/09	101	0	-
15/09	90	2*	7,28
15/09	115	0	-
15/09	105	0	-
15/09	102	0	-
15/09	96	0	-
	Av. = 109 mm.		

* fish found at one location outside the study area

no anosmic fish or blind fish that were released with these normal fish were resighted

Table 7. Comparison of homing success (% resighted in home sites) of Normal fish held in laboratory for 1 day or 51 - 58 days.

Holding time	Displacement Distance (m)	% Resighted	Calculated t_s of difference	Significance p
1 day	19 m.	94.4	4.968	< .001
51 - 58 days	20 m	20.0		

* no blind or anosmic fish held 51 - 58 days in the laboratory returned to their home sites

Table 8a. Resightings of tagged Normal fish displaced immediately following recapture in the home sites.

Total length of fish in mm.	Time in home site (days) before displacement	Displacement Distance (m)	Time (in days) after release that resightings occurred
110	28	13.4	4
90	20	10.9	4
108	14	11.3	7
114	8	11.3	9
95	12	13.1	10
120	24	11.3	15
85	23	9.7	-
110	23	9.1	5
114	15	13.1	13
-	> 365 days	14.3	2
120	63	24.4	6
Av. = 107 mm.		Av. = 12.9 m.	

Table 8b. Resightings of tagged Anosmic fish displaced immediately following recapture in the home sites.

Total length of fish in mm.	Time in home site (days) before displacement	Displacement Distance (m)	Time (in days) after release that resightings occurred
96	8	4.5	5
114	11	10.7	13
121	11	?	-
140	19	7.9	*(found in new home sites)
102	17	7.0	*(found in new home sites)
133	15	?	1
100	38	?	25
114	11	?	13

Av. = 115 mm.

* these fish were found at sites away from their home sites

** 1 blind fish was translocated 10.7 m after spending 15 days in the ocean and was resighted in its home site 8 days later

These fish were not displaced in one constant direction. The home sites were in locations different from the home sites of fish used in the previous homing experiments.

Two of the displaced anosmic fish (Table 8b) were discovered in new home sites outside their collection area. These fish were first resighted at 9 and 12 days following displacement. One fish was observed in the same site on two subsequent occasions.

The fourth group of fish run during July 1977 compared the performance of anosmic fish at short and long displacements. Two of nine fish displaced 12 m were resighted in their home sites. None of the ten anosmic fish displaced 35 m were resighted in their home sites. The calculated t_s of 2.136 in Table 9 shows a significant difference ($p < .05$) in the homing of anosmic fish displaced shorter or longer distances.

Table 9. Comparison of homing in groups of Anosmic fish displaced short (12 m) or long (33 m) distances.

Displacement Distance (m)	Sample Size	% Homed	Calculated t_s	Significance level
12	9	22.2%	2.136	$p < .05$
35	10	0%		

* Critical 't' values taken from Table B of Siegel (1956)

ORIENTATIONS

INTRODUCTION — SECTION III

A major question in understanding the mechanism of homing deals with how the fish orients or 'steers' towards the home site. Hypothesized mechanisms include navigation, random search or directed movements involving sensory contact with the home site (Khoo, 1974) (Adler, 1963).

Green and Fisher (1977) have shown that U. subbifurcata is capable of orienting to a home site from a distance of at least 30 m. They suggested that olfaction is involved in this orientation response but they presented no direct evidence to support this.

To obtain data on the sensory basis of directed movements towards the home site in U. subbifurcata, orientation experiments were conducted. These experiments were carried out with normal, anosmic and blind fish.

METHODS AND MATERIALS

Capture and Treatment

Experimental fish were captured in three areas, each of approximately $4m^2$, located 33 m from a central orientation chamber site (see Figure 1b). Four groups of fish were run in the orientation apparatus. These groups consisted of normal, bilaterally blind, bilaterally anosmic and treatment controls that were unilaterally blind and anosmic. Normal fish were collected at all three capture areas. Blind, anosmic and unilaterally blind and anosmic fish were taken from site C only.

The fish were captured with a slurp gun. Fish from one location were placed in a collecting bag and carried to the surface where they were transferred to a 20 litre bucket and taken ashore. In the shore station at St. Phillip's all fish were anesthetized and sensory impairment was performed. This took place approximately one hour following capture.

All fish were allowed to recover in fresh sea water and then placed in a minnow trap. The minnow trap was then returned to the sea bottom in the area from which the fish were taken.

The numbers of fish used, the length ranges and the approximate mean lengths of the experimental fish used in the orientation study are shown in Table 10.

Table 10. Numbers, size range and mean length of experimental fish in orientation study.

Treatment Groups	Sample Sizes	Range of total length in mm.	Approximate mean size in mm.
Normal	44	80 - 140	106
Blind	38	91 - 120	102
Anosmic	30	86 - 133	109
Unilaterally Blind & Anosmic	19	80 - 106	99

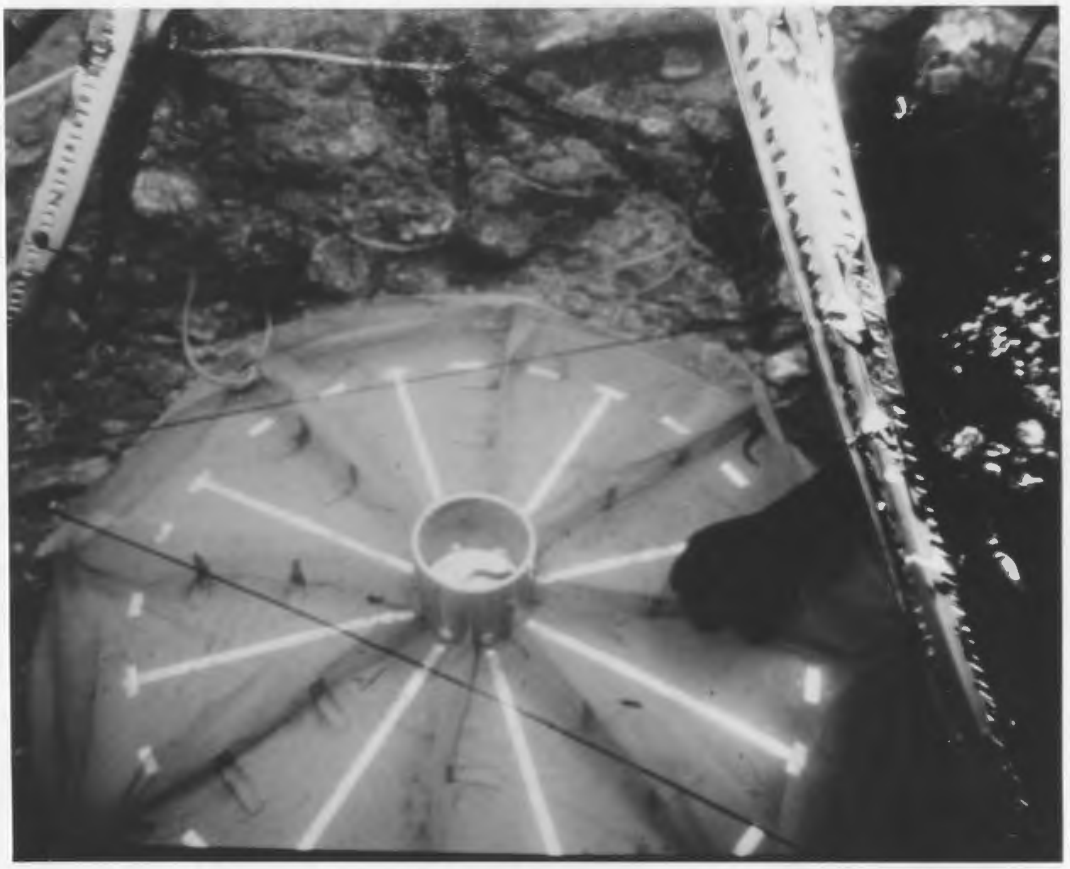
Orientation Apparatus

The basic orientation apparatus was as described by Green and Fisher (1977), but was slightly modified for this study. The apparatus was a 1.3 m diameter PVC disc supporting a 15 cm diameter by 15 cm high PVC pipe with eight 2.5 cm holes spaced equally about its circumference. The holes were 1.2 cm above the surface of the disc. The modification involved the addition of 10 cm high plastic fly screen around the circumference of the disc and as radii from the central release chamber to the disc edge. The mesh was attached with contact cement to 90° PVC bracts attached to the disc. In this manner eight identical compartments were produced. Fish emerging from the holes of the central release chamber were contained within the compartments. The disc, except for the central chamber was covered by a sheet of plastic fly screen which effectively kept other fish out (Figure 7).

Release of the Fish

The orientation experiments were generally conducted between 1300 hours and 1500 hours Newfoundland Daylight Saving Time. The experiments commenced on August 3, 1976 with normal fish being run and ended on September 23, 1976 with the last run of fish that were unilaterally blind and anosmic.

Figure 7. Orientation disc with shanny in central release chamber. (Covering mesh is absent.)



The experiments were run on the afternoon following capture between noon and three-thirty. Prior to their release in the orientation chamber, the fish were held in a minnow trap 5 m to 10 m away from the orientation disc in the direction of the home sites and out of sight of the disc. Fish were individually taken from the minnow trap and carried to the orientation apparatus where they were released into the central chamber of the disc. Fish were observed from a position to the side of the disc. The time to departure of the fish from the central chamber and the direction of departure of the fish were recorded on a slate.

RESULTS AND DISCUSSION

Figures 8a to 8d give the results of the orientations of the fish in each of the four groups. The data for each treatment group were tested for randomness by means of the 'Rao's Test' (Batschelet 1972). This test used the sum of deviations, 'U', as the test statistic. Table 11 gives the U values calculated according to the formula:

$$U = \frac{1}{2}\sum_{i=1}^{n}\left|T_i - \frac{360}{n}\right|$$

(where T_i denotes arc lengths between observed orientations). A table of critical 'U' values found in Batschelet (1972) rejected the null hypothesis of random orientations ($p < .01$) for normal, blind, anosmic and surgical control fish.

A modified Rayleigh test or 'V' test (Batschelet 1972) was then used to determine if the mean direction of orientations (θ) chosen by the test fish differed significantly from the home direction (θ_0). To obtain the mean direction the mean vector of all orientations of each group had to be first calculated. This was required because the mean direction is the angle in the direction of the mean vector.

Figure 8a. Orientations of released Normal fish. Data has been rotated so that home is the home direction of all fish (N = 44).

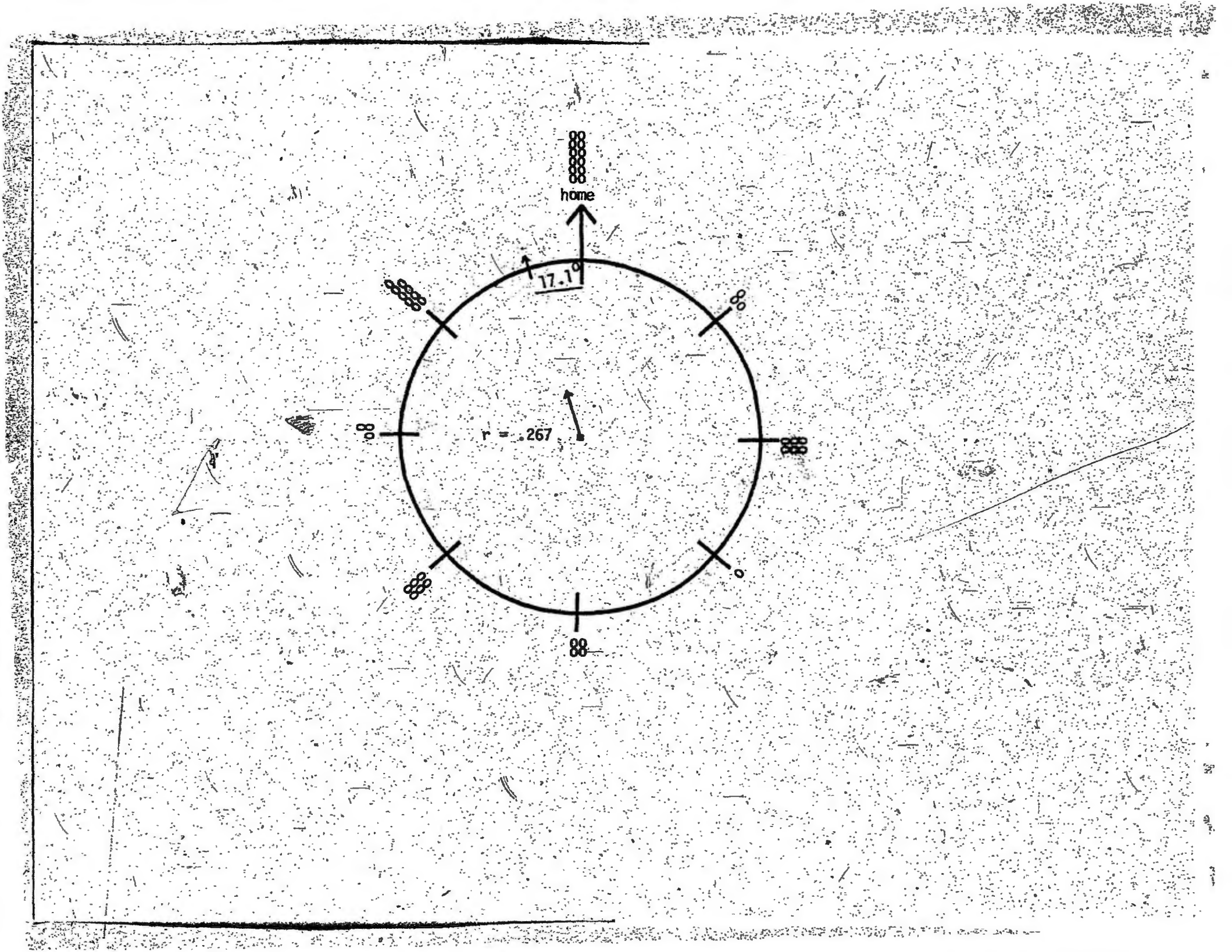

home
17.1°
r = .267

Figure 8b. Orientations of released Blind fish (N = 38).

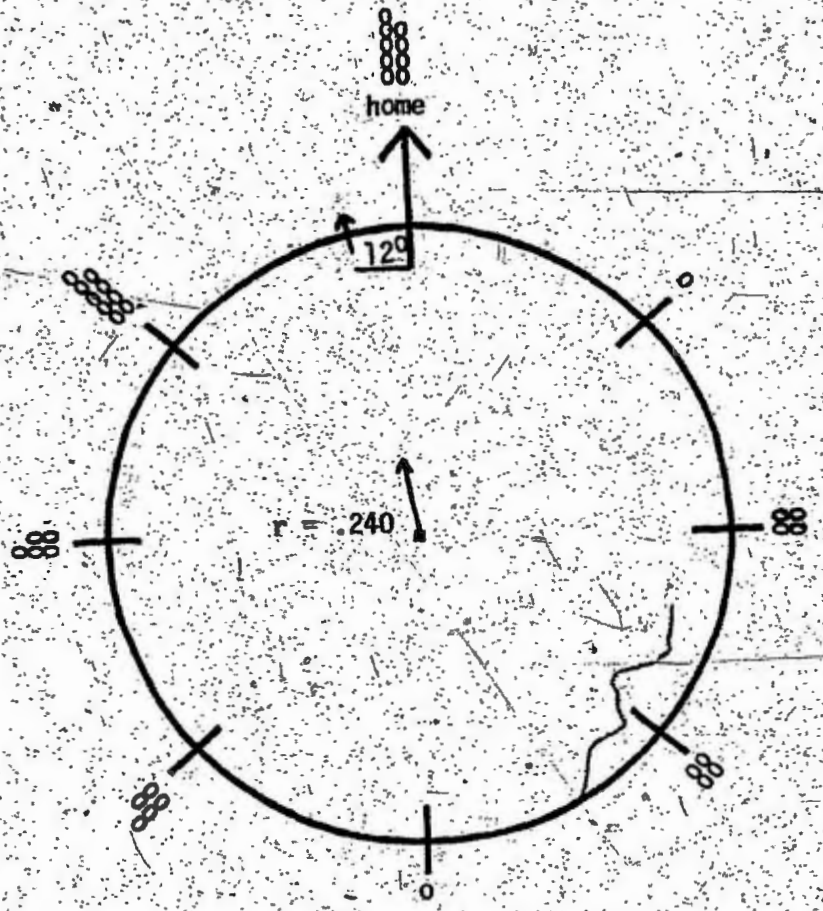

home
12°
r = .240

Figure 8c. Orientations of released Anosmic fish (N = 30).

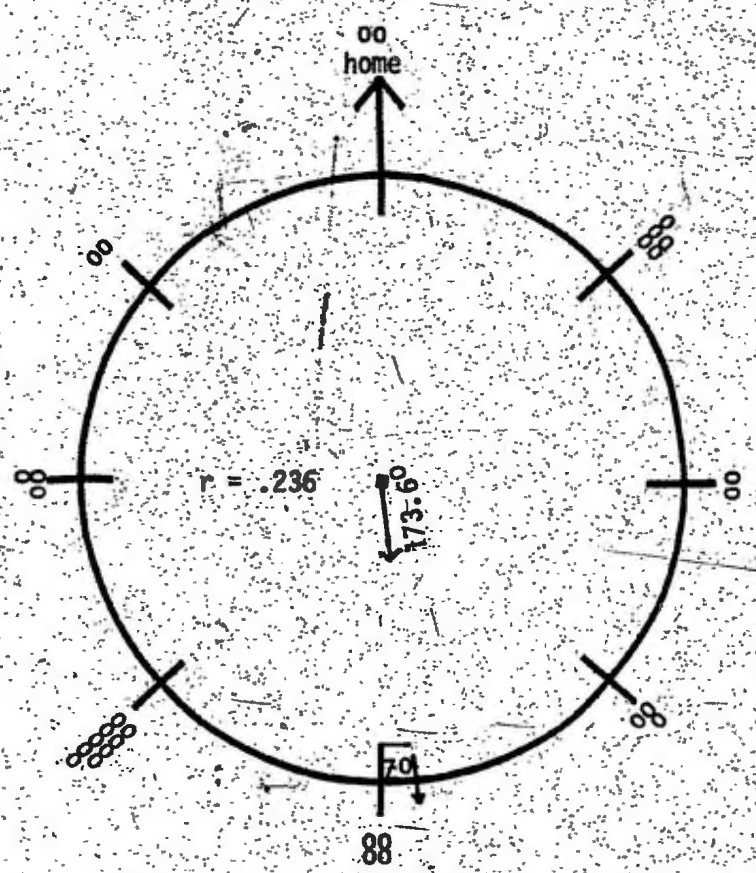

oo
home
oo
oo
oo
oo
oo
oo
r = .236
173.6°
70
88

Figure 8d. Orientations of released fish that were unilaterally blind and anosmic (N = 19).

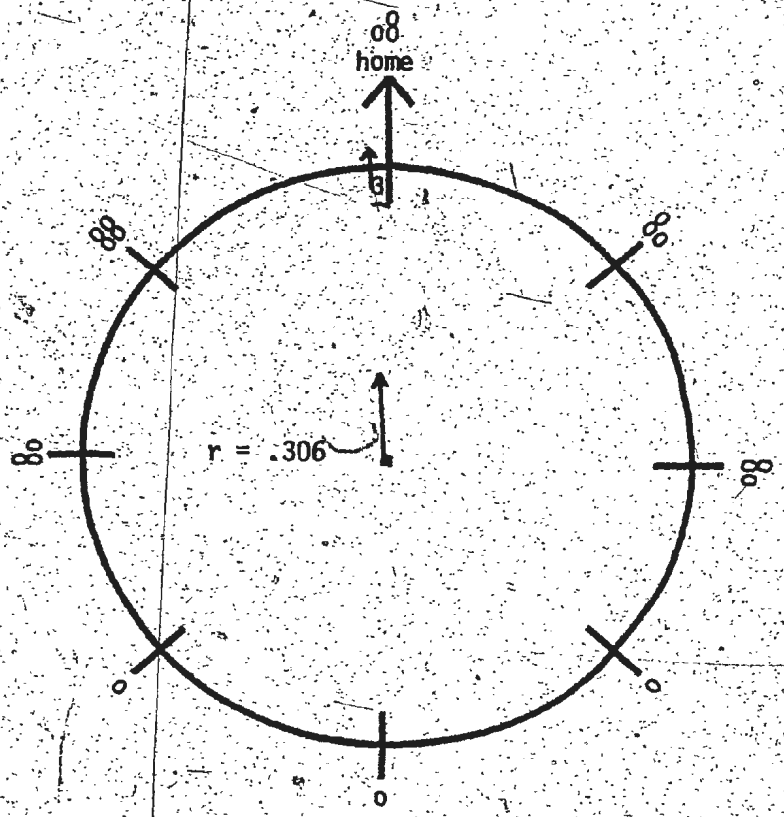

home
θ
r = .306

Table 11. Test for randomness in orientations of released fish by means of 'Rao test'.

Treatment Groups	N	Length of mean vector r *	Calculated U values **	Significance level (p)	Av. latency of orientations (sec.)
Normal	44	.267	294	$p < .01$	4.7
Blind	38	.240	284	$p < .01$	80.1
Anosmic	30	.236	168	$p < .01$	11.7
Unilaterally Anosmic & Blind	19	.306	208	$p < .01$	9.0

* an 'r' value of 1 indicates perfect homeward orientation

** from Batschelet (1972) U = sum of deviations as test statistic

*** Table 6 Batschelet (1972) Critical value for the test statistic U in degrees

The length of the mean vector is denoted by 'r'. An r = 1 represents perfect orientation in one direction and r = 0 represents totally random orientation. It is calculated from:

$$r = \sqrt{\bar{X}^2 + \bar{Y}^2}$$

where $\bar{X} = \frac{1}{n}\sum \cos\alpha_i$; for the angles α_i $(i = 1 \ldots n)$ in a sample of fish run on the orientation disc. Similarly $\bar{Y} = \frac{1}{n}\sum \sin\alpha_i$ (Batschelet 1972).

The mean vectors were corrected by multiplying r by the grouping factor 1.0262. This was required because orientations were limited to eight directions. The grouping factor was obtained from Table 12.1 in Batschelet (1965).

The mean directions (θ) of the orientations were obtained by solving the equations; $\cos\theta = \frac{X}{r}$ and $\sin\theta = \frac{Y}{r}$, for the orientations of each group.

Table 12 gives the calculated 'u' values for the four treatment groups. ('u' is calculated according to:

$$u = \left(\frac{N}{2}\right)^{\frac{1}{2}} \cdot V$$

where V represents clustering of orientations in the home direction and is equivalent to: $r \times n \times \cos(\theta - \theta_0)$. Critical

Table 12. Modified Rayleigh Test (V test) to compare randomness of orientations relative to a predicted direction (home).

Treatment Groups	N	Home direction - mean direction	u* calc.	p Rejection randomness
Normals	44	17.1°	2.395	< .01
Blinds	38	12.0°	2.046	< .05
Anosmics	30	173.6°	0	n.s.
Singly Anosmic + Singly Blind	19	3.1°	1.881	< .05

* $u = (\frac{2}{n})^{\frac{1}{2}} \cdot V$ i V denotes the homeward component of mean vector (Batschelet 1972)

ii $V = R \cos$ (home - mean directions); $(\theta - \theta_0)$

iii when $(\theta_0 - \theta) > 90^0$ the V becomes 0 since $\cos 90^0 = 0$

Table of critical values of the test statistic u of Modified Rayleigh (V) Test from Table 2 Batschelet (1972).

values for the test statistic 'u' were obtained from Table 2 of Batschelet (1972).

The null hypothesis of random distribution of orientations with respect to a home direction was rejected ($p < .05$) for normal fish, blind fish and unilaterally blind and anosmic fish. The alternate hypothesis of a preference of orientations around a predicted home direction is valid for these groups. This indicates that visual contact is not essential for orientation to home sites. It suggests that fish maintain some other sensory contact with the home site.

Although anosmic fish do not orient in the home direction, they did show non-random orientation. A calculated 'u' value of 0 was obtained which indicated random orientations with respect to the predicted home direction. A calculated 'u' value of 0 was obtained in Table 12 for the anosmic fish because when the difference between the home direction and the mean direction is equal to or greater than 90^{0} the homeward component of the mean vector disappears. The calculated 'u' value contains a cosine function and the cosine of $90^{0} = 0$. The inability of olfactory impaired fish to orient in a home direction indicates olfaction is likely the means of sensory contact with the home site.

The latencies with which groups of fish released on the disc orientated are given in Table 11. Normal fish had the shortest

latencies while blind fish had the longest.

ACTIVITY PATTERN OF NORMAL AND SENSORY IMPAIRED FISH

INTRODUCTION SECTION IV

It has been reported (LeDrew and Green, 1975) that Ulvaria subbifurcata is nocturnal but detailed observations of individual fish have not been reported. Recovery data on tagged fish could best be made by sightings of fish when they were out of shelter during peak activity. Therefore field studies of the activity pattern of U. subbifurcata were carried out by night observations on single dives of approximately 20 minutes duration. Activity of the fish over the main hours of night diving was also determined.

In the laboratory attempts were made to determine if groups of normal, anosmic and blind fish show the same temporal pattern of activity. The activity pattern of individual tagged fish was also considered.

Observations on the feeding of normal, anosmic and blind fish were made in the laboratory to give some indication of the ability of sensory deprived fish to survive in the field.

METHODS AND MATERIALS

Field Work

To study the activity patterns of a population of shannies at Broad Cove, dives were carried out every two hours from 2030 hours on August 9 until 0630 hours on August 10. During each dive a check was made of marked home sites known to be occupied by tagged shannies. Tagged fish seen during each dive were recorded.

At the beginning and end of these dives a swim was made 1 - 2 m above the substrate along a 33 m marked transect. An area approximately 1.8 m to each side of the transect line was scanned with a light and the number of exposed shannies was recorded.

To determine the relative proportion of the population of shannies active during the hours that most of the night diving was done, transect counts of exposed fish were made following tag recovery dives between July 16, 1976 and August 13, 1976. The transect counts were taken at times approximately one to five hours after sunset.

Laboratory Work

A. Group Activity Patterns

In the laboratory during March 1977, studies were done to see if groups of normal, anosmic and blind fish showed the same temporal patterns of activity. Twenty-four *U. subbifurcata* ranging in

size from 91 mm to 140 mm were collected at St. Phillip's. These were divided into three equal numbered groups of normal, blind and anosmic fish. The average length for each group was 109 mm, 109 mm and 113 mm respectively.

At Logy Bay a 182.8 cm long x 60.9 cm wide x 10.2 cm deep tray was divided into 15.2 cm squares with transparent nylon line suspended above the water surface (Figure 9). In the centre of the tray a section 30.5 cm x 60.9 cm contained rocks and scallop shells that served as shelters. There was a constant flow of sea water through the tray and an approximate 12 hr l : 12 hr d light cycle was maintained. The tray was separated from the rest of the room by a sheet of black plastic.

Four normal, four anosmic and four blind fish were placed in the tray at a time. Twenty-four to thirty hours following capture and just before dark, observations were begun. At one hour intervals a small hand light was used to note if individuals were out of the shelters and, if so, their position in the tray. A Mann-Whitney U test was employed to compare the data for treated and normal fish.

B. Individual Activity Pattern

To obtain some idea of the amount of time a fish might spend out of shelter during the night and the pattern of resightings of a fish over four separate search intervals, the data for the fish studied

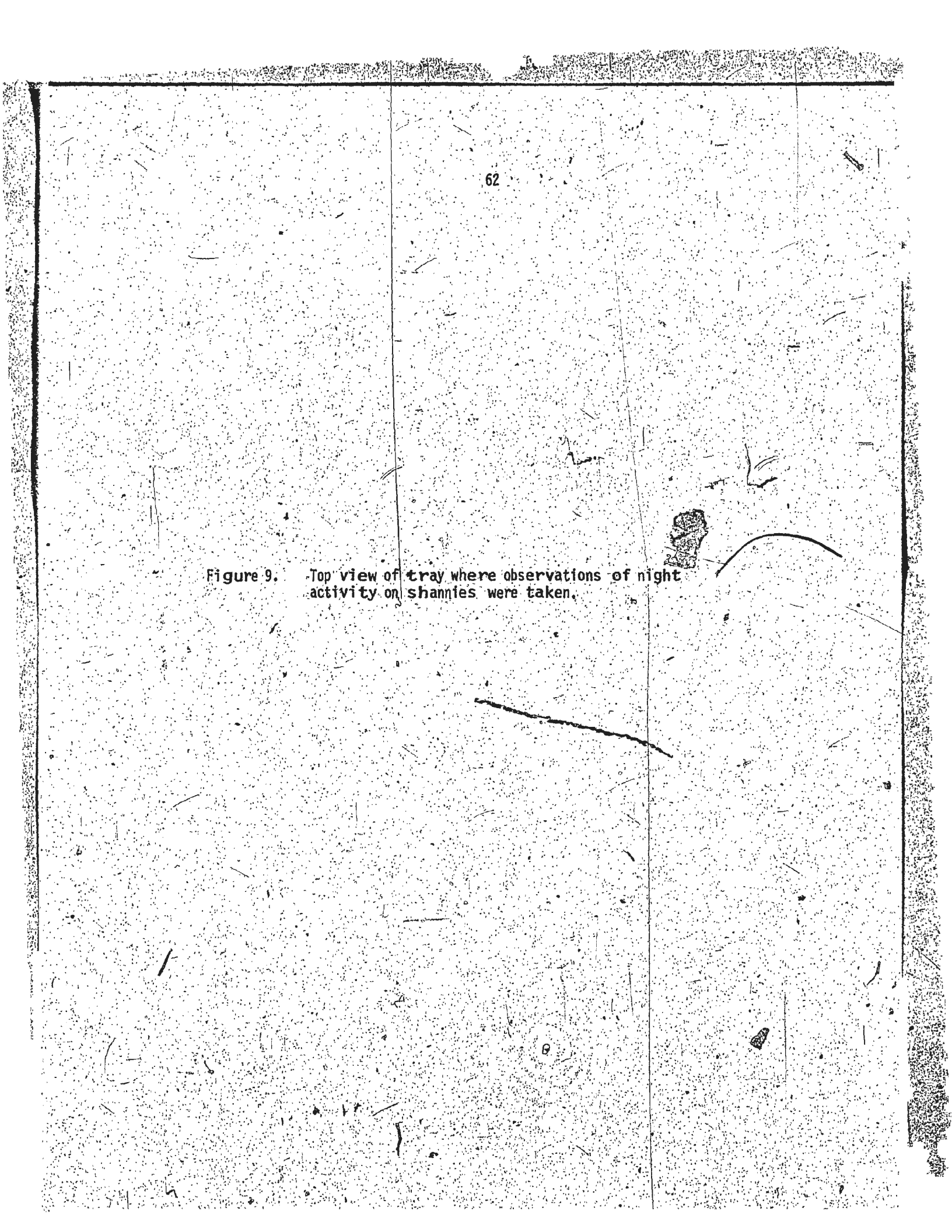
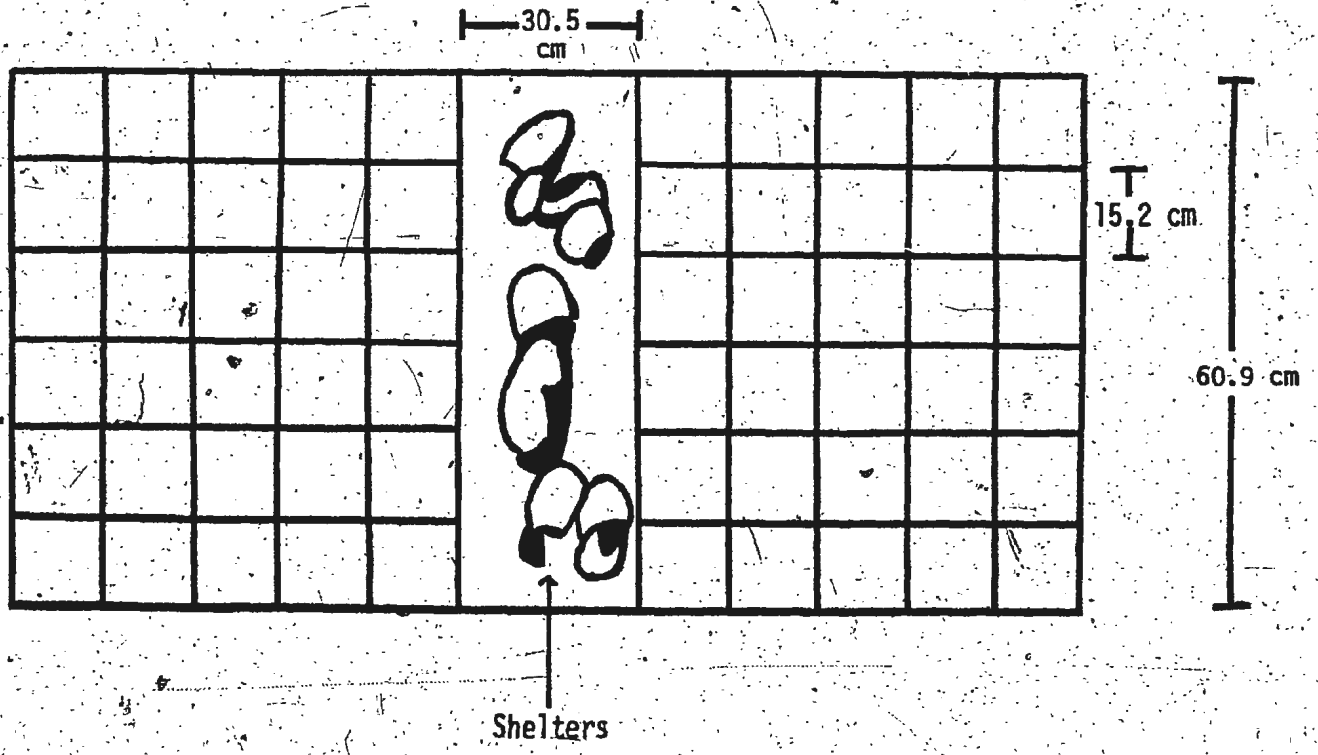


Figure 9. Top view of tray where observations of night activity on shannies were taken.


30.5 cm
15.2 cm
60.9 cm
Shelters

in the laboratory in March 1977 was analyzed in a second manner. The data for twelve normal, twelve blind and twelve anosmic fish were arranged to show the proportions of fish sighted on all four intervals, on three of the intervals, on two consecutive intervals, on two non-consecutive intervals and on one observation interval. Included was the data for another group of fish observed in an identical way in May 1977. This group of four normal, four blind and four anosmic fish ranged in size from 95 to 123 mm. The observation times were chosen to correspond to the times when tagged fish were recovered on the field study of all-night activity pattern.

RESULTS

Field Studies

During the night of August 9-10, 20 sightings of tagged fish were made. The numbers of tagged fish seen on each dive is given in Figure 10. These 20 tag sightings represented 12 of the 16 tagged fish known to be occupying home sites.

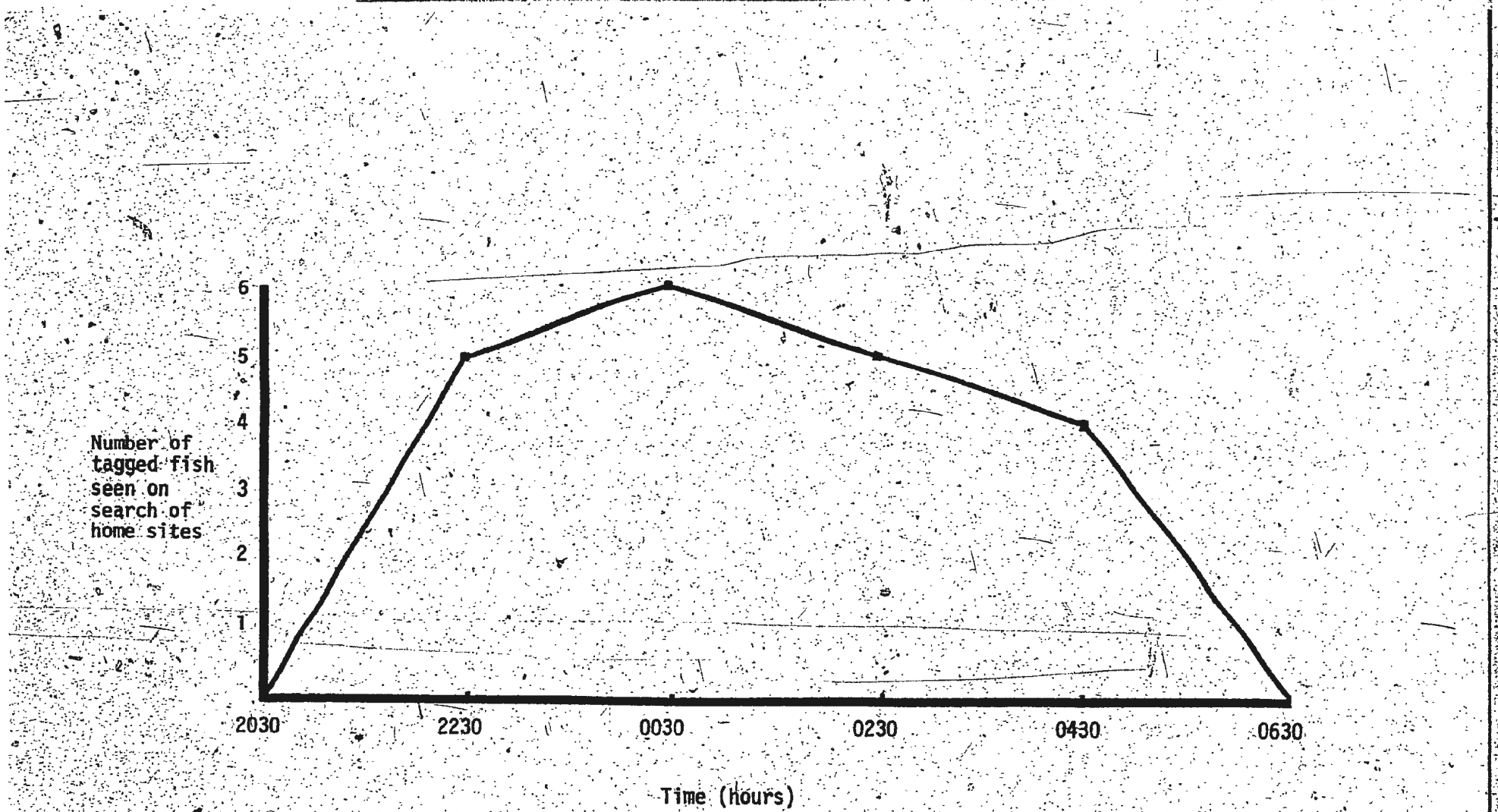
Of the 16 tagged fish in the home sites, 12 were normals, 3 were anosmic and one was blind. Ten (83.3%) of the twelve tagged fish seen on the night dives of August 9-10 were normal fish. The other two were anosmic.

The ten tagged normal fish were seen one to four times during the night. One fish was sighted during each of the four dives, one during three consecutive dives and one during two consecutive dives. (Total 3 fish). Two fish were seen on two non-consecutive dives and five were seen once.

The number of fish seen during the transect counts taken on August 9-10 are given in Figure 11. The largest number of shannies was seen at 0030 hrs. The largest number of tagged fish was also observed on this dive.

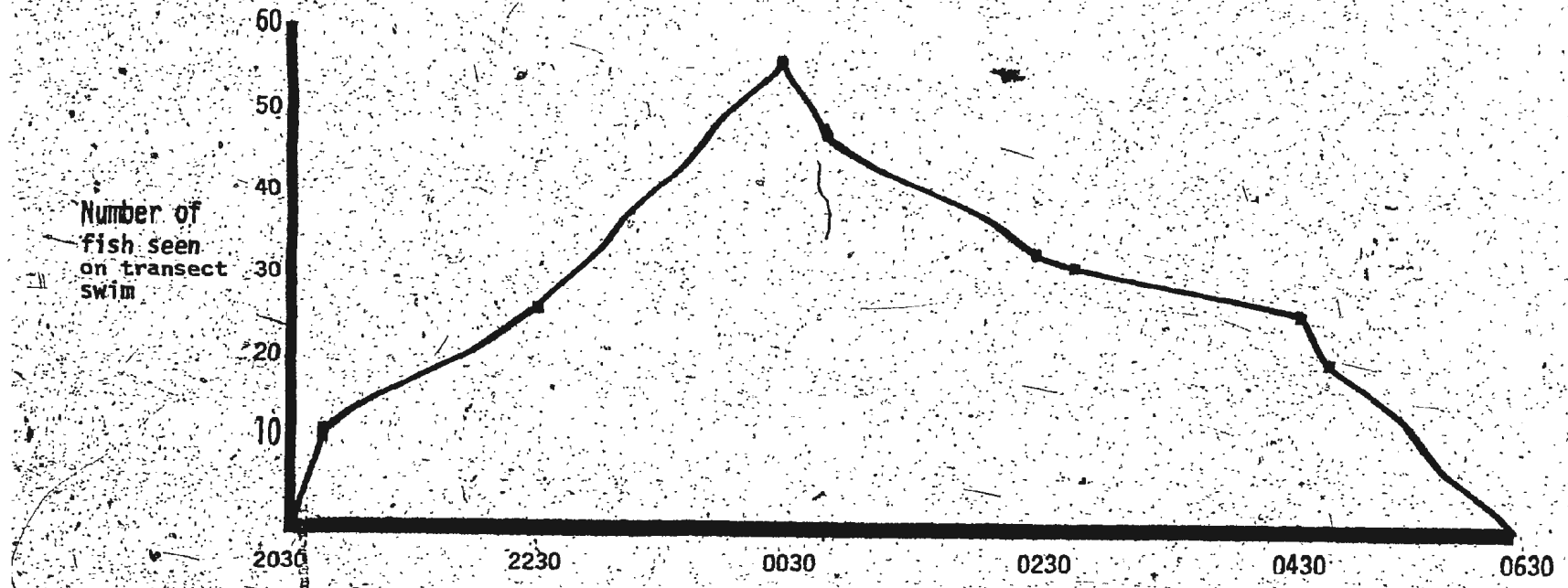
The data for the transect counts made between July 16, 1976 and August 13, 1976 are given in Figure 12. These data are presented

Figure 10. Number of tagged fish observed on each dive to check home sites for pattern of all-night activity in fish.



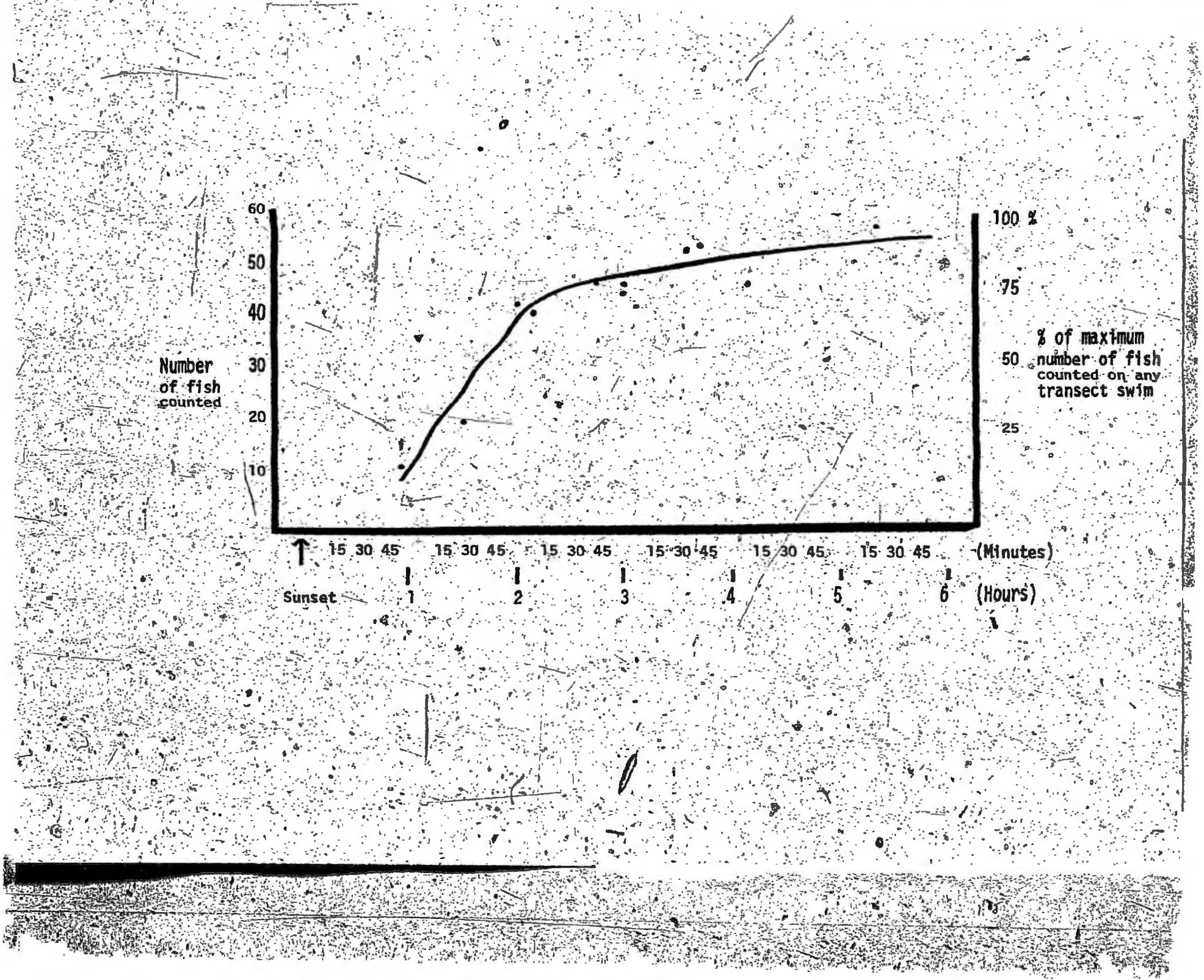
Night of August 9 - 10, 1976

Figure 11. The number of fish observed on transect swims during study of all-night activity pattern. (Night of August 9 - 10, 1976)



Night of August 9 - 10, 1976

Figure 12. Observations of fish exposed on transect from July 16 to August 13, 1976.


60
50
40
30
20
10
Number of fish counted
100 %
75
50
25
% of maximum number of fish counted on any transect swim
15 30 45 15 30 45 15 30 45 15 30 45 15 30 45 15 30 45 (Minutes)
Sunset
1
2
3
4
5
6
(Hours)

as counts at specific intervals following sunset. The time of sunset was obtained from the Atmospheric Environment Service.

Most of the night diving work, both capturing fish and searching for tagged fish, was done 2 to 4 hours after sunset. Seventy percent to ninety-two percent of the maximum number of fish likely to be seen in a given area will be visible during this time period (Figure 12).

Laboratory Studies

The laboratory data on the number of normal, blind and anosmic fish occurring out of shelter at 13 observation periods between 1800 hours and 0600 hrs are represented in Figure 13. When a Mann-Whitney U test is applied to the data the null hypothesis of no significant difference in the occurrence out of shelter of different groups of fish, over the 13 observations, cannot be rejected. Table 13 shows the comparison of the blind and anosmic fish with the normals and with each other. It also gives the calculated and critical U values for the Mann-Whitney U test in each comparison.

When the light was on, no normal or anosmic fish were ever observed to be out of their shelters. Blind individuals were occasionally found resting in exposed sites during hours of light in the laboratory.

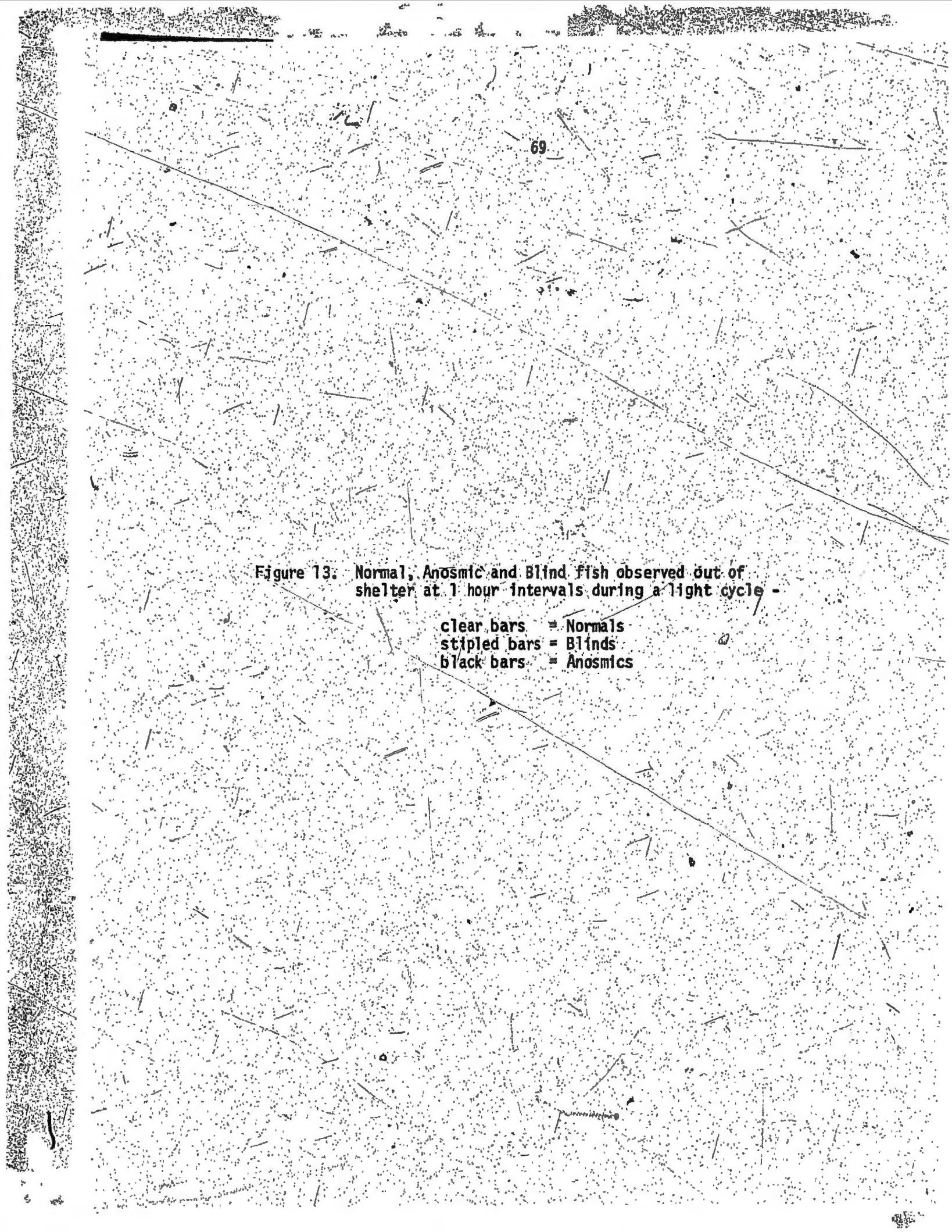


Figure 13. Normal, Anosmic and Blind fish observed out of shelter at 1 hour intervals during a light cycle -

clear bars = Normals
stipled bars = Blinds
black bars = Anosmics

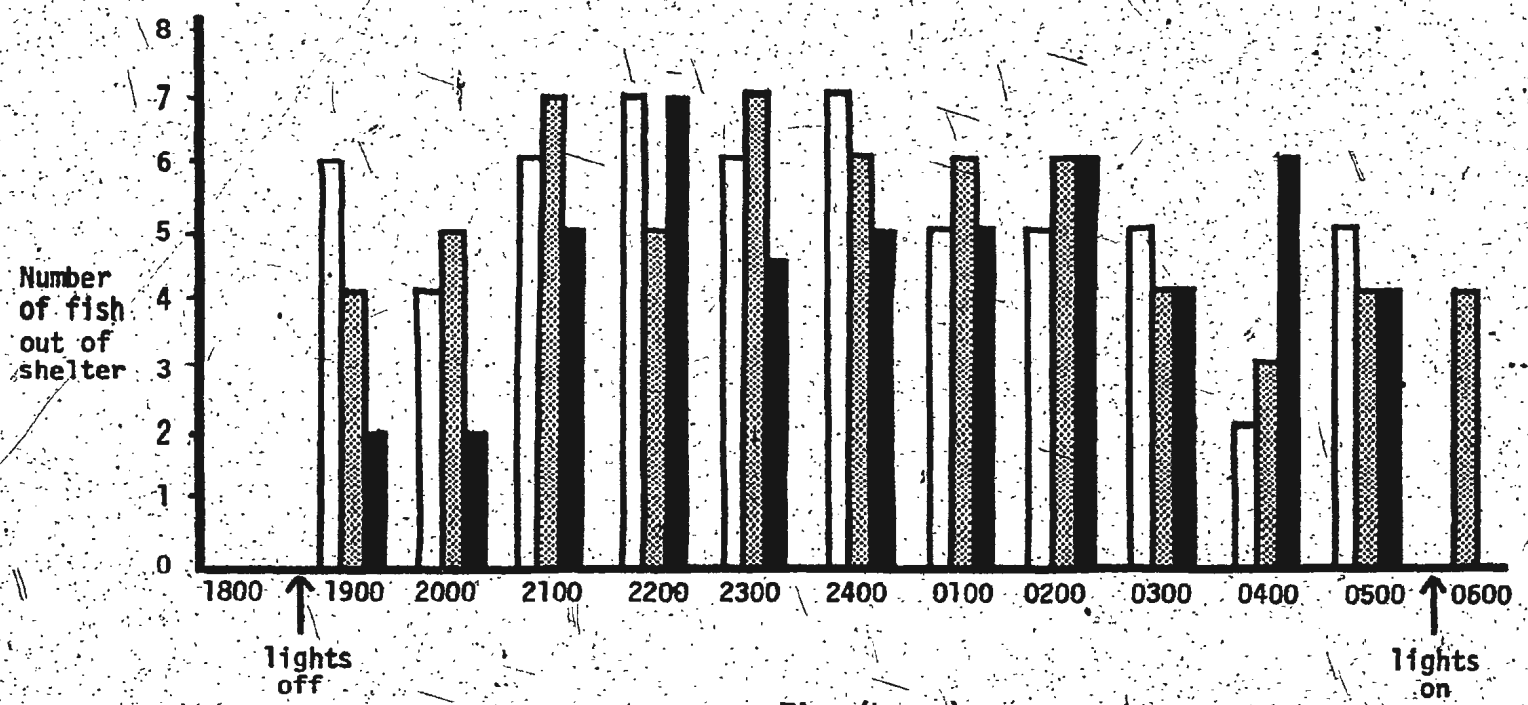

Number of fish out of shelter
0
1
2
3
4
5
6
7
8
1800
1900
2000
2100
2200
2300
2400
0100
0200
0300
0400
0500
0600
lights off
lights on
Time (hours)

Table 13. Comparison of occurrence out of shelter of Normal, Blind and Anosmic fish over 13 observations; from 1800 hrs. to 0600 hrs.

	Mann Whitney U value	Critical U*	P‡ at .05
Normal vs Blind	82.5	45	ns
Normal vs Anosmic	70	45	ns
Blind vs Anosmic	69.5	45	ns

* Obtained from Table K in Siegel (1956).
Obtained table of critical values of U in the Mann-Whitney test tested for a two tailed test at $p < .05$; $n_1 = 13$, $n_2 = 13$

‡ ns - no significant difference

The activity patterns of individual fish are represented in Table 14. Over four observations any one fish may be sighted out of shelter, four times, three times, twice at non-consecutive observations, once during the night or it may not have been sighted at all. A large proportion of individual fish appear to remain out of shelter for an extended period of time during the night. Ten of twelve normal fish, 8 of 12 blind fish and 7 of 12 anosmic fish were sighted on 2 or more consecutive observations. Only 1 of 12 normal fish and 2 of 12 anosmic fish were seen during non-consecutive observations.

Feeding Observations

One consideration in this study was whether surgically treated fish were able to feed when released in the field. Some observations on this question were made in the laboratory between May and August 1976. While only two out of six normal fish held in a tray with flowing sea water would take sea urchin gonads when presented 1 - 2 cm in front of the fish with a pair of tweezers, seven out of nine blind fish would take sea urchin gonads when presented in the same manner. This indicates blind fish are able to take food when available. Fifteen minutes after sea urchin gonad was introduced to the tray, all fish in the tank were out of their shelters. This was done during the night in May.

In August 1976 the fish in the laboratory were being maintained on a diet of sliced frozen caplin. When fish were deprived for

Table 14. Number of tagged fish being observed out of shelter on four observations through the dark period.

	# Times Observed					
	4	3	2 consecutive	2 non-consecutive	1	0
Normals	1	4	5	1	1	0
Blinds	1	3	4	0	1	3
Anosmics	4	2	1	2	2	1

24 to 48 hours, it took approximately 1 - 2 minutes for them to emerge from shelter when food was placed in the tray. This was done during light when the fish normally remain in their shelters. Normal and blind fish were the first to appear when food was presented suggesting that olfaction played a role in identifying the presence of food. The anosmic fish appeared after the blind and normals. They were able to seize a piece of food as quickly as normal fish once it was seen. It took the blind fish more time to seize the sliced caplin and required a series of short movements in various directions before reaching the food. They were successful in obtaining and ingesting the sliced caplin. This behaviour suggested vision plays a role in seizing the food in normal fish.

There was evidence in both May and August of a size dependent priority in obtaining food when a restricted amount was provided.

GENERAL DISCUSSION

In studying the roles of olfaction and vision in the homing and orientation mechanisms of Ulvaria subbifurcata by the displacement methods used in this study, it was first necessary to know the likelihood of resighting tagged fish in their home site. U. subbifurcata is a benthic fish that lives in holes in the sublittoral zone. They come out during the night to forage (LeDrew and Green, 1975). Recovery data on tagged fish could only be made by diving during the night in order to catch fish without disturbing their home site. The results of the experiments described on home site fidelity indicate that normal and anosmic fish did not differ significantly from each other in the likelihood of being resighted when placed in their home sites. A slightly lower proportion of anosmic fish (78%) than normal fish (94%) were resighted following removal for tagging and treatment. Blind fish on the other hand had a significantly lower likelihood of being resighted with only 39% of those blind fish released at their home site resighted.

It was thought that this difference in the recovery of normal, anosmic and blind fish might be related to differences in temporal patterns of activity due to treatment. However, the results of the laboratory observations reported in Section IV indicated that normal, anosmic and blind fish did not differ significantly in activity pattern throughout the night.

This laboratory evidence leads one to believe that if blind fish are in the home site, they are as likely to be seen as are anosmic and normal fish for an equivalent amount of search effort. The fact that blind fish are not seen in as large a proportion or with as many resightings per individual as normal and anosmic fish suggests that blind fish either have a lower fidelity to their home sites or are subject to higher mortalities. The lower proportions of blind fish resighted was not likely to be due to starvation or as a direct result of surgical treatment. Laboratory evidence showed that the removal of the lenses from the eyes of shannies produced no mortalities. The ability of blind fish to feed was indicated by observations in the laboratory. Data on the ability of blind fish to feed in the field was not obtained, however considering that their diet consists of such things as nereid worms and tube feet of sea urchins (LeDrew and Green, 1975) and considering that they are nocturnal, it is likely that vision is not essential to their feeding.

Several things point to the fact blind shannies might be exposed to a higher level of mortality. The laboratory results in Section IV showed that normal and anosmic fish were never observed out of shelter during periods of light while blind fish sometimes were out. If blind fish stayed out longer in the field at elevated light intensities, it is likely that they would be subjected to predation by *Tautogolabrus adspersus* and *Myoxocephalus octodecemspinosus*.

The behaviour upon release of blind fish in home sites described in Section I supports the idea of predation mortality. When released to home sites, blind fish remained exposed for varying periods of time before seeking shelter. This was frequently longer than two minutes. By comparison, normal fish were the quickest to seek permanent shelter thought to be their home sites. Anosmic fish were quick to seek the shelter of the substrate but moved around somewhat before they obtained permanent shelter. Because of the time spent out of shelter, blind fish were susceptable to predation by Myoxocephalus octodecemspionosus which were active in the study area at night.

The likelihood of being resighted after seven days for fish known to be in their home site decreased by the largest percentage for blind fish compared to normal and anosmic fish. It is thought that this decrease reflects to some degree the level of predation on each group since starvation would not be a factor during this time period.

The time period used to search for tagged fish (results Section IV), was considered a good time to search for fish in their home site. Seventy to ninety-two percent of the maximum number of fish out of shelter at any one time were present at 2-to-4 hours following sunset. A large proportion (50%) of normal, blind and anosmic fish remained out of their shelters for longer than two consecutive hours. A repeated number of searching dives made throughout the 2 - 4 hour post-sunset time interval was expected to allow resighting of the

majority of tagged fish present in their home sites of all groups.

The results of the displacement experiments described in Section II confirm the work of Green and Fisher (1977) that U. subbifurcata will home after displacement. Ninety-four percent of normal fish displaced approximately 19 m were resighted in their home sites. The effect of sensory impairment was to decrease the number of displaced tagged fish resighted in their home site. The decreased proportion of tagged blind fish resighted following displacement was not significantly different from the proportion of those resighted following replacement in the home site. However the proportion of anosmic fish resighted following displacement was significantly lower than the proportion of fish resighted following replacement in their home site. Thus the importance of olfaction is indicated in the homing mechanism. Vision does not play an essential role in the homing process.

The suggestion that anosmic fish may have been able to return to their home site but not recognize it is not supported by the observations of anosmic fish released at their home sites. These fish were more quick to enter the home shelter than were blind fish. It is likely that these fish use visual cues to recognize and move about the home site. The evidence of anosmic fish released to their home site remaining there and the fact that there was no significant difference between the normal and anosmic fish remaining in the home site, supports the suggestion that the fish may use visual cues to recognize the home site.

Homing experiments done with fish that had been tagged and returned to home sites for a period of time (longer than 8 days), before being displaced an average of 7.6 m show a higher homing was obtained with anosmic fish. Five of eight (62%) fish homed over 7.6 m compared to 5 of 17 (29%) fish homing when displaced approximately 19 m suggesting a visual recognition over short distances or possible olfactory regeneration.

An increased ability of anosmic shannies to home over short distances could occur in two ways. (1) It is possible that visual recognition of an area larger than the home area occurs and when displaced a short distance anosmic fish are able to home using visual cues. Familiarization with visual landmarks of an area larger than the home range could occur during a juvenile stage of development or through the move to a new home site. (2) Return to the home site by chance through random movements would have a much greater probability for fish displaced a short distance.

The long distance (35 m) and short distance displacements (12 m) in one direction of anosmic fish show there was significantly better ($p \leq .05$) homing in fish displaced 12 m. Two of nine fish displaced 12 m were resighted while none of 10 fish displaced 35 m were resighted. Green and Fisher (1977) demonstrated that normal fish easily home 33 m and recoveries after 285 m displacement were reported.

It is also possible that some degree of olfactory regeneration may have occurred during the eight or more days in the ocean. This could have allowed homing. Von Baumgarten and Miessner (1968) reported regeneration in teolost olfactory system. However their regeneration was studied 60 to 90 days following surgery.

The return of a fish to a place formerly occupied implies the acquisition of a familiarity with a restricted area. This requires that the fish are able to perceive, learn and remember features of the restricted area and be able to distinguish them from 'strange' areas (Gibson, 1969): U. subbifurcata has been shown to be able to remember and distinguish familiar features of a home site when removed for twenty-four hours. But what is the effect on homing of fish removed from the home site for a longer period of time.

When shannies were removed from their home sites for 51 to 58 days only 3 of 15 (20%) normal fish homed. No blind or anosmic fish homed. This initially suggests an inability of the shannies to remember features of the home site for this length of time. However there is also the possibility that competition is involved. During the 51 to 58 day absence of the fish it is likely the home sites were occupied by other shannies. Recent laboratory studies have demonstrated that shannies are highly aggressive at least during spring and summer (Green, personal communication). Newcomers could have obtained dominance in the sites by the time the original occupants returned.

Two dives were made one and three days prior to the release of the original residents, to remove competitors from the home sites of the original fish. It seems unlikely however that a large number of newcomers would be removed from the area on only two dives.

In this study straying occurred three times. Two instances involved displaced anosmic fish that were occupying new home sites outside the area of their previous home ranges. These two fish were found in home sites from which the fish had been collected for another experiment. The third straying fish was a normal fish that had been held out of its home site 51 - 58 days. Its occupancy of a new home site may have been due to an inability to recognize its home site or it may have been displaced from its original home site through competition.

To know that olfaction is involved in homing is only part of understanding the homing mechanism(s). The mechanism of homing could involve a random search for the home site, directed movements by means of sensory contact with the home site or by navigation which is the ability to determine position relative to the home site when out of contact with it (Khoo, 1974, Adler, 1963). Khoo (1974) presented evidence that olfactory cues were involved in the homing behaviour of O. maculosus but he did not determine specifically the role played by olfaction. Gibson (1967) suggested that Blennius pholis and Enophrys bubalis are capable of recognizing their home pool after

coming in contact with it following random movements. Green (1971) suggested that O. maculosus exhibit directed movements back to their home pool. These conclusions however were based on indirect evidence such as the amount of straying and the time required to home. The previous work of Green and Fisher (1977) demonstrated that U. subbifurcata can orient or 'steer' in the direction of a home site from well outside its home range. Indirect evidence from that study suggested olfaction was involved in the orientation response.

The further orientation experiments described in this study obtained direct evidence on the sensory mechanisms involved in homing and orientation. These orientation experiments demonstrated that normal, blind, anosmic and unilaterally blind and anosmic fish oriented non-randomly upon release. The orientations of normal, blind and unilaterally blind and anosmic fish did not differ significantly from the home direction. The orientation of the anosmic fish did differ significantly from the home direction.

These results indicate that homing does not occur by random search for normal fish orient in the direction of the home site upon release. Sensory contact with the home site, that is not visual, is indicated. The inability of anosmic fish to orient in the home direction suggests that olfaction is the sense involved.

The ability of unilaterally blind and anosmic fish to orient in the home direction indicates that bilateral sensory input is not

required in homing.

It is possible that orientation through reception of local electrical or magnetic fields may be occurring. It has shown that fish (Anguilla anguilla) are able to perceive electric fields (McCleave and Rommel, 1972) and that catfish (Ictalurus nebulosus) are able to use electric fields for directional information (Peters and van Wijland, 1974). Cauterization of the olfactory rosettes of U. subbifurcata could interfere with perception of such cues by the fish. However this awaits further study.

The cue to which the anosmic fish were orienting in the orientation chamber (Results, Section III) was unknown.

Khoo (1974) outlined three basic problems that have to be considered when dealing with the mechanism of homing. The first problem is concerned with the orienting or 'steering' mechanism. The results of the present study indicate that olfaction is the orienting or steering mechanism and that U. subbifurcata homes by means of sensory contact with the home site. The second problem deals with how a fish recognizes the home site when it arrives. Again the results reported here indicate that olfactory identification with blind fish allows U. subbifurcata to recognize the home site. However visual recognition may also play a role in actual home site recognition. This is evidenced by the ability of anosmic fish replaced in their home site to remain there, and the ability of anosmic fish displaced short

distances to home. The third problem deals with the source of the cues. Recent laboratory evidence (Green and LeBlanc, personal communication) suggests there is something in the water of a home site that the fish is able to discriminate. Other authors (Cooper and Scholtz, 1976; Cooper et al, 1976) have been able to successfully imprint Salmo gairdneri and Oncorhynchus kisutch to a single olfactory stimulus. However the specific substance that provides the olfactory cue for U. subbifurcata is unknown.

LITERATURE CITED

Adler, H. E. 1963 Sensory factors in migration. Anim. Behav. 11: 566 - 577.

Batschelet, Edward 1965 Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. American Institute of Biological Sciences, Washington, D.C. Monograph 1: 57 p.

Batschelet, Edward 1972 Recent statistical methods for orientation data. In- S. R. Galler (et al)(eds.) Animal Orientation and Navigation. National Aeronautics and Space Administration (N.A.S.A.), Washington, D.C.

Bebe, W. 1931 Notes on the gill-finned goby, Bathygobius soporator, Zoologica XII: 55 - 56.

Carlson, H. R. and Haight, R. E. 1972 Evidence for a home site and homing of adult yellowtail rockfish, Sebastes flavidus, J. Fish. Res. Bd. Canada 29: 1011 - 1014.

Cooper, J. C. and Scholz, A. T. 1976 Homing of artificially imprinted steelhead (rainbow) trout, Salmo gairdneri. J. Fish. Res. Bd. Canada 33: 826 - 828.

Cooper, J. C., Scholz, A. T., Horrall, R. M., Hasler, A.D., and Madison, D. M., 1976 Experimental Confirmation of the Olfactory Hypothesis with Homing, Artificially Imprinted Coho Salmon, Oncorhynchus kisutch. J. Fish. Res. Bd. Canada 33: 703 - 710.

Gerking, S. D. 1959 The restricted movements of fish populations, Biol. Rev. (Camb.) 34: 221 - 242.

Gibson, R. N. 1967 Studies on the movements of littoral fish, J. Anim. Ecol. 36: 215 - 234.

Gibson, R. N. 1969 The biology and behaviour of littoral fish, Oceanogr. Mar. Biol. Ann. Rev., 7: 367 - 410.

Green, J. M. 1971 High tide movements and homing behaviour of the tidepool sculpin, Oligocottus maculosus, J. Fish. Res. Bd. Canada 28: 383 - 389.

Green, J. M. 1973 Evidenee for homing in mosshead sculpin, Clinocottus globiceps, J. Fish. Res. Bd. Canada 30: 129 - 130.

Green, J. M. 1975 Restricted movements and homing of the cunner, Tautogolabrus adspersus (Walbaum) (Pisces: Labridae), Can. J. Zool. 53 (10): 1427 - 1431.

Green, J. M. and Fisher, R. 1977 (in press) A field study of homing and orientation to the home site in Ulvaria subbifurcata (Pisces: Stichaeidae), Can. J. Zool.

Gunning, G. E. 1959 The sensory basis for homing in the longear sunfish, Lepomis megalotis megalotis (Rafinesque), Invest. Indiana Lakes Streams 5: 103 - 130.

Khoo, H. W. 1974 Sensory basis of homing in the intertidal fish Oligocottus maculosus, Girard, Can. J. Zool. 52(8): 1023 - 1029.

LeDrew, B. R. 1972 Selected aspects of the biology of the radiated shanny, Ulvaria subbifurcata (Storer) 1839 (Pisces Stichaeidae), M.Sc. thesis. Memorial University of Newfoundland, St. John's, Newfoundland.

LeDrew, B. R. and Green, J. M. 1975 Biology of the radiated shanny, Ulvaria subbifurcata, Storer in Newfoundland (Pisces: Stichaeidae), J. Fish. Biol. 7: 485 - 495.

McCleave, J. D. and Rommel, S. A. 1972 Oceanic electric fields perception by American eels. Science, Vol. 176 (4040): 1233 - 1235.

Peters, R. C. and van Wijland, F. 1974 Electro orientation in the passive electriccatfish, Ictalurus nebulosus, J. Comp. Physiol. 92(3): 273 - 280.

Siegel, Sidney 1956 Nonparamentric Statistics for the Behavioural Sciences, McGraw-Hill Book Company, Toronto.

Sokal, Robert R. and Rohlf, R. James 1969. Biometry: The Principles and Practice of Statistics in Biological Research, N. H. Freeman and Co., San Francisco.

Von Baumgarten, R. J. and Miessner, H. J. 1968 Regeneration in teolost olfactory system in "The Central Nervous System and Fish Behaviour", Ed. David Ingle, University of Chicago Press, Chicago.

Williams, G. C. 1957 Homing behaviour of California rocky shore fishes, Univ. Calif. Publ. Zool. 59: 249 - 284.

Winn, H. E., Salmon, M. and Roberts, N. 1964 Sun compass orientation by parrot fishes, Z. Tierpsychology 21: 798 - 812.