AGGRESSION AND TERRITORIALITY IN STICHAEUS PUNCTATUS (PISCES: STICHAEIDAE)

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AGGRESSION AND TERRITORIALITY IN *STICHAEUS PUNCTATUS* (PISCES: STICHAEIDAE).

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ABSTRACT

Laboratory experiments demonstrated that underyearling Stichaeus punctatus are territorial in tanks of 4050 cm^2 total bottom area or more for the periods September to January and July through August. In the field, territory holders won a significant number of encounters with intruding fish and were observed to occupy territories from August to November. In laboratory experiments, prior residency was found to be a factor in the territoriality of underyearlings. Older fish were never observed to establish territories in the laboratory or field during the study but appeared to show area affinities for a particular area of the substrate in the field.

Underyearling aggressiveness was influenced by time of year, water temperature and photoperiod. Aggressive levels were low for the period January to June and high from July to December. Photoperiod affected the intensity of underyearling aggressiveness but not the seasonality of it. The aggressive level decreased sharply in August when the underyearlings completed their first year of benthic life. Older fish were less aggressive and no seasonal influences were noted. The rate of interaction between the two age groups was low and in all encounters between them the older fish were always dominant.

Underyearlings preferred a rocky habitat when presented with a choice. The isolation and social aspects of aggression and territoriality were examined but the relative importance of these two factors in the territoriality of this species was not determined.

The social organization operating between the two age groups and its ecological implications during their period of inshore life are discussed.

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GENERAL INTRODUCTION

Stichaeus punctatus, the arctic shanny, is a benthic, circumpolar arctic species. Farwell et al., (in press) describe the known aspects of the species' life history in the Northwest Atlantic. Spawning probably occurs during mid-winter. Larval S. punctatus appear in the plankton in Logy Bay around the beginning of June each year. The larvae settle from the plankton onto the substrate from mid-July to the beginning of August. Older arctic shannys appear in the inshore areas of Logy Bay (> 30 m) around the beginning of July. The inshore populations of S. punctatus have varied greatly from year to year. A high mean number of 8.3 shannys per square metre was reported in August 1972 while at the same site in 1973 a mean number of 1.4 shannys per square metre was reported. S. punctatus disappears from shallow water in Logy Bay between November and January of each year. Farwell (1970) and Farwell and Green (1973) have published the only accounts of the species' behaviour.

> It would seem self-evident that an animal can respond only to the environment that its sense organs, its motor equipment and its central nervous organization, both innate and acquired make accessible to it; and hence any enquiry designed to describe, understand or explain its behaviour should necessarily use this environment as one of the variables that conditions the behaviour. (Adams, 1962).

This statement rationalizes the association between the behaviour (aggression and territoriality) and environment of Stichaeus punctatus which formed one of the basic questions in this enquiry. That question briefly stated was: How does the aggression of S. punctatus relate to its survival in the natural environment, namely Logy Bay, Newfoundland?

Aggression or agonistic behaviour typically disperses animals through the environment. The resulting dispersal often is related not only to intraspecific aggression but also to other features of the environment. One of the common results of intraspecific aggression is the formation of territories. The literature dealing with aggression and territoriality in fish is quite extensive (Greenberg, 1946; Carpenter, 1958; Zumpe, 1965; Van dem Assem, 1967; Gibson, 1968; Itô, 1970; Farwell, 1970; Stephens, 1970; Clarke, 1970 and 1971; Myrberg, 1972; Phillips, 1971; and Ewing et al., 1973) with the majority of papers dealing with the occurrence of these behaviours in adults. The apparent reason for this is that few underyearling fish display both aggression and territoriality. This study was concerned with these behaviours in underyearlings as well as adults. Only two of the above authors have dealt with these behaviours in underyearlings. Gibson (1968) in a paper on the behaviour of Blennius pholis dealt entirely with agonistic behaviour as the fish were not observed to be territorial. Farwell (1970) dealt with the agonistic behaviour of underyearling S. punctatus and suggested that these fish are territorial.

Farwell stated that underyearlings appeared to be territorial when given ample space. He found that in a tank with a bottom area of 1075 cm^2 the status of the fish depended on the area in which the agonistic encounter took place. Further he found that the fish occupied certain grids of the tank to the almost total exclusion of the other member of the pair. His experiment, however, lasted only six days, thus important questions regarding the seasonal occurrence and spatial requirements of territories in underyearling S. punctatus were left unanswered. This study examined both the seasonal and spatial aspects of territoriality in underyearling and older _S. punctatus_.

As mentioned previously, territories are often the result of intraspecific agonistic interactions. Further to this, aggression is the most common behaviour used to control spacing areas (territories) (MacBride, 1971). The idea that the aggressive levels of underyearlings appear to be influenced by seasonal factors (Farwell, 1970) formed the basis for an experiment on aggressiveness in this study. Factors such as water temperature, photoperiod and season were examined to determine their influence on the aggressive levels of underyearling and older _S. punctatus_. It was assumed that fluctuations in the aggressive levels should correlate with the occurrence of territoriality in the species.

Underyearling _S. punctatus_ begin their benthic life in Logy Bay around the end of July and beginning of August when they settle from the plankton. During this time of settlement, the density of underyearlings is at its highest (Pepper, 1974). When densities are high among animal populations there is often intense competition for "favorable" habitats. The substrate in Logy Bay is rocky with many boulders and crevices. There are also scattered areas of gravel among the rocks. It has been observed that underyearlings appear to favor the rocks and boulder substrate as opposed to the gravel areas (personal observation). Whether this is a "preference" or simply a result of dispersal is unknown. One of the functions of aggression and territoriality is to distribute animals evenly through the environment, with surplus animals forced to leave or inhabit marginal areas. It was felt that this "favorable area" concept was important in the survival and territorial behaviour of underyearlings and experiments were set up to determine if underyearlings demonstrate a "preference" for a certain habitat.

Closely related to this "habitat selection" experiment was one dealing with the prior residency effect. Larval S. punctatus settle from the plankton during a period of a few days to a week (Farwell et al., in press). It was felt that because of this time difference involved in settlement, fish that settle early may have an advantage in securing and maintaining territories over fish that settle later. Experiments were run to determine if this prior residency effect could be a factor in the life of underyearlings.

The diverse functions of territories have been dealt with by many authors but most deal with the occurrence of territories in connection with nesting and reproductive behaviours. Feeding territories have been suggested for reef fishes (Zumpe, 1965; and Clarke, 1970) and salmonids (Jenkins, 1969; and Symons, 1971). Myrberg (1972) suggested that territories allow the territory holder to learn specific path habits to escape predators. Further to these suggestions as to the functions of territories in various fish species, a function of isolation may be operating in S. punctatus. Observations in Logy Bay had indicated that underyearlings tend to be visually isolated from one another. Whether this apparent isolation is a function of the behaviour of the fish or is a result of the substrate characteristics was felt to be worthy of examination if an accurate idea of the function of territorial behaviour in this species was to be arrived at. Experiments were set up to determine the social aspects of aggression and territoriality as it related to this apparent isolation factor.

In examining these aspects of aggression and territoriality in both underyearling and older S. punctatus it was hoped that a clearer picture of the functions of these behaviours would be ascertained and that their relationship and importance to the survival of the species would be determined.

GENERAL MATERIALS AND METHODS

FIELD STUDY

Stichaeus punctatus were observed and collected while using SCUBA. A slurp gun and a fine mesh hand net were used to collect specimens. Live specimens were transported to the laboratory in a plastic bucket containing approximately 15 l of seawater. Dyer's Gulch, Logy Bay, was used regularly as a collecting and observation site from September 1972 until January 1975. Mitchell's Brook, Salmonier, St. Mary's Bay, was visited on an irregular basis from August 1973 until January 1975.

Field Area Description

Dyer's Gulch, Logy Bay, is adjacent to the Marine Sciences Research Laboratory. The gulch is characterised by nearly vertical rock sides with the bottom composed mainly of boulders and gravel. The gulch extends from a depth of 1 m at its shoreward origin to a depth of 22 m approximately 170 m seaward. All field experiments were carried out in the depth range of 1 to 6 m, (referred to henceforth as the shallow area). Underyearling *S. punctatus* were quite numerous in this area from August through November 1974 but few were present after November 1974. During the above period the shallow area was used for all field experiments while the deep area (9 to 22 m) was used for collecting purposes only. These two areas, shallow and deep, are separated by a narrow corridor which extends for approximately 30 m seaward. A detailed description of the submarine characteristics of

Dyer's Gulch is given by Himmelman (1969). From August through November 1973, underyearlings were not numerous in the Gulch and apart from one experiment, both the shallow and deep areas were used for collecting purposes. Observations involving older fish were carried out in the deep area in 1973 and in the shallow area in 1974. At no time were S. punctatus observed in Dyer's Gulch in significant numbers after November or before June in 1973 and 1974. In 1972 the population of underyearlings was larger than in 1973 (Pepper, 1974).

Mitchell's Brook, Salmonier, was visited 4 times over the two-year period. A rock and pebble beach continues subtidally to a depth of approximately 5 m. At this depth a sand and silt bottom continues offshore. Underyearling S. punctatus were collected along the rock-sand interface. Specimens from this site were noted to have a white ectoparasitic nematode on their pectoral and anal fins. These ecto-parasites had no observable effect on the host's behaviour and were useful in distinguishing Mitchell's Brook fish from Logy Bay fish and in identifying individuals in the laboratory experiments.

LABORATORY STUDY

Fish Holding Conditions

Fish were held at the Marine Sciences Research Laboratory where all laboratory experiments took place. The holding conditions for all fish prior to their placement in experimental tanks were the same. Holding tanks for underyearling S. punctatus were 45 X 30 X 25 cm fiberglass tanks with glass fronts. The bottom was covered with gravel and a few rocks. Seawater was maintained on a continuous flow basis. Illumination was provided by overhead fluorescent lights plus sunlight from the laboratory windows which provided a natural light cycle. Tanks were situated in the main room of the laboratory thus fish were exposed to activity in the laboratory. Water temperature was maintained to within a degree or two of the temperature in Dyer's Gulch. Older _S. punctatus_ were maintained in 60 X 29 X 29 cm tanks which contained gravel and a few rocks. These tanks were maintained under the same conditions as those described for the underyearlings. The densities of the underyearling fish in the holding tanks were never above 15 per tank while the densities of the older fish were never above 8 per tank. Individual fish which were to be placed in the observation tanks were taken from different holding tanks to minimize, as much as possible, the chance of placing the same pair of fish together in subsequent trials. Fish were moved from the holding tanks to the observation tanks in small, 19 X 19 X 11 cm, clear plastic aquaria.

The fish fed on foods occurring naturally in the seawater supplying the tanks. The most commonly eaten food items were copepods and amphipods. Supplemental feedings were also provided twice a week during the warm months (mid June through November) and once a week the remainder of the year. Food was introduced into the holding tanks without regard to disturbance but care was exercised to minimize disturbance when introducing food into the observation tanks. Feedings occurred at irregular times to avoid conditioning the fish to a certain time period. The supplemental food was crushed _Strongylocentrotus droebachiensis_ gonads.

Experimental Tanks

The sizes of experimental tanks varied with the different studies from as small as 30 X 21 X 20 cm to as large as 150 X 51 X 43 cm. The bottoms of the experimental tanks were covered with a layer of gravel and a continuous flow of seawater was maintained in each tank. Experiments were carried out in a constant temperature room (maintained at 17°C) in the basement of the MSRL and in a room that was partitioned off from the main laboratory by a black plastic curtain. Tanks were maintained on a constant light cycle. Those tanks that were maintained under different conditions than those described will be described under individual experiments.

EXPERIMENTAL PROCEDURES AND RESULTS

EXPERIMENT I. SELECTED ASPECTS OF TERRITORIALITY AND DOMINANCE

Farwell (1970) concluded that underyearling S. punctatus were territorial when given ample space, but did not specify the spatial requirements needed. This experiment utilized both the field and laboratory environments to determine if underyearling and older S. punctatus are territorial as Farwell suggested. The experiment also dealt with selected aspects of territoriality and social dominance in the species.

Territorial species typically exhibit several classes of behaviour in connection with territory maintenance. Two of these behaviours, defense of an area (Noble,1939) and attachment to a particular area (Mayr,1963), were used as criteria for territoriality in S. punctatus. Littoral fish, such as the arctic shanny which do not possess a swim bladder typically remain close to the substrate and perform only short excursions from one place to another on the substrate. Fish that show this restricted movement usually display territoriality during some period of their life (Myrberg,1972). It was hypothesised that S. punctatus is territorial.

Territorial behaviour also has to be understood in relation to time (Leyhausen,1971) as territoriality is typically a seasonal phenomenon. This experiment was run on a yearly basis so that seasonal related changes in the behaviour would be noted.

Farwell (1970) further noted that when space is limited underyearlings form a constant dominant-subordinate hierarchy. The hierarchies formed in these cases are reputed to be a nip-right hierarchy (dominant fish nips and is never nipped by a subordinate) as opposed to a nip-dominant hierarchy (steady reciprocal nipping between two fish with the dominant fish winning the majority of nip contacts) (Allee,1942). Thus when space is limited S. punctatus should form a nip-dominant hierarchy in which social status is determined by individual encounters.

Farwell (1970) reported that underyearling S. punctatus dominate older fish during times of warm water temperatures. He hypothesized that this allows more underyearlings to set up territories and hence survive than would otherwise be possible. This observation of dominance of older fish by younger ones has not been shown to exist in other fish species so experiments were set up to examine this particular observation.

Materials and Methods

Field. During the period August - November 1974, field work was centered around the manipulation of underyearlings into encounter situations to determine if a resident fish would chase an intruding fish out of its area, thus providing evidence of territoriality in underyearlings. These observations were carried out in the shallow portion of the gulch.

Using SCUBA, the substrate was scanned until two fish, less than 2 m apart, were located. One fish was then "herded" into the other's area. The "herded" fish was designated the intruder while the other fish was considered the resident. Both fish were then observed from a distance of 2 - 4.4 m. The winner of the bout, if any, the distance the winner chased the loser and whether or not either fish returned to its original area were recorded. The pair of fish were observed for at least 10 minutes after the intruding fish had been herded into the resident's area.

Laboratory. Four tanks were selected to provide the fish with four different total bottom areas in which to set up territories. The tank sizes were as follows:

Small ----	60 X 34 X 34 cm	Total Bottom Area - 2040 cm^2
Medium ---	90 X 45 X 40 cm	Total Bottom Area - 4050 cm^2
Large ----	120 X 45 X 48 cm	Total Bottom Area - 5400 cm^2
X-Large---	150 X 45 X 43 cm	Total Bottom Area - 6750 cm^2

The tanks were all maintained under a 12 hour dark - 12 hour light cycle. A green plexiglass panel was placed over each tank. The tanks were separated from the observation room by a black plastic curtain. Horizontal slits were cut in each curtain and one-way viewing glass was placed in the slits. During observation periods all lights were off in the observation rooms. The smallest tank was divided into 6 equal grids while the larger tanks were divided into 8 grids. These grids were marked by a lengthwise rope through the center of each tank, just under the gravel, and by marks on the outside of each tank, 3 in the small tank and 4 in the larger tanks.

A pair of fish of the same size and age (underyearlings or older fish) were placed in each tank for each trial. There were two trials that were run using an underyearling-older fish combination. One fish of each pair went through a marking procedure which consisted of anaesthetizing the fish with MS_{222} (Sandoz, Ltd.) and then marking it with a nylon thread. The thread was inserted by needle through the dorsal musculature just under the posterior portion of the dorsal fin, looped and tied over the fin so as not to interfere with the movement of the fish's dorsal fins. Pseudosurgery was performed on the second fish of the pair in each trial. It consisted of the standard marking procedure with the exception that the thread was simply pulled through the musculature without being tied. Both fish were allowed 2 hours recovery time before being placed in the experimental tanks. Fish were allowed 1 day acclimation period in the tank before observations began.

Daily 30 minute long observation periods were made during which each fish's position was recorded every 5 minutes. Thus if a fish remained stationary for the total observation period one position would be noted 7 times, however, if a fish was active throughout the observation period then 7 different positions would be noted. The grids enabled a precise recording of positions of each fish in relation to tank bottom. The position and outcome of any encounters were also noted.

These data, once collected, were analysed to determine if either "positional stereotypy" or defense of an area were demonstrated by either fish. If these two criteria were evident, either for one or both fish, territoriality was considered to be demonstrated in the tank. Positional stereotypy is the affinity of a fish for a specific area and was determined using frequency of occurrence data. A significant frequency of occurrence was set as twice the expected occurrence value of a fish in one grid of the tank. For example: if 160 observations were recorded in the large tank then an expected frequency of occurrence would be 12.5% or 20 positions per grid for one fish. If, however, a fish was recorded in one grid on 40 occasions (25% of the total) or more, then it met the criterion for positional stereotypy. The defense of an area could be determined by the positions and outcomes of the encounters between the two fish in the tank.

If these two criteria were not met in a tank, then territoriality was not considered to be demonstrated by either fish. In this case the data would be totalled with other non-territorial data and placed with data from other trials of the same tank.

The length of time a pair of fish were in the test aquarium was usually determined by either the results to date or the survival of the fish. The majority of trials lasted for at least a month.

Using this standard procedure three trials were run in which manipulations of the fish took place. In two trials, one in the medium tank (90 cm) and one in the X-large (150 cm) tank, a third fish was introduced into the tank after the trial had been running a month. The trials ran for 10 days after the third fish was introduced. In another trial in the medium tank the pair of fish were removed for two days then placed back in the tank.

These territorial experiments ran from March 1973 to January 1975.

Results

Field. From August 20 until October 23, 1974, 22 encounters were staged in the gulch. Of these, 18 were won by the resident fish, 2 were won by the intruding fish and 2 resulted in no agonistic encounter between the fish. These results are significant ($X2=23.28$, 2d.f., $p<.01$).

The distances that the resident fish chased the intruding fish were noted on 10 occasions. The maximum distance was 83 cm while the minimum distance was 15 cm. The majority of the chase distances fell in the range of 34 - 68 cm. On one occasion a resident fish came out 68 cm to meet an intruding fish but no encounter ensued.

Intruding fish, after losing an encounter, returned to their original area on 8 occasions. The 10 instances in which the intruding fish did not return immediately to their area were those in which they were chased further than 50 cm in the opposite direction to their original area. The 10 minute observation period used after the encounter was not long enough to allow these fish to be observed returning to their original areas.

One chance encounter was observed between an underyearling and an older fish in Dyer's Gulch. This occurred as the underyearling was approaching the older fish from the side. The older fish turned towards the underyearling when it was approximately 15 cm away. The older fish then moved towards the underyearling which, in turn, fled.

Laboratory. The criteria for territoriality were met in the three larger tanks. Table I gives the results for the trials run in the four tanks.

TABLE I

Results from Trials, in Percentages, indicating the Type of Social System observed and Positional Stereotypy.

Tank Size	N (Trials)	Territoriality	Hierarchy	Positional Stereotypy
60 cm	4	0	100%	100%
90 cm	7	14%	86%	100%
120 cm	3	33%	66%	100%
150 cm	4	25%	75%	100%

The 90 cm tank was the smallest one in which territories were set up and maintained (total bottom area 4050 cm^2). Positional stereotypy and defended areas for this particular ~~trial are shown in~~ Figure I-A and I-B. The tank was almost evenly divided between the two fish as indicated by the theorized territory boundary in Figure I-B. Fish A had a frequency of occurrence of 80.5% on the side of the tank where it was dominant while Fish B had a 68% frequency of occurrence in its dominant area.

In the 120 cm tank, in the trial in which territories were set up (see Figure V, Appendix), Fish A had an 86.5% frequency of occurrence in its territory while Fish B had a 71.9% frequency of occurrence in its territory. Both of these trials were run from September 30, 1974 to January 8, 1975. At the onset of both of these trials, the fish were less than 2 months old and were placed directly into the experimental tanks from the field.

FIGURE I

Results from 90 cm tank for positional stereotypy and encounters from September 30, 1974 to January 5, 1975.

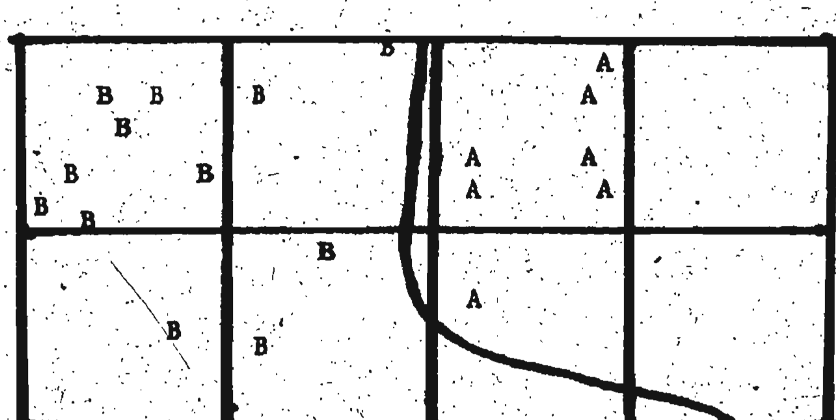
A. Total percent values of occurrence for individual fish in the grids of the 90 cm. tank. Values for Fish A are in the upper left corner while values for Fish B are in the lower right corner.

B. Positions and winners of encounters in the grids of the 90 cm tank. The dark line forms a hypothesised territory boundary between the individual fish's territories.

A

2.7% 27.1%	3.6% 8.9%	12.3% 14.7%	23.1% 6.2%
5.8% 11.1%	4.5% 10.8%	5.8% 20.4%	42.2% 0.8%

B



The third instance of territoriality occurred in the 150 cm tank. Results are given in Figure II-A and II-B. A third fish was introduced briefly into the tank but had no apparent effect on the original pair. The results again indicate that the original pair were territorial but a number of differences exist between this trial and the two previous instances of territoriality. In this trial the fish were over 10 months old (as calculated from settlement date) thus they were approaching yearling status. Initially there was a hierarchy evident in the tank but on July 19 (trial started June 12) the subordinate Fish B won two encounters. From this date until August 14, 1973 territories were being maintained in the tank by both fish. Figure III-C, III-D and III-E gives the positional stereotypy of the two fish for the pre-territorial period, the territorial period and the post-territorial period. After August 14 both fish won encounters in the other's previous territory. Unfortunately Fish A developed a fungus on its fins and died on November 7, 1973.

From Figure II-C and II-D it appears that both fish showed positional stereotypy from the onset of the trial but only Fish A defended its area. Fish A had a frequency of occurrence in its eventual territory of 78% before territoriality and 70.6% during territoriality. Fish B was not observed defending its area before July 17 but still had a frequency of occurrence of 47.6% in its eventual territory. After B began to defend its area the frequency of occurrence was 85%. The introduced fish was a newly settled young of the year and was observed being attacked by both Fish A and B shortly after its introduction into the tank. It died a week after it was placed in the tank, probably from

FIGURE II

Results from the 150 cm tank for positional stereotypy and encounters from June 12 to November 6, 1973.

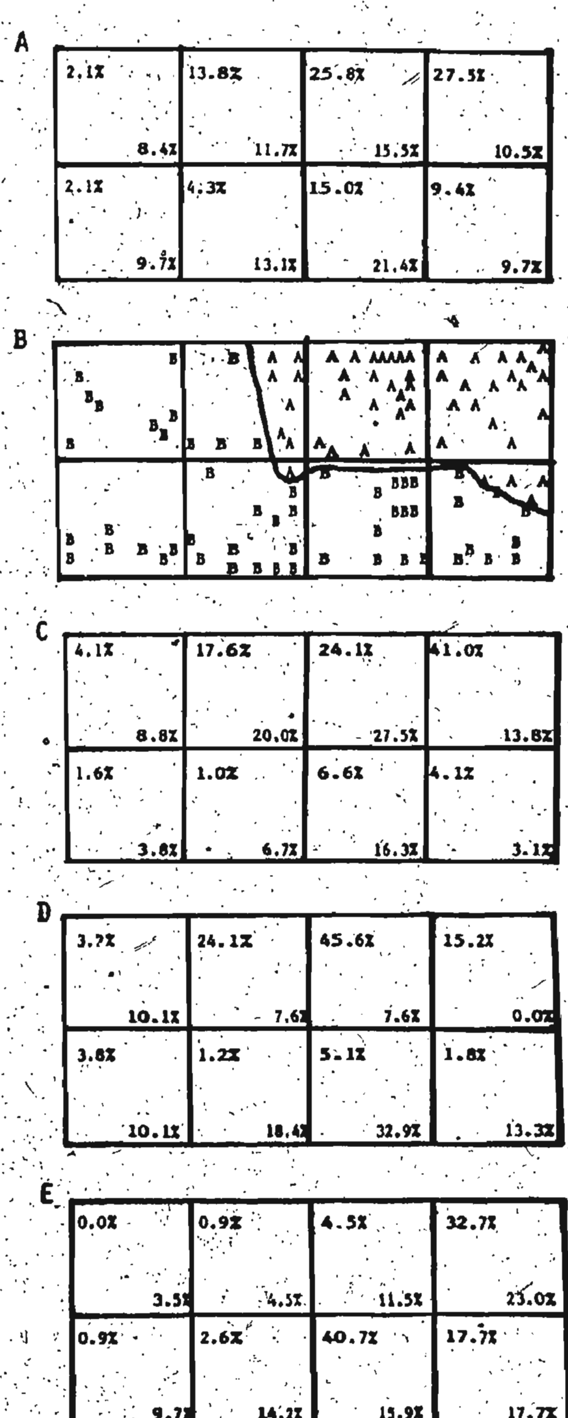
A. Total percentage values of occurrence in grids of the 150 cm tank for underyearling fish. Values for Fish A are in the upper left corner and values for Fish B are in the lower right corner.

B. Positions and winners of encounters in grids of the 150 cm tank. The dark line forms a hypothesised territory boundary between the individual fish's territories.

C. Percentage values of occurrence in grids of the 150 cm tank for Fish A and B <u>before territoriality</u>. Values for Fish A are in upper left corner and values for Fish B are in lower right corner.

D. Percentage values of occurrence in grids of the 150 cm tank for Fish A and B <u>during territoriality</u>.

E. Percentage values of occurrence in grids of the 150 cm tank for Fish A and B <u>after territoriality</u>.


A
2.1% 13.8% 25.8% 27.5%
8.4% 11.7% 15.5% 10.5%
2.1% 4.3% 15.0% 9.4%
9.7% 13.1% 21.4% 9.7%
B
C
4.1% 17.6% 24.1% 41.0%
8.8% 20.0% 27.5% 13.8%
1.6% 1.0% 6.6% 4.1%
3.8% 6.7% 16.3% 3.1%
D
3.7% 24.1% 45.6% 15.2%
10.1% 7.6% 7.6% 0.0%
3.8% 1.2% 5.1% 1.8%
10.1% 18.4% 32.9% 13.3%
E
0.0% 0.9% 4.5% 32.7%
3.5% 4.5% 11.5% 23.0%
0.9% 2.6% 40.7% 17.7%
9.7% 14.2% 15.9% 17.7%

the attacks by the two territory holders.

Dominance hierarchies were evident in 14 of the 17 trials run with underyearling fish. These hierarchies were uni-directional with one fish always being dominant over the other. Once the hierarchy was established there was never any observed reversal in the status of the two fish. Overall positional stereotypys were shown by both underyearling fish in the small tank (See Figure VI Appendix), by the dominant fish in the X-large tank (see Figure VII-B Appendix) and the subordinate fish in both the large and medium tanks (see Figures VIII and IX-B, Appendix).

In one trial in the small tank and one in the medium tank the two hierarchies were not established until the fish had been together for 6 days. Both of these trials started in mid-July and ran until the middle of August. Both of the fish were dominant in bouts, thus initially a nip-dominant hierarchy was evident but after 6 days this was replaced by the nip-right hierarchy. During these trials the fish were approaching yearling status as determined by their settlement date.

In the two yearling-underyearling combination trials the yearlings were dominant over the underyearlings. In the majority of encounters observed between the fish the underyearling would flee from the approach of the yearling. In only one instance was there an attack by the yearling. There were area affinities shown by these fish. (See Figure VI-A, Appendix).

In the three trials using older fish only one dominance hierarchy was observed. This hierarchy was in the X-large tank. During trials run in the large tank no agonistic encounters were observed between the pairs. The observed hierarchy was similar to those formed between underyearling pairs with the exception that the agonistic encounters did not involve as complex a sequence pattern as was observed for underyearling pairs. The sequence involved in the encounters between older fish was composed of an approach, display and flatten while underyearlings typically had a sequency of approach, display, attack, flee and chase (Farwell and Green, 1973). Activity levels were quite low for the older fish when compared to the underyearlings. All older fish showed positional stereotypy. (See Figures VII-A and IX-A Appendix).

Social manipulations were performed in two trials in the medium tank. In one trial a third fish was introduced after the original pair had been in the tank for 6 weeks. There was a dominance hierarchy in existence before the introduction and, immediately after placement, the third fish was attacked by both of the original pair. Positional stereotypy was shown by the original pair before and after the introduction. (See Figure X, Appendix). The dominant fish shifted its positional stereotypy during the two periods while the subordinate retained the same area. The third fish likewise showed a positional stereotypy during the trial.

The other manipulation also took place in the medium tank. After 3 weeks both fish were removed for 2 days and then returned to the same tank. A dominance hierarchy was in effect the entire time. The status of the fish remained the same but there was a shift in the positional stereotypy of the two fish (see Figure XI, Appendix).

Discussion

The results from laboratory and field trials indicate that under-yearling *S. punctatus* are territorial at least during a portion of their first year of life. Field results indicated that resident fish have a distinct advantage over intruding fish as they won most of the staged encounters. The possibility that the intruding fish were stressed by the experimental "herding", thus placing the fish at a disadvantage, is of course a possibility. However, the stress involved in being in an area recognized as a neighboring territory is no doubt great also and as Lorenz (1966) points out in some species, territorial neighbors are learned as well as the borders of the neighboring territories. On two occasions (unrecorded) two fish met on neutral ground and no encounter ensued. Both these fish were observed to return to their original areas.

The fact that in 8 of the 18 encounters the intruding fish returned to their original area within 10 minutes suggests that there is an attachment to a particular area. As mentioned in the results section, the 10 occasions when the intruding fish did not return to its original area were those in which it was chased more than 50 cm in the opposite direction from its original area. Thus territories are maintained by underyearlings in the field during their inshore stay, they are defended, and displaced underyearlings tend to return to their original area.

Animals tend to orient themselves along natural lines in the environment which are easily accepted as natural boundaries (Leyhausen, 1971). Dyer's Gulch is characterised by many large boulders, crevices, and small gravel patches. It is among these rocks and boulders that underyearlings set up and maintain territories. The field experiments showed that resident fish chased intruders a maximum distance of 83 cm and a minimum of 15 cm. The majority of chases fell in the range of 34 - 68 cm. The size of a territory appeared to be dependent on the substrate, thus the boundaries of territories appear to be determined to a large extent by the substrate.

The laboratory trials likewise showed that underyearlings are territorial when given ample space. Territories were set up and maintained in the three larger tanks. The territories set up in the medium and large tanks were by fish which were less than 2 months old, thus they were quite small in size (less than 4 cm.). It is reasonable to assume that in confinement the larger the fish the larger the spatial requirements for a territory. In these two instances of territoriality the fish were quite small and young, and both these aspects may be important in the establishment of territories in the laboratory. Once set up the territories were maintained from September 1974 to January 1975. It appears that underyearlings are territorial for a period of time which is greater than the inshore portion (about 5 months according to Pepper 1974) of their first year of benthic life.

The territoriality that was evident in the X-large tank was different than in the other two instances. The fish in the X-large tank were becoming yearling fish at the time of the territoriality. Also there was a period of over a month when it appeared that a dominance hierarchy existed between the two fish. The territoriality lasted for a month and then appeared to break down as both fish won encounters in the other's former territory. It is possible that both fish were territorial from the onset of the trial but not in an aggressive manner. As shown in Figure II, before Fish B began to actively defend its territory it had maintained an exclusive occupancy of the area. Fish B occupied the grids of its territory more than twice as often as Fish A did, thus it appears that territoriality was in effect before any active defense of the area was observed. When the territoriality broke down it was not replaced by a nip-right hierarchy as would have been expected but appeared to be replaced by a nip-dominant hierarchy. The status of the fish was not determined by the area in which the bout took place but by the outcome of each individual bout.

In the majority of trials hierarchies were set up in the experimental tanks. However, in both the small and medium tanks, for the period of mid-July to mid-August, the hierarchies were not set up until the fish had been together for a week. This is contrary to Farwell's (1970) and the author's observation that the hierarchy between fish is established during the first few bouts. This observation suggests that the fish were possibly setting up territories in these tanks but that the area was too small and hierarchies finally resulted. The time period (July – August) corresponds to the time when territories were established in the X-large tank by a pair of fish that were the same age as those in the small and medium tanks. It thus appears that fish which are approaching yearling status are territorial and will establish and maintain territories for a period of at least a month from July through August.

The hierarchies established in all tanks were of a nip-right type in which the dominant fish always nips and is never nipped in return by the subordinate fish. Allee (1942) and Braddock (1945) found that in chickens the peck (nip) dominant order is related to territoriality in that birds are dominant in their own territories. In this type of hierarchy the status of the individual is determined by each bout. However, in this experiment, the hierarchies are of the nip-right type even though territoriality will be evident if ample space is provided. Once the hierarchy is established between the pair of fish there is never any reversal in status except when they display territoriality.

In respect to hierarchies it is apparent from both field and laboratory observations that yearling and older fish dominate underyearling fish. This is not based on an absolute dominance by the older fish, but rather on an avoidance by the underyearling of the older fish. In the field the underyearling fled from the approach of the older fish while in the laboratory only one attack was noted by the older fish against the underyearling. In all the other encounters underyearlings fled from the approach of the older fish. This is in contrast to Farwell's (1970) finding that underyearlings tended to dominate yearlings. The findings from the present experiment indicate that the two age groups interact infrequently in the field.

Hierarchies among older S. punctatus were observed on two occasions and these were both of the nip-right type. The establishment and maintenance of these did not involve as much nipping and overt aggression as was evident in underyearling hierarchies. The relationship was simplified to submission by the subordinate at the approach of the dominant fish. This simplification of the behavioural sequence involved in the encounters is the same as observed by Farwell and Green (1973) for underyearlings.

The temporal sequence of territoriality in underyearling _S. punctatus_ is evident from the laboratory and field results. Territories were established in the medium and large tanks in September and continued until January. In both instances the fish were small and less than two months old. It appears that there may be a critical time, dependent upon size or age, when underyearlings will set up territories in tanks. Trials during all the other months in these tanks resulted in no territories. Territories are set up by the underyearlings in the field during August and maintained at least until November. After this there appears to be an offshore migration of the underyearlings and whether they maintain territories offshore is unknown but seems unlikely. The reasons for the failure of the underyearlings to set up and maintain territories in the three larger tanks when placed there after September could be due to size or age of the fish, individual differences among the fish, or the past history of the fish. The size and age factor has been mentioned previously. Individual differences among the fish due to physical condition could affect level of aggression. The past history of the fish may also be important. It was impossible to place totally naive fish in the experimental tanks. Each fish had some pretest experience as either a subordinate or dominant fish or both. Thus if one fish of a pair had a past history of being a dominant and the other a history of being a subordinate fish then a hierarchy would no doubt result in the tank. In both instances of territoriality in the medium and large tanks the fish were placed there directly from the field. In the field they would be occupying territories, thus their past history would be comparable. In the X-large tank, however, the fish were also placed in directly from the field but no territoriality resulted. In this case the individual differences among fish may have come into play, thus one fish of the pair may have been more aggressive and a dominance hierarchy resulted. Thus even though underyearling S. punctatus exhibit territoriality in both the field and laboratory, there appears to be a number of factors which may preclude the establishment of territories in both situations.

The other instance of territoriality took place during the period July through August, when the underyearlings were just over 10 months old. This time period appears to be quite important, for even in the tanks in which hierarchies were set up during this time, there was much fighting and the hierarchies took much longer than normal to be established. This territoriality lasted only one month and was followed by a nip-dominant order. It thus appears as if there is a temporal sequence to the establishment of territories and this sequence could take one of two forms.

One possibility is that the underyearlings are territorial throughout their first year of benthic life. The gap that exists in the laboratory for the period January through July in the establishment of territories by underyearlings may be due to factors described above. As this is also a time of low activity by the fish, territories may not be as actively defended as at times of warm water temperatures thus the criteria for territoriality would not have been met.

The other possibility is that underyearling S. punctatus are territorial only during the inshore portion of their first year of benthic life. Laboratory results support this to an extent but the fact that territories were set up and maintained until January in the laboratory while the offshore migration of the underyearlings appears to take place in November is not in total agreement. Underyearlings have been recorded in Dyer's Gulch in January (Farwell, 1970), however, and the offshore migration is still speculative so this second possibility is perhaps the more acceptable of the two offered.

EXPERIMENT II. AGGRESSIVENESS

Although environmental stimuli, such as water temperature and photoperiod, are often suggested as influencing the intensity or frequency of aggressive behaviour, few actual data are available on the subject. Hartman (1966) found that the rate of aggression was reduced in underyearling coho salmon and steelhead trout as a result of lower water temperatures. Farwell (1970) suggested that this could be the case as well with underyearling S. punctatus. The present study was set up to try to expand Farwell's observations as to the causes of the seasonal fluctuations in the aggressive levels of underyearlings. Seasonal fluctuations in aggressiveness, especially in littoral fish, have been shown (Gibson, 1968; and Phillips, 1971) thus it was hypothesised that seasonal fluctuations in the aggressiveness of underyearling and older S. punctatus, due to changes in water temperature, photoperiod and time of year, would be evident.

In the experiment on territoriality (Exp. I) a difference was evident in the occurrence of this behaviour in underyearling and older fish. There was no territoriality noted for older fish and fewer agonistic encounters were observed between older fish as compared to underyearlings. This difference in territoriality and rate of aggression between the two age groups was thought to be based on lower aggressive levels in the older fish. This finding was further supported by field observations where no agonistic encounters have been observed between older fish (personal observation). Part of this experiment was concerned with quantifying this difference in aggressiveness between older and underyearling S. punctatus.

Underyearling and older S. punctatus are found inshore in Dyer's Gulch together from mid-August through December. Observations on this population have indicated that the two age groups interact infrequently in the field. However, in the majority of instances where different age groups of the same species inhabit the same area, some form of social order usually exists. Part of this experiment was set up to determine the rate of interaction between the two age groups and to further discern from the results and observations the type of social system in operation in the field between older and underyearling S. punctatus.

Materials and Methods

Four groups of fish were studied: underyearlings (natural light cycle - NLC), underyearlings (constant light cycle -CLC), older fish (NLC), and an older fish-underyearling combination (NLC). All fish were maintained under the conditions described previously. The fish under the constant light cycle (12 hour dark - 12 hour light) were maintained in two small, 30 X 21 X 19 cm, fiberglass tanks and densities of these fish were kept at approximately 10 per tank. The NLC groups were tested from November 1973 until December 1974 while the GLC group was tested from April to December 1974.

Four pairs of fish were run at a time, three times a week. Fish were selected randomly from the holding tanks. Each member of the pair was taken from a different holding tank. Each month 24 pairs of underyearlings (NLC), 16 pairs of underyearlings (CLC), and 4 pairs each of older fish and the older fish-underyearling combination were tested. There were two months when fewer fish were tested. A total of 310 pairs of underyearlings (NLC), 128 pairs of underyearlings (CLC), 60 pairs of older fish and 47 pairs of older fish - underyearling combinations were run.

Observation tanks were small, 30 X 21 X 19 cm, fiberglass tanks with glass fronts. The tanks were partitioned in two areas, measuring 15 X 21 X 19 cm, by grey PVC sheets with the top portion constructed of wire mesh to allow seawater to flow throughout the entire tank. Recordings by the experimenter were made while seated in front of the tanks using a pen and special observation sheets.

Measures of aggressiveness were "latency" to the first observed bout and "number of bouts per 15 minute period". The use of latency as an indicator of aggressiveness was based on the assumption that the more aggressive fish would initiate agonistic encounters sooner (low latency) than less aggressive fish. The number of bouts a fish engaged in during a 15 minute period (which began with the first observed bout) should likewise be influenced by the aggressiveness of the fish. The more aggressive the fish the greater the instance or rate of encounters during the test period.

A pair of fish were placed in each tank area together. After a 60 minute acclimation period observations began. In March 1974, the behavioural sequence involved in the initial observed encounters were noted to be very simple, i.e. involved only an approach-flee sequence. This simplification of the sequence involved in encounters indicated that a hierarchy had been established during earlier bouts and fighting was simplified after this (Farwell and Green, 1973). The acclimation period was reduced to 30 minutes as a result, to insure that the first observed bout would be one of the early ones between the pair of fish. The observation period lasted for 120 minutes or until each pair of fish being run (4) had encounters. If no encounters were observed then latency was recorded as 120 minutes and number of bouts 0. All fish were measured after each trial and water temperatures recorded.

In August, 1974 newly-settled underyearlings were brought into the laboratory from the field. These fish replaced the underyearlings who had turned a year old in August. These "new" yearlings were then used in the older fish trials. Prior to this the ages of the older fish in the trials had varied from 1+ to 3+ year old fish as determined by size.

Results

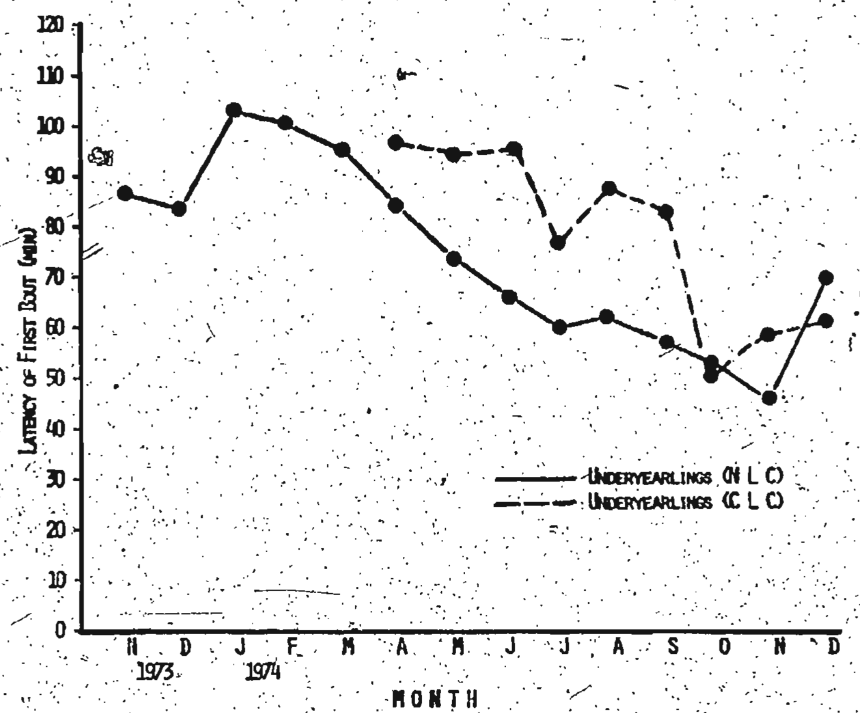
Underyearlings (NLC). Monthly mean values for latency and number of bouts per 15 minute period (bout frequency) were plotted and are shown in Figure III-A and III-B and Table II. There is a definite cycle

FIGURE III

A. Monthly mean latency to first observed bout for underyearlings under natural light cycle and constant light cycle.

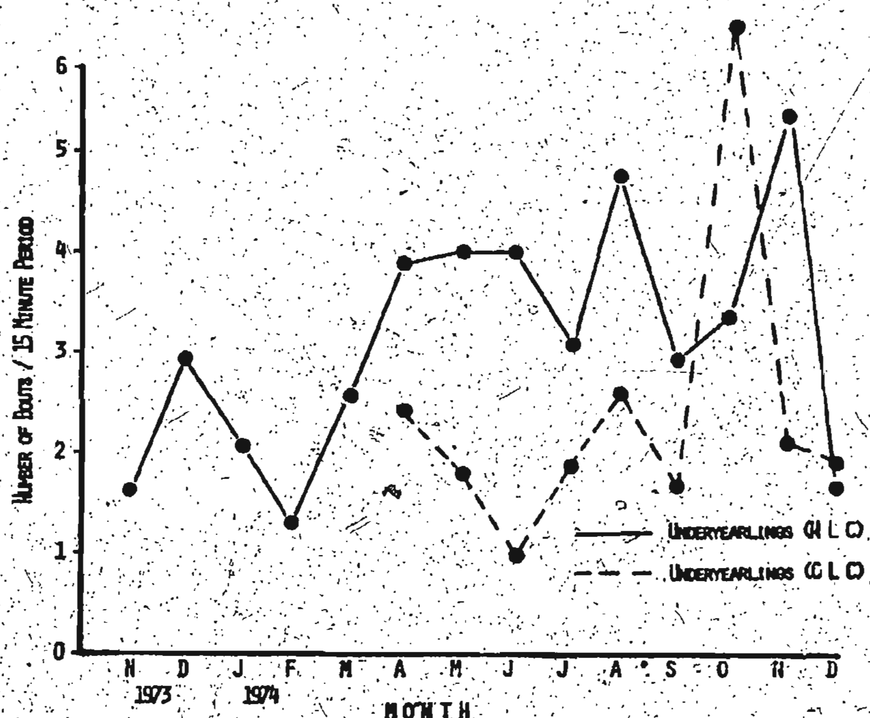
B. Monthly mean number of bouts per 15 minute observation period for underyearlings under natural light and constant light cycles.

A



120
110
100
90
80
70
60
50
40
30
20
10
0
Latency of First Bout (min)
Underyearlings (N L C)
Underyearlings (C L C)
N D J F M A M J J A S O N D
1973 1974
MONTH

B



6
5
4
3
2
1
0
Number of Bouts / 15 Minute Period
Underyearlings (N L C)
Underyearlings (C L C)
N D J F M A M J J A S O N D
1973 1974
MONTH

evident in the latency values. The mean values for January (103 min),

TABLE II

Monthly Mean Values and Standard Deviation for Latency to First Observed Bout and Number of Bouts per 15 Minute Period for Underyearlings (NLC).

Months	Fish N	Mean Latency Values (in min.)	SD	Mean # of Bouts	SD
November 1973	20	87.0	37.33	1.6	2.80
December	48	84.7	30.49	2.96	3.34
January 1974	48	103	22.5	2.04	2.65
February	24	101.6	23.99	1.24	1.82
March	48	96.9	23.28	2.58	2.73
April	48	84.8	19.45	3.92	5.05
May	48	74.5	25.04	4.0	3.99
June	48	66.0	24.55	4.0	4.36
July	48	61.1	28.41	3.13	3.08
August	48	63.6	22.27	4.79	2.09
September	48	57.5	19.54	3.0	2.09
October	48	55.1	19.25	3.42	4.44
November	48	46.2	19.77	5.5	5.70
December	48	69.5	36.38	1.75	2.21

February (101 min) and March (96 min) are the highest followed by a general decline until November (46 min). The slight increase between July (61 min) and August (63 min) is likely due to the use during this period of newly caught fish who were unfamiliar with the laboratory conditions. There is likewise a large difference between the values obtained in November (87 min) and December (84 min) 1973 and November (46 min) and December (69 min) 1974. This difference could have been caused by two factors:

one is the difference in acclimation periods between the two test periods and the second is the fact that the 1974 fish were more familiar with the testing conditions. In 1974 the fish had been exposed to the testing procedure for three months while in 1973 the fish were still quite naive in respect to the testing procedure. These two factors could have influenced the results but would not have altered the fact that a cycle exists in latency and bout frequency values. The monthly mean curve for both would have been slightly depressed for the period November 1973 to March 1974 but would not have been eliminated.

Figure III-B gives the results for bout frequency. There appears to be a decrease in bouts between December 1973 and February 1974 which corresponds to an increase in latency values for this same period. The bout frequency increased from March to June which again corresponds to a decrease in latency for this period. From June until December there is a general decrease in bout frequency. Again the high value for the month of August may be due to the use of newly-settled fish in the trials. The use of the bout frequency data is questionable since in the majority of months tested the standard deviation is greater than the means. However, in using it as support for the latency data and not by itself this obvious shortcoming is not as serious.

To simplify further analysis of the data three procedures were followed. First the months of November and December 1973 were eliminated to allow the data to be analysed for one complete year, from January to December 1974. Next, because a seasonal influence was being examined the results were divided into four quarters. These four quarters were as follows: (1) January to March, (2) April to June, (3) July to September, (4) October to December. The quarters approximated periods of low, intermediate and high water temperatures in Logy Bay. Periods of low temperatures being represented by quarters 1 (0.2°C mean temp.) and 2 (2.8°C), intermediate temperatures by quarter 4 (6.1°C) and high temperatures by quarter 3 (10.7°C). Thirdly, because of unequal numbers of observations between the quarters a number of the results had to be discarded to equalize the observations. This was done by numbering each observation from 1 to 72. Since the lowest number of observations in a quarter was 60, 12 had to be discarded. A table of random numbers was consulted (Winer, 1962). The last two digits of the random number were taken and the result with the corresponding number was discarded. The table of random numbers was read vertically until 12 observations had been eliminated. The quarters thus had equal observations and a Student-Neuman-Keuls test was performed to determine where the significant difference between the quarters existed. The Student-Newman-Keuls test was only performed if the data were found to be significant by a one-way analysis of variance test.

One-way analysis of variance on the latency data ($F=36.95$), d.f.=13, $p<.001$) was significant. The Newman-Keuls test showed that quarters 3 and 4 (July to December) were not significantly different from each other but were from the rest of the year. Quarter 1 (January to March) was significantly different from quarter 2 (April to June) and both these were different from quarters 3 and 4. An omega squared (Ω^2) value was calculated from the variance values (Hays, 1963). This test is designed to approximate the percent variance accounted for by the independent variable, in this case the seasonal quarters. An Ω^2 value of 32.7% was obtained which suggests that season contributes quite significantly to the variance found in the data. Results of the bout frequency data ($F=1.929$, d.f.=13, $p>.01$) were not significant.

Temperature was the other variable examined using the ANOVA tests. Temperatures were broken down into 15 cells, each cell of 0.9°C. The cells ranged from -1°C to +15°C. The results for latency ($F=9.562$, d.f.=14, $p>.001$) showed a significant difference existed between the cells. An Ω^2 value of 28% was obtained from the variance values. Bout frequency results also showed a significant difference ($F=2.272$, d.f.=14, $p<.01$) with an Ω^2 of 5.6%. The temperature data were not analysed further due to the extremely unequal number of observations which existed between the various temperature cells.

Underyearlings (CLC). The monthly mean latency and bout frequency values are given in Figure III-A and III-B and Table III below. There is an overall decrease in latency from June through October. The values increase from October until December when the trials were terminated. There is not a definite trend for the mean monthly bout frequency values. The extremely high mean for October appears to be atypical and the reason for this is unclear. Again the usefulness of the bout frequency data is questionable due to the high standard deviations obtained. It will be used only as supportive evidence for the latency data.

TABLE III

Monthly Mean Values and Standard Deviation for Latency to First Observed Bout and Number of Bouts per 15 Minute Period for Underyearlings (CLC).

Month	Fish N	Mean Latency Value (min.)	SD	Mean # of Bouts	SD
April 1974	16	98.9	23.80	2.4	2.67
May	32	97.3	19.98	1.8	2.40
June	32	98.6	30.35	1.0	1.46
July	32	77.6	33.43	1.9	1.89
August	32	88.3	27.30	2.6	3.18
September	32	84.2	26.79	1.8	2.32
October	32	53.9	16.16	6.4	8.17
November	32	60.6	27.68	2.2	1.47
December	16	61.9	28.36	1.9	1.88

Analysis of the latency data was carried out using the same procedure as employed in the previous group. However, since this particular experiment was only run from April to December there were only three quarters used. These were as follows: (1) April to June, (2) July to September and (3) October to December. Again these quarters approximated periods of low (quarter 1 - 2.8°C mean temp.), intermediate (quarter 3 - 6.1°C) and high (quarter 2 - 10.7°C) water temperatures. Latency data were significant ($F=23.75$, d.f.=2, $p<.001$). The Student-Neuman-Keuls test showed that quarters 1 and 2 (April to September) were not significantly different from one another but were different from quarter 3(October to December). Quarter 3 in turn was significantly different from both the other quarters. The bout frequency data were also significant ($F=3.11$, d.f.=8, $p<.01$) but were not analysed quarterly. These were analysed on a monthly basis. Further analysis of the bout frequency data was not carried out due to its questionable worth. An Ω^2 value of 27% was obtained for the latency data.

Analysing the data according to temperature a significant difference ($F=3.01$, d.f.=13, $p<.01$) was found for latency. No significance was found for the bout frequency ($F=1.62$, d.f.=13, $p>.05$) data. An Ω^2 value of 16% was obtained for the latency data.

Underyearlings (NLC and CLC). The monthly means for latency of both the natural light and constant light cycle groups of underyearlings were compared using the "t" test. Results are shown in Table IV. Small significant differences were found in four of the nine months compared. Monthly means were plotted in Figure III-A and III-B for both

TABLE IV

Mean and "t" Values Obtained for the Natural and Constant Light Groups of Underyearlings in the Aggressiveness Experiment for the Period April to November 1974.

Month	Mean Latency (NLC)	Values (in min.) (CLC)	DF	"t"	p
April	84.8	98.9	30	1.68	>.01
May	73.5	97.3	38	4.02	<.01
June	66.0	98.6	38	3.75	<.01
July	61.1	77.6	38	1.68	>.01
August	63.6	88.3	38	3.13	<.01
September	57.5	84.2	38	3.64	<.01
October	55.1	53.9	38	.207	>.01
November	46.2	60.6	30	.542	>.01

groups. The overall curve for the constant light group is slightly higher than the curve for the natural light group. There are two months, October and December, when the constant light curve is lower but overall the natural light group curve is lower.

Older Fish (NLC). Four pairs of older fish were run for each month with the exception of October and November when eight pairs were tested.

The monthly mean values for latency and bout frequency are given in Table V and the monthly mean curve for latency and bout frequency is shown in Figure XII (see Appendix). There were no encounters

TABLE V

Monthly Mean Values and Standard Deviation of Latency to First Observed Bout and Number of Bouts per 15 Minute Period for Older Fish

Month	Fish N	Mean Latency Value (min.)	SD	Mean # of Bouts	SD
November 1973	8	120	0	0	0
December	8	120	0	0	0
January 1974	8	120	0	0	0
February	8	120	0	0	0
March	8	120	0	0	0
April	8	120	0	0	0
May	8	120	0	0	0
June	8	103.8	19.50	.75	.96
July	8	87.0	38.81	.50	.58
August	8	64.5	38.87	1.50	1.73
September	8	120	0	0	0
October	16	89.7	39.37	.80	1.67
November	16	79.3	36.23	1.40	1.43
December	16	96.1	45.96	0.38	.74

between the older fish for the period November 1973 to May 1974. There is an overall decrease from July to October in latency values with the exception of September. The values begin to increase in December. A low number of bouts were recorded in this group for all months tested. A high frequency of bouts (1.5) was recorded in August which also corresponds to the lowest latency value recorded (64.5).

Results of ANOVA tests for latency ($F=1.967$, $d.f.=13$, $p>.05$) and bout frequency ($F=1.558$, $d.f.=13$, $p>.05$) were not significant. Analysis of the data according to temperature for latency ($F=2.006$, $d.f.=14$, $p>.01$) and bouts ($F=2.296$, $d.f.=14$, $p>.01$) were likewise not significant.

<u>Older Fish and Underyearling Combination (NLC)</u>. This study ran from December 1973 to December 1974. The results for December 1974 are not included as less than half the required number of fish were tested due to deaths caused by saturation of the seawater with dissolved gases at the MSRL.

Results are shown in Table VI below and Figure XIII (see Appendix). The latency values decrease overall from April through October, with the exception of July. An increase in latency begins in November and continues until March. The bout frequency means are quite low with the exception of November (3.5). These low means reflect the fact that there was very little interaction between the two age groups throughout the experiment.

TABLE VI

Standard Deviation and Monthly Mean Values for Latency to First Observed Bout and Number of Bouts per 15 Minute Period for Older Fish - Underyearling Combination

Month	Fish N	Mean Latency Value (in min.)	SD	Mean # of bouts	SD
November 1973	6	98.3	37.52	2.33	4.04
December	8	120	0	0	0
January 1974	8	120	0	0	0
February	4	120	0	0	0
March	8	120	0	0	0
April	8	107.5	25.00	2.00	1.00
May	8	110.0	20.00	.75	1.50
June	8	106.5	27.00	.25	.50
July	8	120	0	0	0
August	8	98.7	42.50	2.25	4.50
September	8	101.7	36.50	.50	1.00
October	8	81.0	45.10	1.75	2.36
November	8	89.75	35.33	3.50	6.35

Results of the monthly data for latency ($F=1.33$, $d.f.=12$, $p>.01$) was not significant as was the case with the bout frequency data ($F=1.227$, $d.f.=14$, $p>.01$). There was likewise no difference noted in the temperature for either latency ($f=.836$, $d.f.=14$, $p>.01$) or bouts ($F=.829$, $d.f.=14$, $p>.01$).

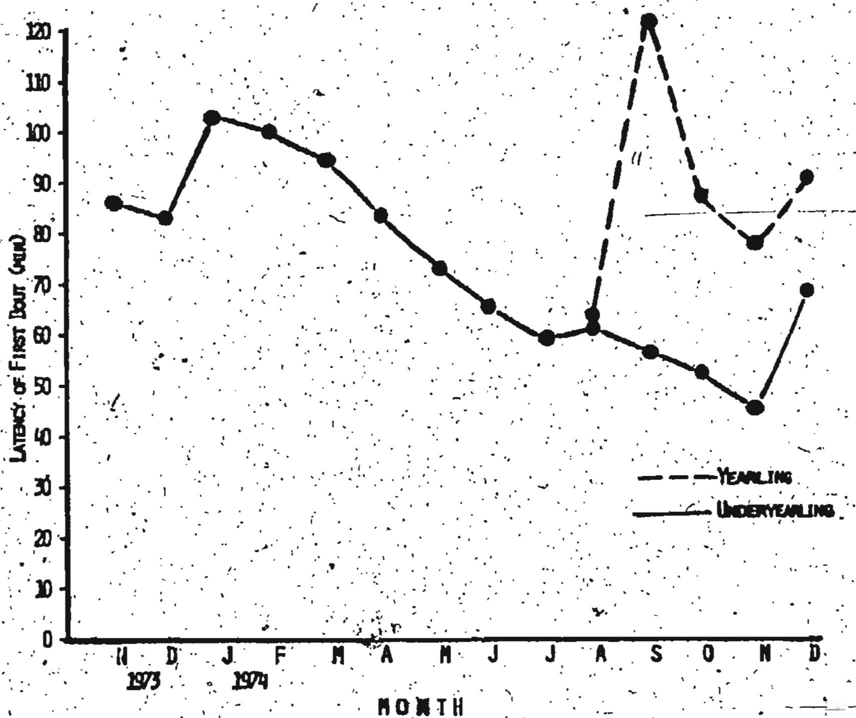
Age and Aggressiveness. Figure IV-A and IV-B combine the monthly means from the underyearling (NLC) and yearling (NLC) trials. In August 1974 the latency and bout frequency are slightly higher for yearlings than underyearlings. The latency value for August is quite similar for both age classes but in September the latency value for

FIGURE IV

A. Monthly mean latency values for underyearlings (NLC) for the period November 1973 to December 1974 and for yearlings from August to December 1974.

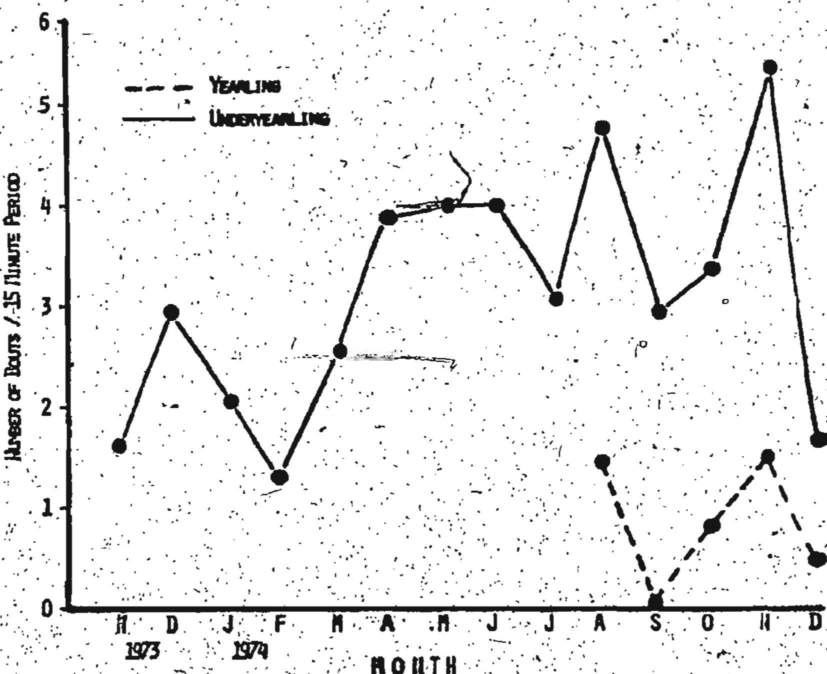
B. Monthly mean number of bouts per 15 minute observation period for underyearlings for the period November 1973 to December 1974 and for yearlings for the period August to December 1974.

A



Latency of First Bout (min)
Yearling
Underyearling
N D J F M A M J J A S O N D
1973 1974
MONTH

B



Yearling
Underyearling
Number of Bouts / 15 Minute Period
N D J F M A M J J A S O N D
1973 1974
MONTH

yearlings is high while the values for underyearlings decreased. Both latency curves follow a similar trend, decreasing from September to November with an increase in December, but the overall latency values for yearlings are much higher than the values for underyearlings.

The bout frequency follows comparatively the same trend. The number of bouts for yearlings is much lower from September through December than for underyearlings. This again indicates a much reduced level of aggressiveness for yearlings when compared to underyearling *S. punctatus*. The yearlings used in the trials for the period August through December 1974 were newly turned yearlings or 1+ fish.

Size versus Outcome of Encounters. All fish in the underyearling (NLC) group were measured after each trial. The sizes of the fish were then compared to the status (winner or loser or no encounter) of the fish by a 2 X 3 Chi-square contingency table analysis. Table VII shows the results.

TABLE VII

Chi-Square Contingency Table Analysis of Size of Underyearling Fish (NLC) with Outcome of Encounters

	Won	Lost	No Encounter
Large	53	14	24
Small	14	53	24

Large fish won significantly more (x^2=45.403, d.f.=2, p<.01) encounters than small fish.

Discussion

There is a definite seasonal fluctuation in the level of aggressiveness of underyearling S. punctatus. During the months when the water temperatures are highest, July to December, the latency values are low indicating a high level of aggressiveness. Likewise during this period there is an overall increase in the number of bouts per test period. The average water temperature during this period was 8.4°C in the laboratory while the average for the period January to June was 1.5°C. The results from the multiple comparison test (Neuman-Keuls) further support this finding. The period July to December was significantly different from the rest of the year. The period April to June was likewise different from the period January to March. It thus appears that the rate of aggression is subject to seasonal changes but whether this is due to water temperature, age, time of year or a combination of these factors cannot be determined from this experiment. The omega squared (Ω^2) values for season 32.7% and temperature, 28%, were both quite high. To suggest that a single factor controls aggressive levels seems risky as multiple factors are undoubtedly at work. Hartman (1966) noted in his work on two salmonid species that aggression appeared to be related to water temperature, the higher the temperature the more aggressive the fish. He only analysed this one factor however, and his data were based on only a few months of study.

With seasonally increasing water temperatures, aggression in the arctic shanny increases. The activity of the fish likewise increases with warming temperatures and in the experimental tanks this would mean that the members of the pair would come into close proximity sooner and more often thus resulting in more opportunities for agonistic encounters. During the warm water period the underyearlings settle from the plankton onto the substrate, thus densities are also highest at this time. Aggression has repeatedly been demonstrated as resulting from high population density. A high level of aggression at this time would aid in the establishment and defense of territories.

Results indicate also that aggressive levels are lowered by a constant light cycle (see Figure III-A and B). The constant light cycle used corresponds roughly to that which occurs during the winter season (December to April). The lower aggressive levels due to this light scheme reflect the low aggressive levels found in the natural light group for the winter season.

The months of August and September were found to be significantly different between the natural light and constant light groups. This period is important in the life history of the underyearlings (setting up territories, high densities) and their aggressive levels are quite high. However, under the constant light cycle which corresponds to the winter season the aggressive levels were significantly lower. However, the latency means follow a curve which is roughly similar to the curve for the natural light group, only higher. It appears that photoperiod affects the level of aggressiveness but not the seasonal nature of it.

Older S. punctatus show a lower aggressive level than underyearlings. There were no observed aggressive interactions between older fish for a seven-month period which extended from November 1973 to May 1974. Water temperatures are low during this period and the activity levels of the older fish were likewise low. Aggressive levels increased in June and continued to increase until December. The mean latency curve followed the same general trend as that for the underyearlings but as was the case with the constant light group, the curve was higher overall. There was no significance noted for months or temperatures. Seasonal fluctuation of the magnitude of that observed in underyearlings was not apparent. The period June to December is the inshore period for the older fish in Logy Bay thus the increase in aggression associated with this time period is reasonable. Another change noted in the aggression of older fish is the behavioural sequence involved in the encounters. Rarely did an agonistic encounter between two older fish involve an Attack. In the majority of encounters there was a Display by the dominant fish and a Flatten by the subordinate. In only 5 of 19 encounters between older fish was there an Attack. In comparison with encounters between underyearlings, there was an Attack during almost every encounter situation (initial bout only). It appears as if there is a simplification of the agonistic sequence involved in encounters between older fish.

The interaction between the two age groups, underyearlings and older fish was found to be low. There does not appear to be any seasonal cycle evident, as such, but there is a general decline in latency from April to October. The agonistic interactions between the two groups rarely involved an Attack. The older fish were always dominant and underyearlings would seem to "avoid" the older fish in the majority of encounters. Underyearlings would Flee from the Approach of the older fish and in only 2 instances was there an Attack by the older fish.

Upon completion of one year of benthic life, the aggressive level of S. punctatus is lowered considerably. The latency values for yearlings and underyearling fish are quite close in August but in September the yearling values increase sharply in comparison to the values for underyearlings which decrease. For the period September to December, the latency values are high for yearlings compared to underyearlings values. The latency values are higher for yearling and older fish over the year than those for underyearlings. This is comparable to the findings of Zumpe (1965) for butterfly fishes (Family, Chaetodontidae).

Despite the tendency of the older fish to be less aggressive than the underyearlings, in agonistic encounters between the two groups the older fish dominate. This is reasonable when the results of the size versus outcome of encounter data is considered. The larger member of a pair engaged in an agonistic encounter won a significantly greater portion of these encounters than did the smaller member. Other authors have found this as well (Braddock, 1949; MacDonald et al., 1968; Gibson, 1968; Greenberg, 1946 and Boer and Heuts, 1973).

EXPERIMENT III: HABITAT SELECTION

Habitat selection may be defined as the repertoire of behavioural responses to environmental stimuli by means of which an animal locates its preferred habitat (Meadows and Campbell, 1972). Habitat selection and territoriality may seem like unrelated behaviours but as Pitelka (1959) stated, territories are fundamentally an ecological phenomenon and not just a behaviouristic one. Thus in this respect the territories of animals are objects in the environment and the question as to whether an animal defends any area or selects an area to defend is one that deserves attention.

Underyearling S. punctatus settle in Dyer's Gulch and have little apparent choice but to live among the rocks and boulders found there, as this is the only habitat available in the study area. Behaviourally (thigmotaxis) (Gibson, 1968) and morphologically (compressed and elongated body, modified fins, reduced scales and body mucus) these fish are adapted to life among the rocks and crevices found inshore. In fact, however, it has never been shown whether habitat selection plays a part in their settlement among the rocks and boulders or if the fish will take up residency in any habitat they settle in. This study was designed to determine whether or not underyearling S. punctatus do select the habitat in which they live.

Material and Methods

Laboratory. The laboratory portion of this experiment ran from July 31 to August 22, 1973 which corresponded to the time of the field study. Underyearling S. punctatus were brought in directly from the field and placed in two wet-benches in the laboratory. The largest of these measured 223 X 70 X 9 cm and the other 184 X 58 X 9 cm. These were divided into 6 equal sections, those on the larger bench measuring 74 X 35 X 9 cm and those on the smaller bench 61 X 29 X 9 cm.

The three habitats used were:

1. Rocky --- 3 cm layer of gravel with rocks of a diameter greater than 4 cm scattered about.

2. Gravel --- 3 cm layer of gravel with no rocks greater than 4 cm in diameter present.

3. Bare ---- bare wet-bench top of fiberglass with no rocks or gravel present.

The three different habitats were of equal size and each habitat occurred twice on each wet-bench. Placing of habitats, in relation to one another, on the wet-benches was done for all possible placement combinations. The fish had equal access to each habitat. A constant light cycle was provided and food was placed in each section. When recording the positions of fish in each habitat, the disturbance to each was constant.

A total of 75 fish were observed during the study with a maximum of 6 fish per bench. The amount of cover present in each bench was sufficient for 6 fish but with numbers above this a crowding effect would be noted. This crowding would result in the more dominant fish occupying the preferred areas while the subordinate fish would be forced to occupy the less preferred areas.

Field. This portion of the experiment was run from July 20 to August 20, 1973. Two substrates, rocky and gravel were used. Two tables, both with a surface area of 1 m^2 and legs 30 cm long, were constructed of dexion and placed 1 m apart in Dyer's Gulch at a depth of 6 m. The table tops were constructed of fiberglass painted black to prevent light from being reflected back up through the tables from the substrate. Small buckets of cement were attached to each leg for weight.

One table surface was covered with an 8 cm layer of gravel (no rocks with a maximum diameter of over 4 cm). The other top (rocky substrate) was covered with a layer of rocks between 4 - 45 cm in maximum diameter. The two tables were visited on 13 occasions between July 23 - August 20, 1973. On the last date only the rocky table remained as rough sea had destroyed the gravel table.

Results

Laboratory. The results were analysed using a chi-square contingency table and are presented in Table VIII.

TABLE VIII

Chi-Square Contingency Table Analysis of Habitat Preference for Underyearlings in the Laboratory.

	Rocky	Gravel	Bare
Observed	51	13	11
Expected	25	25	25

The results (x^2=40.64, d.f.=2, p<.01) indicate a significant difference exists in the choice of habitats by the fish. The overall preference is for the rocky habitat over the other two.

Field. A total of 34 underyearling *S. punctatus* were recorded on the two tables during this study. Of the 34 fish observed, 33 of them were recorded on the rocky table and 1 on the gravel table. Chi-square results showed a significant difference (x^2=19.30, d.f.=1, p<.01) existed between the two tables.

Discussion

Territories are areas of the substrate which are occupied and defended by the territory holders. The results of the laboratory and field portions of this experiment show that underyearling S. punctatus do select a specific habitat and prefer this area over others equally available. The habitats available in the two studies were quite different and the rocky habitat was selected over the other two habitats of gravel and fiberglass.

Territoriality not only involves a type of behaviour (aggression) but also involves an object, the territory. Animals do not normally defend areas that are unfavorable to them. In the field, during storms, underyearlings remain under rocks and in crevices. They also use these areas to escape predators (personal observation). There appears to be no survival value for underyearlings to defend a patch of gravel if there are no crevices available in it for the fish to take refuge in. To be able to select a habitat that will offer a better chance of survival and to defend this area confers a definite advantage to the territory holder.

EXPERIMENT IV: TAGGING AND RELEASE OF OLDER FISH

Territoriality among older S. punctatus has been shown to exist in the laboratory only for a short period after they become yearlings (see Exp. I). Aggression among older fish has been shown to exist in the laboratory for the period July through November but instances of aggression in the field have not been noted. Older fish are dispersed throughout Dyer's Gulch from July to November and the mechanism which is responsible for this dispersion is unknown. King (1973) stated that agonistic behaviour is necessary for even dispersal of animals in an environment. Whether this agonistic behaviour results in territoriality or a form of home range behaviour depends upon the animal in question.

Territoriality and home range behaviours both disperse animals throughout the environment. The basic difference between the two is one of aggression. Territories typically involve aggression to defend an area while a home range is a passively occupied area. Burt (1943) stated that a home range is an area which is covered by an animal in its normal activities of food gathering, mating and care of young. Noting that the aggressive levels of older fish are much lower than underyearlings and further noting the lack of observed aggression in the field, this experiment was designed to provide an idea as to the type of dispersion in older fish.

Materials and Methods

Older S. punctatus were tagged by the method outlined by Pepper (1974), and released into Dyer's Gulch. These fish had been held in the laboratory over the winter and some were Mitchell's Brook specimens. Observations of the location of tagged fish were recorded once on each dive made in the Gulch.

Nineteen fish were tagged and released into the Gulch on four occasions: August 19, September 20 and 23 and October 10, 1974. The 4 released on August 19 were not individually marked but could be identified by the white ectoparasites on their fins. The remaining

15 were all individually marked.

The tagged fish were released at two sites on the substrate, (Site A and B) each approximately 4 m in diameter and 3 m apart. These two sites were the only areas extensively searched on subsequent dives for tagged fish.

Results

Results from the tagging were sparse but deserve mention. Of the 4 unmarked fish released on August 19, 1 was observed in the original release site, A, on October 23. Of the 4 released September 20, in Site A, 2 were recorded in the area on October 21. The 4 released September 23 in Site B were observed only on the day following their release in the release site. Of the 7 released October 10, 3 in Site A and 4 in Site B, 1 was observed in Site A and 2 in Site B on October 23.

In summary, of the 19 fish released, 7 were never observed again and 5 were observed in their release sites on the last dive (October 23) before a prolonged period of rough seas terminated diving until mid-November.

Discussion

The results suggest that older fish do show restricted movements for a period of at least a month. Five of the 19 fish were observed at least 4 weeks after their release in the original release sites. In late November, when conditions were again suitable for diving, no tagged fish were noted but at this time the inshore population of <u>S. punctatus</u> was quite low and by the end of the month no fish were observed in the study area.

During the two months of observation there were always tagged fish in the release sites. The two release sites were only 4 m in diameter. It would be unlikely for all the released fish to remain in these sites. The fact that 2 of the 19 released fish remained in the release sites for almost 2 months suggests that possibly the areas were only large enough for a small number of older fish. This observation agrees with other field observations which indicated that density levels of older fish were quite low and older fish were more spread out on the substrate than were underyearlings (personal observation). Pepper (1974) found that 4 of 11 tagged older fish showed an affinity for the capture-release area. Thus it does appear that older fish have an affinity for a particular area but whether this area is occupied passively or is a defended territory is still unknown from field observations.

EXPERIMENT V: VISUAL ISOLATION

The aggression observed in Dyer's Gulch between underyearling _S. punctatus_ often resulted in the fish being visually isolated from one another. The territories that resulted from the underyearling's aggression were likewise often visually isolated. In the Gulch the substrate is rocky with many large boulders and crevices. This type of habitat has been shown to be preferred by underyearlings (see Exp. III). The substrate thus provides many areas in which underyearlings can be visually isolated from conspecifics.

Whether this isolation is a result of the substrate or is in fact a function of the behaviour that results in the formation of territories is unknown. This experiment was set up to determine if underyearlings will tend to isolate themselves visually when given the opportunity to be alone or with other individuals of the same species. The hypothesis was that visual isolation does occur in the species and that it is a function of the territorial behaviour of underyearling S. punctatus.

Materials and Methods

Two tanks were used in the study. One measured 60 X 34 X 34 cm while the smaller one measured 34 X 34 X 34 cm. The tanks were each divided into 4 equal sections by opaque PVC tubing having a diameter of 8 cm. When these tubes were placed in the tank substrate they extended approximately 5 cm above the substrate. Thus if a fish swam into one of the sections it was visually isolated from the other 3 sections. The tanks were separated from the main laboratory by a black plastic curtain. A natural light cycle was maintained for all trials except for one which was under a 12 hour light - 12 hour dark cycle. The study was carried out from May to October 1974.

Four fish were placed into each tank for each trial. Individual fish were identified by size and also by the presence or absence of white ectoparasites on their fins. The length of the trials varied from 2 days to one month. Thirty observations were carried out for each trial. Observations consisted of recording the position of each fish in the tank and were carried out on a random basis throughout the day. Generally a minimum of 4 per day were done, with a maximum of 15. Different fish were placed in the tanks at the conclusion of each trial. In 4 trials, however, fish from the large tank (60 cm) were placed in the small tank (34 cm) and 4 new fish were placed in the large tank. Fish were allowed to acclimate for 24 hours before observations began.

Sixteen trials (8 per tank) of 30 observations per trial were run in the tanks. Two additional trials, also of 30 observations, were run in a large tank under constant light conditions. A total of 72 fish were tested. Results were examined to determine if the fish spent a significant number of observations either Alone or With 1 or more other fish. Individual fish that did not demonstrate any significant "preference" (as determined by chi-square) for either of the two conditions were classified as demonstrating No preference. The percentage of fish that "preferred" each condition was calculated.

The initial two trials in each tank were run using "old" (more than 10 months) underyearlings, while the remaining trials used newly-settled or "young" underyearlings. The results from these two groups were compared to determine if underyearling "age" affected their occurrence in each condition.

Of the 18 trials run, 5 were run for 2 days or less. The results of these "short run" trials were compared to the "regular run" trials which lasted from 10 days to a month.

Encounters between fish in the experimental tanks were noted to determine the effect of social status on the occurrence of the fish.

Results

Results from the small tank are shown in Table IX. Over 59%

TABLE IX

Observed "Preferences" of Underyearling S. punctatus Expressed as a Percentage in Small Tank of the Visual Isolation Experiment.

Social Condition	N (fish)	Percent	p
Alone	19	59.4	< .05
With 1 or more fish	7	21.8	< .05
No preference	6	18.8	> .05

of the fish tested demonstrated a "preference" for the Alone condition. The other condition accounted for over 21% while almost 19% had No preference for either of the conditions.

The results for the "old" underyearlings in the small tank and for the "young" underyearlings are shown in Table X below. A higher

TABLE X

Observed "Preferences" of "Old" and "Young" Underyearling S. Punctatus Expressed as a Percentage in the Small Tank of the Visual Isolation Experiment.

	"Old" Fish			"Young" Fish		
Social Condition	N (Fish)	Percent	p	N (Fish)	Percent	p
Alone	6	75.0	<.05	13	54.2	<.05
With 1 or more fish	1	12.5	<.05	6	25.0	<.05
No preference	1	12.5	>.05	5	20.8	>.05

percentage of the "old" underyearlings were observed Alone (75%) than were the "young" underyearlings (54.2%).

There were 6 encounters observed in the small tank in which 3 winners and 6 losers were designated. This could occur as one fish could win encounters with as many as 3 different fish. The results indicated that social rank does not influence the designated preference of the fish.

Results for the short and regular run trials are compared in Table XI below. In the short run trials, 25% of the fish preferred the Alone condition compared to almost 71% in the regular run trials.

TABLE XI

Observed "Preferences" of Underyearling S. punctatus Expressed as a Percentage in the Small Tank for Short Run and Regular Run Trials in the Visual Isolation Experiment.

Social Condition	Short Run			Regular Run		
	N (fish)	Percent	p	N (fish)	Percent	p
Alone	2	25.0	<.05	17	70.8	<.05
With 1 or more fish	5	62.5	<.05	2	8.4	<.05
No preference	1	12.5	>.05	5	20.8	>.05

Approximately 63% of the fish tested in the short run trials preferred the With 1 or more fish condition while only around 8% preferred this condition in the regular run trials.

Area preferences (determined if the frequency of occurrence of individual fish in the grids was twice the expected value) were demonstrated by 19/32 (59.4%) of the fish tested.

Results from the large tank were examined in the same manner as those for the small tank. Table XII below shows that again over half of the fish tested (56.4%) demonstrated a preference

TABLE XII

Observed "Preferences" of Underyearling S. punctatus Expressed as a Percentage in Large Tank of the Visual Isolation Experiment

Social Condition	N (fish)	Percent	p
Alone	18	56.4	< .05
With 1 or more fish	7	21.8	< .05
No preference	7	21.8	> .05

for the Alone condition. The other condition and the No preference condition accounted for the remaining 43.6% of the fish. These values compare quite closely to those obtained in the small tank.

In the large tank there was one complete hierarchy observed and the preferences of the four fish involved were as follows: the alpha, beta and omega fish preferred the Alone condition while the gamma preferred the With 1 or more fish condition. The gamma and omega fish were observed together on numerous occasions and seemed to prefer (though not significantly) to be together as opposed to with the other two higher ranking individuals. There were three incomplete hierarchies noted and the results showed that all the winners preferred the Alone condition while 66.7% of the losers preferred this condition.

Table XIII gives the results for the "old" and "young" fish tested in the large tank. Again the "old" underyearling fish had a higher percentage (66.6%) in the Alone condition than did the "young" underyearlings (50%).

TABLE XIII

Observed "Preferences" of "Old" and "Young" Underyearling S. Punctatus Expressed as a Percentage in the Large Tank of the Visual Isolation Experiment

	"Old" Fish			"Young" Fish		
Social Condition	N (Fish)	Percent	p	N (Fish)	Percent	p
Alone	8	66.6	<.05	10	50.0	<.05
With 1 or more fish	2	16.7	<.05	5	25.0	<.05
No preference	2	16.7	>.05	5	25.0	>.05

Table XIV gives the results of the short and regular run trials. As was the case in the small tank, more fish preferred the Alone condition in the regular run trials (58.3%) than in the short run trials (50%). Likewise more fish preferred the With 1 or more fish condition in the short run trials (50%) than in the regular run trials (12.5%).

TABLE XIV

Observed "Preferences" of Underyearling S. punctatus Expressed as a Percentage in the Large Tank for Short Run and Regular Run Trials in the Visual Isolation Experiment

	Short Run			Regular Run		
Social Condition	N (fish)	Percent	p	N (fish)	Percent	p
Alone	4	50.0	<.05	14	58.3	<.05
With 1 or more fish	4	50.0	<.05	3	12.5	<.05
No preference	0	0		7	29.3	>.05

Area preferences were found for 21 of the 32 fish tested (63.7%).

The results of the t-test carried out on the four trials in which fish from the large tank were switched into the small tank showed no significant difference. Results of the 8 trials in the small and 8 trials in the large tank were also compared and no significant difference was found.

The results from the constant light trials were found to compare quite closely to those obtained for the large tank in the previous section. Of the 8 fish tested, 6 preferred the Alone condition (75%) while the remaining 2 showed No preference.

Discussion

The results support the hypothesis that underyearling _S. punctatus_ tend to visually isolate themselves from conspecifics but observations did not determine fully if this isolation is a function of the territorial behaviour of the species. In both experimental tanks over half of the fish tested "preferred" to be alone in a section of the tank. The next most observed social condition was the No preference condition.

"Old" underyearlings tended to "prefer" the Alone condition more than the "young" underyearlings. This result is unexpected as from earlier experiments (see Exp. II) the "younger" fish were found to have higher aggressive levels than the "older" underyearlings. One might expect that the "young" underyearlings would be observed more in the Alone condition than would the "older" underyearlings if this isolation was due to the aggressive behaviour of the species. Thus the result could suggest that the Alone condition is in fact a "preferred" one and not simply the result of an aggressive act. Further to this the isolation resulting from an agonistic encounter would be immediate, it would occur right after the bout. The fact that relatively few bouts were observed during the experiment suggests that the observations reflect the positions of the fish long after any encounters took place, thus the "preferences" are due more to the social factor than the results of agonistic encounters. The fish could isolate themselves without engaging in any agonistic encounters but when encounters do occur one result may be to visually isolate the pair. It thus appears that visual isolation may be a factor in the territorial behaviour of underyearlings.

The length of the trials appeared to affect the "preferred" social conditions of the fish as well. In the short run trials the Alone condition was "preferred" by fewer fish than in the regular run trials. This appears to be reasonable in that initially the social system would be relatively unstable and much fighting would be taking place. After a period of time the hierarchies would be established and fighting would be lessened. Chases and fleeing would be reduced as appeasement behaviour is present when a social order has been established. A subordinate fish showing the appeasement behaviour of flattening would be less likely to be forced or chased from a section when a dominant fish entered it. This reduction in movement of the fish would probably result in the Alone condition being the most observed which in fact was the case. Also when fish are first introduced into a tank there is much movement involved in exploratory behaviour, which gradually disappears.

The status of the fish did not appear to affect their "preference" for a certain social condition. In total, 67% of winning fish and 55% of losing fish preferred the Alone condition.

The question as to whether the visual isolation observed in underyearlings is a result of substrate or one of the functions of territorial behaviour was not totally determined from the experiment. The fact that underyearlings do prefer a habitat that affords them the physical means to visually isolate themselves has been shown (Exp. III). The fact that the fish are aggressive and territorial has likewise been shown (Exps. I and II). It is suggested from the observations in this experiment that visual isolation is a component of the territoriality of the species and is not just a result of agonistic encounters. More experimentation along these lines however needs to be carried out to determine fully the role of this "apparent preference" in the life and behaviour of the fish.

EXPERIMENT VI: MIRROR IMAGE AND ISOLATION

The visual isolation experiment (Exp. V) indicated that the territorial behaviour may result in the visual isolation of underyearling S. punctatus. However, the relative importance of substrate and territoriality was not fully determined in regard to this apparent preference. (See Discussion, Exp. V). This experiment was designed to expand upon the results of the previous experiment and determine the preference of underyearlings.

This experiment utilized mirror areas and non-mirror areas, thus the fish had a choice between two "stimulus offering" areas. Farwell (1970) found that 10 of 10 underyearling S. punctatus displayed aggressively to mirror images. This aggressive response to visual stimuli, provided by the mirror image, is a social response. The mirror areas in this experiment provided a social stimulus to the fish while the non-mirror areas offered no social stimulus, but rather an isolation effect. Based on the results from Experiment V, the hypothesis was that underyearlings would prefer the non-mirror areas over the mirror areas.

Materials and Methods

Three tanks were used in the experiment, one measured 60 X 34 X 34 cm and was divided into two equal sections by a 5 cm high PVC sheet. This sheet did not prevent the fish from entering or leaving either section. One section had pieces of mirror, 5 cm high, along 3 sides. The PVC sheet across the middle of the tank had a mirror on one side. The other section of the tank had no mirrors and was left clear. The other two tanks measured 45 X 34 X 34 cm. Each was divided into two sections in the same manner as the large tank. In one of the tanks the two sections consisted of mirrors on one side and PVC sheeting on the other. The two sections in the third tank were of PVC sheeting and a clear section. The three tanks therefore were arranged in three different ways: Tank 1 - Mirror versus Clear, Tank 2 - Mirror versus PVC and Tank 3 - PVC versus Clear. The experiment ran from May to August 1974. All tanks were on a natural light cycle with the exception of one tank that was on a constant light cycle for two trials.

A trial consisted of placing a designated grouping of fish (either a single fish or a pair of fish) into each tank. The tanks were observed randomly throughout the day (generally two or four times per day) and recordings made of which sections of the tank the fish were in. After 30 observations the sections were switched to control for any position bias, i.e. if the mirror section was on the left side of the test area it was switched to the right side. The fish were then replaced in the tank and 30 more observations were recorded. The fish were removed at the end of each trial. A total of 19 fish was tested in the 3 tanks.

Three trials were run using a pair of fish. In these trials, two fish were placed into each tank and recordings made of which section each member of the pair was in. Experimental procedure was the same as that already described.

Four trials were run in the large tank with single (1) fish and 1 trial with a pair (2) of fish. There were 4 trials run using single (1) fish and 3 trials run using pairs (2) in the other 2 tanks. There were 2 trials run under a constant light cycle in the large tank using single (1) fish.

Results

All data was analysed by chi-square. Results for the large tank are given in Table XV. There was no significant difference noted in the constant light trials (x^2=2.20, 1 d.f., p>.01). For both the single (x^2=98.82, 1 d.f., p<.01) and the paired fish (x^2=12.03, 1 d.f., p<.01) trials significant differences were noted. When the paired fish were analysed individually, however, only one member of the pair showed a significant preference for the mirror side over the clear side.

TABLE XV

Preferences of Single and Pair Groupings of Underyearling S. Punctatus in the Large Tank of the Mirror Image and Isolation Experiment

Grouping	N Fish	Light	Mirror Side	Clear Side	p	N Trials
Single	2	Constant Light	69	51	$>.05$	2
Single	4	Natural Light	197	43	$<.01$	4
Pair	2	Natural Light	79	41	$<.01$	1
P-A **			54	6	$<.01$	
P-B **			25	35	$>.01$	

** Denotes individual member of the pair (2) of fish trial.

In the PVC versus clear side, a laboratory effect was noted in the single fish trials. In 3 of the 6 trials in which significance was noted, the left side was preferred regardless of the condition of the side (PVC or clear). This effect was noted only in the single fish trials. Table XVI gives the results for the PVC versus Clear side trials (all natural light).

No significant preferences were noted in the single fish trials ($x^2=0.80$, 1 d.f., $p>.05$). However, in the pair of fish trial significance was noted in both the pair data ($x^2=36.3$, 1 d.f., $p<.01$) and the individual members of the pair data ($x^2=17.07$, 1 d.f., $p<.01$) and ($x^2=19.29$, 1 d.f., $p<.01$). These preferences were in all cases for the PVC side over the Clear side.

TABLE XVI

Preferences of Single and Pair Groupings of Underyearling *S. Punctatus* in the PVC Versus Clear Side of the Mirror Image and Isolation Experiment

Grouping	N Fish	PVC Side	Clear Side	p	N Trials
Single	3	96	84	> .05	3
Pair	2	93	27	< .01	1
P-A **		46	14	< .01	
P-B **		47	13	< .01	

**Denotes individual member of the pair (2) of fish trial.

Table XVII below gives the results for the PVC versus Mirror side.

TABLE XVII

Preferences of Single and Pair Groupings of Underyearling *S. Punctatus* in the PVC Versus Mirror Side of the Mirror Image and Isolation Experiment.

Grouping	N Fish	PVC Side	Mirror Side	p	N Trials
Single	4	71	169	< .01	4
Pair	2	41	79	< .01	1
P-A **		36	24	> .05	
P-B **		5	55	< .01	

** Denotes individual member of the pair (2) of fish trial.

Significant preference was demonstrated by the single fish (x^2=40.02, 1 d.f., p<.01) for the mirror over the PVC side. This preference was shown also in the pair (2) of fish trial (x^2=12.03, 1 d.f., p<.01). In the pair of fish trial, however, only one member of the pair (P-B) showed a significant preference (x^2=41.07, 1 d.f., p<.01) for the mirror over the PVC side. The other pair member (P-A) showed no preference (x^2=2.40, 1 d.f., p>.05) for either side.

Discussion

Mirror areas were found to be preferred over other non-mirror areas, thus the hypothesis was rejected. That mirror areas were preferred suggests that the visual stimulus provided by the mirrors is perhaps important as a social factor.

The image presented by the mirror to the fish would mean that the fish would always be in close proximity to "another" fish. This social contact between the fish and its image could have been the factor causing the preference for the mirror area. Aggression and territoriality are both social behaviours and both function in or as a social order. Lorenz (1964) and King (1973) stated that the apparent positive correlation between gregariousness and frequency of aggressive encounters in animals could be interpreted to mean that aggression enhances group cohesion. The visual proximity offered by the mirror area could be one of the factors resulting in the preference but there are other contributing factors as well.

The opportunity to behave aggressively can act as a reinforcer as Thompson (1963) discovered with <u>Betta splendens</u>. Farwell (1970) found that 10 of 10 underyearling <u>S. punctatus</u> acted aggressively to mirrors presented to them. Thus underyearlings are aggressive to mirror images and this chance to behave aggressively could act as a reinforcer to remain on the mirror side as opposed to remaining on the non-mirror sides. Clayton and Hinde (1958) found in their study with <u>B. splendens</u>

that after 10 days the positive reinforcement of the mirror image waned. In this study there was no difference in preferences between those trials run in less than 10 days and those run in more than 10 days (see Appendix, Table XVIII). Both groups showed preferences for the mirror areas over the non-mirror areas. Habituation, therefore, does not appear to be a factor in underyearlings S. punctatus' preference for the mirror over non-mirror area.

So far two factors have been examined in reference to the cause of the preference for the mirror area, social proximity to another fish and the opportunity to behave aggressively which may act as a positive reinforcer.

A third factor could be that the mirror area offered a large "visual plane" to the fish. The reflection of the gravel in the tank would present a very large gravel area to the fish which it may prefer to the small visual area offered by the non-mirror area.

In all the trials with paired fish, one member of the pair showed an overwhelming preference for the mirror area over the non-mirror area. This finding further supports the fact that the mirror area is more preferred than non-mirror areas. In all situations where two underyearlings were placed together in other experiments, a hierarchy would develop. It is reasonable to assume that a hierarchy was set up in these instances also and it is further assumed that the dominant fish occupied the mirror area as that was shown to be the preferred area in trials using single fish. This situation appears to have occurred in the trials in the tanks which had mirror areas and where pairs of fish were tested.

In the trials involving the PVC and Clear areas, it is only among the paired fish trials that any significant preference was noted. Both individuals of the pair preferred the PVC area over the clear area, which may indicate a hiding effect. The PVC area would allow the fish to hide from the laboratory behind the PVC sheets along the sides while in the clear area the fish would be exposed to the routine of the laboratory.

As mentioned earlier, the results disprove the original hypothesis and are contrary to the results from the Visual Isolation Experiment (Exp. V). The reason for the preference of the mirror area over the other area could be any one of the three factors mentioned, a combination of them, or another so far unthought of factor. The findings may point out the contrary nature of agonistic behaviour and territoriality as being social behaviours. Eibl-Eibesfelt (1971) stated that often an animal species is both sociable and aggressive at the same time. The results from this experiment and Experiment V indicate the need for more work to be carried out on the social aspects of aggression and territoriality in underyearlings. The role of the substrate in respect to this problem must also be considered.

EXPERIMENT VII: PRIOR RESIDENCY

Prior residency is a well-documented aspect of territoriality and aggression, (Braddock, 1949; Phillips, 1971; Myrberg, 1972; Boer and Heuts, 1973) and this behaviour occurs among many fish of the littoral zone of the sea. Allee (1938) stated that the fact that dominance relationships between animals of the same size depend on visual characteristics of the environment indicates that dominance is not merely a function of so-called "physiological factors" but that a "psychological factor" is present as well. Prior residency basically makes use of the fact that the first fish to adapt to its environment will have an advantage over an intruding fish unfamiliar with the area.

Larval S. punctatus settle out of the plankton over a 2 or 3 day period in Logy Bay (personal observation). The present experiment was set up to try and determine if prior residency is a factor in the territoriality of underyearling S. punctatus. It is reasonable to assume that if prior residency is a factor the first fish to settle on the substrate will have an advantage over those that settle later. It was impossible to test naive fish from the field so laboratory fish were used. The fact that all the fish tested had had some prior experience as either a dominant or subordinate fish meant that both groups had to be tested. It was determined that prior residency could only be determined by the effect on the subordinate group as the dominant group was already dominant. It was hypothesised that if prior residency was an important factor in the aggressive behaviour of underyearling S. punctatus it would confer enough of an advantage that a formerly subordinate fish would become dominant after being a prior resident.

Materials and Methods

The two tanks used in the experiment were the same ones as those used in Experiment II (Aggressiveness). They were maintained under constant light conditions. A pair of fish was placed in each partitioned section of the tanks (2 tanks, 4 sections). All pairs consisted of equal sized fish. The fish were observed until a dominant-subordinate relationship was established. One member of each pair was then removed and isolated in a clear plastic aquarium. The remaining member of the pair was placed in the other tank. The other tank had a section which had a few bits of rock and coral in it thus presenting a "new environment" to the fish. This fish was designated the prior resident and was allowed to remain alone in the new environment for 24 hours. After the 24-hour period the isolated member was placed into this environment. Dominant and subordinate members of the pairs were used in the trials as the prior resident fish.

Observations were carried out after the isolated member had been replaced with the prior resident. Recordings consisted of the latency of encounters and the social status of each fish after the encounters. In one trial the fish were allowed to remain together for 24 hours then separated again but with the other member as the prior resident. After 24 hours the pairs were reunited and observed.

Thirty-six pairs (72 fish) of underyearling S. punctatus were observed in the experiment. These were broken up into two groups, 18 pairs with a dominant prior resident and 18 pairs with a subordinate prior resident. The study ran from November 1974 to February 1975.

Results

The dominant prior residents won 18/18 of their trials. The mean latency time for the encounters was 12 minutes. During the trials the dominant fish would approach the intruding fish (subordinate) which would in turn flee from the approach. There were no encounters which consisted of more than an Approach, Nip and Flee sequence. In 10 trials the sequence consisted of only an Approach and Flee sequence.

The subordinate prior residents won 7/18 trials. The mean latency time for these encounters was 7 minutes, and the encounters were usually very intense (a long sequence was involved). There were 4 instances where the subordinate prior resident fled from the approach of the dominant intruder. During 4 other trials, the subordinate prior resident attacked the intruder first but eventually the intruder became the dominant fish. In these 4 trials the encounters were very intense and the sequence involved Approach, Threat Posture, Body Shakes, Attack (by both fish) and eventually a Fleeing by the prior resident (subordinate fish). It was not until the prior resident fled that the social status of the fish could be determined. In the remaining 3 trials, the encounters were not as intense as the others involving only Approach, Display, Nip and Flee.

One other series of trials was run which utilized subordinates as prior residents after they had been tested as intruders. In this trial the hierarchy was very well established with the pair of fish having been together for over 24 hours. Of the 4 pairs tested, 1 subordinate prior resident became dominant. The encounters were very intense and the sequence quite long. The mean latency time for the encounters was 6 minutes.

Discussion

That 7 of 18 subordinate fish reversed their social status after being a prior resident indicates that a prior residence effect exists and confers an advantage in encounter situations to the prior resident among underyearling S. punctatus. Gibson (1968) found in pairs of juvenile B. pholis, of equal size, that the first fish to adapt to its surroundings eventually proved to be dominant. In the present experiment the intruding fish had to adapt to a "new" environment before interacting with the prior resident. In those trials in which the prior subordinate fish were the intruders, the prior residents won all the encounters, suggesting that the combination of being in a new environment plus the past social experience of being a subordinate fish resulted in this dominance by the prior resident. When the prior dominant fish were the intruders this combination of past social experience and being in a new environment resulted in very long (behavioural sequence involved a number of behaviours) and intense agonistic encounters between the intruder and the prior resident. This indicates that the aggressive drives of the two fish were quite similar thus suggesting something had affected the drive of either the prior dominant or the prior subordinate. This "effect" was again evident in those trials with the prior subordinate as the prior resident. The subordinate fish reversed its status after spending 24 hours alone in the new environment, in 7 of 18 trials, suggesting it had gained an advantage. The prior resident "effect" can thus be expressed in two ways: it could confer an advantage to the prior resident or it could inhibit the intruding fish. Both of these "effects" would interact on the aggressive drives of the fish.

Phillips (1971) found in his study that prior residency is an important aspect of territoriality of <u>Chasmodes bosquianus</u>. This fish is a seasonal inhabitant of the shallow water areas of rivers which flow into Chesapeake Bay, Maryland. Phillips theorized that the first fish to arrive in these areas would be more successful in setting up and maintaining territories than later arrivals. This so-called "resident effect" could likewise be applied to the situation found in underyearling <u>S. punctatus</u>. The first fish to settle from the plankton onto the substrate could be more successful in securing and maintaining territories than those who settle later.

GENERAL DISCUSSION

Territoriality typically involves aggression as a means of excluding conspecifics from a particular area. Territoriality among underyearling fish is not typical, however, and in the majority of species studies by various authors, underyearlings are aggressive without being territorial. This study was mainly concerned with showing that underyearling S. punctatus are territorial as Farwell (1970) suggested and with defining some of the parameters of the behaviour. Aggression is associated with territoriality, in this species, so a study of the aggressiveness of S. punctatus was necessary for a more complete understanding of territoriality. The first experiment examined the territoriality of both underyearling and older shannies. The experiment dealt mainly with the spatial requirements for the territory and the seasonal occurrence of it, both in the field and laboratory. The second experiment dealt with the yearly levels of aggressiveness for both underyearling and older fish. Environmental factors such as temperature, time of year and photoperiod were examined to determine their influence on the aggressive behaviour of the fish. Other experiments dealt mainly with the social aspects of the aggressive behaviour, the prior residency effect, habitat selection and behaviour of both underyearling and older fish in Logy Bay. A fairly complete picture of the aggressive and territorial behaviour of this species was determined and the sequence of these behaviours and their possible significance in the life history of the species can be suggested.

Experiment I demonstrated that underyearlings are territorial for the period September through January and from July to August. This territoriality was evident in tanks which had a total bottom area of 4050 cm^2 or more. In tanks with less than this area, dominance hierarchies were set up and maintained. It appeared from the laboratory experiments that only underyearlings will set up territories as no territories were set up by either yearlings or older fish during the experiment. Field work done with underyearlings showed that resident fish won significantly more encounters than did intruding fish. It appeared that the resident fish had an advantage, that of being a territory holder, which enabled them to be dominant in encounters with intruders. The size of the territories in the field were found to be largely determined by the substrate and not by the aggressiveness of the territory holder. It was further noted that underyearlings maintain territories from August through October in the field. There were no encounters observed between older fish in the field. In the laboratory experiment on territoriality, the size and past history of the fish were suggested as factors which may explain why territories were not set up by more fish. The presence of a critical time for territory formation in the laboratory is suggested as a possible reason for this lack of territoriality. The results suggest that underyearlings may be territorial throughout their first year of benthic life. Older fish do not appear to set up territories, at least in tanks with a total bottom area of 6750 cm^2 or less and they were not observed defending territories in the field.

Underyearling S. punctatus were found to be aggressive throughout the study period of November 1973 to December 1974. There was a definite seasonal change in their aggressiveness as it was quite low for the period January through June 1974 and higher for the period July through December 1974. These two periods were further shown to be statistically different from one another in latency of aggression. Both temperature and time of year (season) appear to be influencing factors. Which of these is the more important was not determined as they are so closely interrelated that separating their influence on the behaviour was not possible from these studies. Aggressive levels for fish under a constant light cycle were found to be lower overall than levels for fish under a natural light cycle. Photoperiod appears to affect the intensity but not the seasonality of aggressive behaviour in underyearlings. Older fish had a much lower overall aggressive level than underyearlings. When an underyearling completes its first year of benthic life (August) the aggressive level decreases sharply. This age of transition between underyearling and yearling status appears to be important in respect to aggressiveness in the species. The interaction between older fish and underyearlings was quite low but in all encounters between the two age groups the older fish were dominant.

Prior residency was found to be a factor in the territoriality of underyearlings. A significant number of previously subordinate fish, after spending 24 hours alone in a new environment, became dominant over their previously dominant pair member. In the majority of the other trials the encounters were very intense.

Underyearling fish, on settlement, select an environment when presented with a choice. In both laboratory and field experiments a rocky habitat was chosen over two other different habitats. Underyearling fish, therefore, select a particular habitat after settlement and metamorphosis. The arctic shanny probably selects a habitat which provides cover as this appears to be an important aspect of the habitat.

Tagging results indicate that older fish appear to show an affinity for a particular area of the substrate. This area affinity has never been observed, in the field, to be accompanied by aggression thus older fish appear to occupy a home range as opposed to a defended territory.

Older arctic shannies arrive inshore in Logy Bay by the end of June or beginning of July each year. Young-of-year fish settle from the plankton around the end of July or beginning of August. Upon settling onto the substrate they set up territories which they defend against other underyearlings. The first to establish territories have an advantage over those fish who settle later. These territories are not defended against older fish but rather older fish are avoided by the underyearlings. In Dyer's Gulch, therefore, a social system exists in which underyearlings maintain territories against underyearlings while older fish appear to occupy home ranges. These two systems overlap to the extent that underyearlings have territories in the home ranges of older fish. This can occur as the two age groups apparently do not compete directly for the area's resources. Older fish have been shown to feed mainly on amphipods while the major food item of underyearlings is copepods (Farwell et al., in press). Older fish also require larger rocks and boulders under which to seek cover than are required by the smaller underyearlings.

The temporal sequence of territoriality in underyearlings and its relationship to the complete social system of S. punctatus has been suggested but what of the function of this territoriality? Marler and Hamilton (1967) state that fighting is basically a means of competing more effectively for any commodity in short supply. Unless something is gained, fighting is, at best, a waste of energy. Territories are gained by the aggression of the arctic shanny and factors associated with these territories could be space, food, site familiarity and cover.

As Farwell (1970) suggested the territorial behaviour of underyearling S. punctatus would limit the numbers in a given area. The mechanism by which this is accomplished would be as follows. Underyearlings have been shown to select a preferred habitat. Once in this habitat they defend it and occupy it exclusively. Intruders are thus forced to inhabit less favorable areas or leave the area entirely. Those fish who inhabit the marginal areas would be more likely to be preyed upon or killed due to rough seas. In effect then, numbers of underyearlings are limited by those which can occupy territories in favorable areas.

The spacing of the animals is a prime consequence of territoriality in underyearling S. punctatus. However, as mentioned previously the substrate plays an important role in determining the size of the territory. Further to this the substrate was shown to be an important factor in the isolating aspect of territoriality. It was shown in the visual isolation experiment that underyearlings prefer to be alone rather than with other conspecifics when given the choice. This particular aspect of territoriality depends on the substrate as does the size of the territory. It thus appears as if the substrate is important in determining the spacing of individual shannies. The importance of the substrate relative to the territorial behaviour of the fish has yet to be fully determined.

Gibson (1968) showed that adult <u>Blennis</u> <u>pholis</u> demonstrate individual distances that vary in accordance with the level of aggression of the fish. Underyearling <u>S. punctatus</u> have a certain minimum distance within which they will react aggressively to conspecifics. At times of high densities in Logy Bay, the individual territories could shrink to a certain minimum size. It has been observed that there was a surplus population in Dyer's Gulch of non-territorial underyearlings in 1974 (personal observation), when densities were high. These non-territorial fish appeared to remain in another fish's territory only as long as they were undetected. Once they were observed by the territory holder they were driven out. However the possibility exists that if these fish remained undetected for a day or more they could defend the area they were in as their territory against the original resident, as a result of the prior residency effect, thus reducing the size of the original territory by half.

The various aspects of space as an area have been discussed but what of the quality of that space in terms of food and cover? Underyearlings, as mentioned before, feed mostly on copepod and less on amphipods (Farwell et al., in press). As these foods occur fairly evenly throughout Dyer's Gulch, the territories of underyearlings do not appear to be solely for feeding. This is supported by laboratory observations. The area in the tank where food was introduced was in all three instances of territories, shared by the pair of fish present. Both territory holders would feed regardless of which territory the food happened to fall into. Only after feeding would the territory holder chase the intruder out of its territory. In no instance was there an observed case of a fish being prevented from feeding because the food was in the other fish's territory.

Site familiarity would provide yet another survival benefit to the territory holder. Familiarity with an area would allow the animal to learn specific path habits to escape predators more effectively (Myrberg 1972). In Dyer's Gulch juvenile Gadus morhua, Myoxocephalus octodecemspinosus and M. scorpius are potential predators of the underyearlings. Although S. punctatus has not been observed in the stomach contents of these species (Pepper, 1974), this apparent lack of success of these species may be due to the escape responses of the shanny.

Provision of cover is the last of the possible functions of territoriality to be discussed and it may be the most important in the survival of the species. The territories of underyearlings provide cover not only from predation but perhaps more importantly from wave turbulence caused by storms. If an underyearling's territory provided protection during these storms, its chances of survival would be greatly enhanced. It is during this period of early November to January that the inshore population of S. punctatus disappears from

Dyer's Gulch. This reduction in population could be due to storm mortality and/or an off-shore migration. It is known that the older fish migrate inshore (personal observation) in July but an off-shore migration of underyearlings is still largely speculative. These winter storms drastically alter the substrate in Dyer's Gulch and only those fish with access to shelter are likely to survive the storms in shallow water.

The territories of the underyearlings likely do not serve a single function. Territories do provide food and site familiarity to the territory holder so in this regard the number of underyearlings who survive the first year of benthic life could be related to the quality of their territories. In turn the qualities of their territories could be related to the settlement time of the larvae from the plankton. As previously mentioned the first fish to settle have the prior residency advantage plus the opportunity to select the site of their territories. The earliest settlers are mobile enough to find or select the best area and defend this area successfully. Thus there appears to be an adaptive benefit to early settlement as well as to territoriality.

The survival advantage of territorial underyearlings has been suggested but what of the older fish? Why is their aggressive level so low in comparison and why are they not territorial?

Davis (1958) found in house mice that territoriality and dominance hierarchies are two poles of a continuum of behaviour that is dependent upon density. The density levels of underyearling

S. punctatus are quite high at times, 8.3 per meter in 1972 (Pepper, 1974), while the density levels of older fish are quite low in comparison (personal observation). It appears as if the aggressiveness involved in territorial behaviour in underyearlings is an adaptive behaviour related to density levels. It is known among animals that the highest mortality usually occurs during the first year of life, thus any behaviour which would increase survival success during this stage of development would be selected for. It is obvious that, at high densities, underyearlings which have territories have a better chance of survival than the non-territorial underyearlings or those which have poor quality territories. The density levels of the older fish are low, thus the need for high aggressive levels associated with territoriality does not confer any significant survival advantage to the older fish. The density levels in these older fish are such that there is ample space, thus older fish do not have to spend time fighting for territories. The low level of aggression noted in older fish suffices to spread them throughout the environment.

It thus appears that through behavioural differences between the underyearling's aggressively defended territories and the older fish's passively occupied home ranges, the survival sucesss of individual S. punctatus in Logy Bay is maintained.

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APPENDIX

TABLE XVIII

Preferences of Single and Pairs of Underyearling S. Punctatus in the Mirror Image and Isolation Experiment for Short and Long Run Trials.

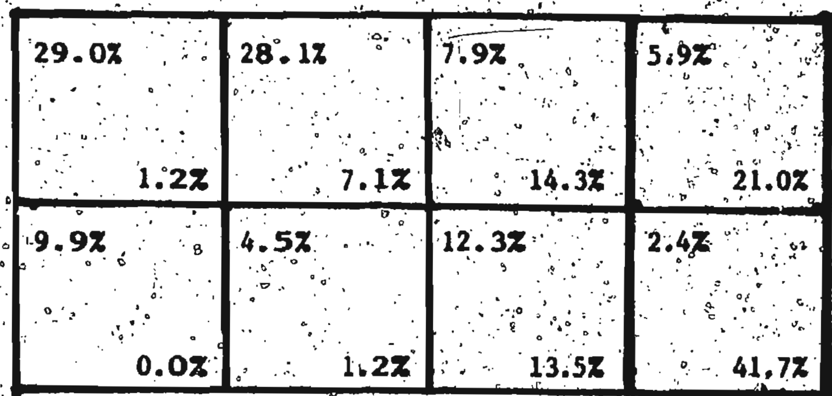
Time Period	Condition	N	Clear	PVC	Mirror	PVC	Mirror	Clear
10-30 days	Single	4	51	69				
10-30 days	Single	5			110	40		
11-14 days	Single	6					147	33
2-8 days	Single	3	42	48	63	27		
2-8 days	Single	2					50	10
9-10 days	Pairs	8	27	93	79	41	79	41

FIGURE V

A. Positional stereotypy values in grids of the large tank for Fish A and Fish B. Values in upper left corner are for Fish A and values in lower right corner are for Fish B.

B. Winners and positions of encounters observed in the large tank. Dark line forms theorized territory boundary between Fish A and Fish B's territories.

A


29.0%
1.2%
28.1%
7.1%
7.9%
14.3%
5.9%
21.0%
9.9%
0.0%
4.5%
1.2%
12.3%
13.5%
2.4%
41.7%

B

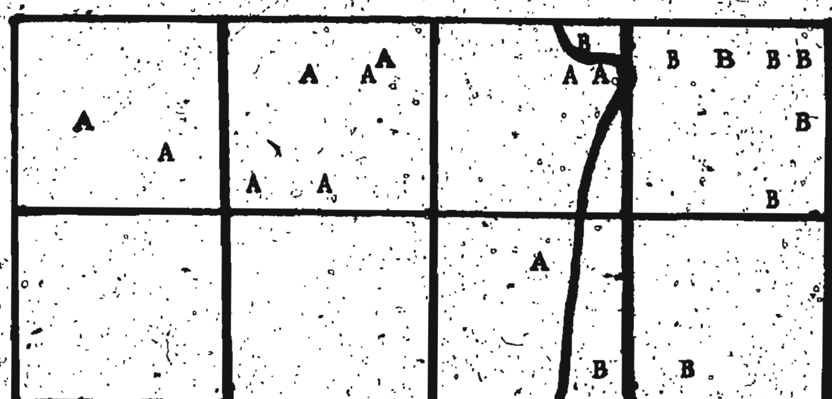

A A A
A
A
A A
B
A A
B B B B
B
B
A
B
B

FIGURE VI

A. Positional stereotypy values of individual fish in the grids of the small tank for the underyearling-older fish combination. The percent values for the underyearlings are in the upper left corner and the percent values for the older fish are in the lower right corner.

B. Positional stereotypy values of individual fish in the grids of the small tank for the underyearling pairs. The percent value for dominant fish are in the upper left corner while the percent values for subordinate fish are in the lower right corner.

A

14.5% / 4.8%	33.9% / 8.9%	13.7% / 34.7%
5.6% / 20.2%	15.4% / 4.8%	16.9% / 26.6%

B

3.7% / 9.6%	5.5% / 10.9%	21.3% / 36.7%
13.2% / 7.3%	21.5% / 11.1%	34.8% / 24.4%

FIGURE VII

A. Positional stereotypy values in the grids of the X-large tank for older fish. Values in the upper left corner are for fish A and values in the lower right corner are for fish B.

B. Positional stereotypy values in grids of the X-large tank for underyearling fish. Values in the upper left corner are for dominant fish and values in the lower right corner are for subordinate fish.

A

19.3% 6.2%	4.8% 3.4%	5.7% 3.9%	18.1% 36.0%
11.9% 41.9%	1.7% 1.2%	1.4% 1.2%	37.1% 6.2%

B

4.6% 7.8%	6.8% 6.9%	9.9% 9.0%	20.2% 13.0%
8.9% 11.1%	8.2% 13.4%	12.9% 16.6%	28.5% 20.2%

FIGURE VIII

A. Positional stereotypy values in the grids of the medium tank for dominant and subordinate fish. Values in the upper left corner are for dominant fish while values for subordinate fish are in lower right corner.

A

21.1% 11.3%	4.8% 6.7%	4.1% 9.7%	12.6% 16.1%
17.2% 11.3%	7.5% 4.5%	13.1% 8.3%	19.6% 32.1%

FIGURE IX

A. Positional stereotypy values in the grids of the large tank for the older fish. Values for fish A are given in the upper left corner and values for fish B are given in the lower right corner.

B. Positional stereotypy values in the grids of the large tank for underyearling fish. Values for the dominant fish are given in the upper left corner and values for the subordinate fish are given in the lower right corner.

A

34.7% 17.7%	8.1% 3.3%	19.4% 4.1%	29.8% 43.5%
4.8% 10.5%	0.0% 0.0%	0.0% 0.0%	3.2% 20.9%

B

14.9% 9.4%	6.5% 8.2%	9.2% 10.9%	7.9% 14.5%
21.1% 12.1%	5.9% 7.7%	9.7% 11.1%	24.8% 26.1%

FIGURE X

A. Positional stereotypy values of individual fish in the grids of the medium tank for introduced third fish trial. Values for dominant fish are in upper left corner and values for subordinate fish are in lower right corner.

B. Positional stereotypy values of the third fish in the grids of the medium tank.

C. Positional stereotypy values of the dominant fish in grids of the medium tank before and after the introduction of the third fish. The before values are in upper left corner and after values are in the lower right corner.

D. Positional stereotypy values in the grids of the medium tank for the subordinate fish before and after introduction of the third fish. The before values are in upper left corner and the after values in the lower right corner.

A

5.5% 14.5%	4.7% 0.4%	3.1% 4.7%	7.5% 14.1%
31.0% 16.9%	3.9% 0.8%	11.0% 5.9%	33.3% 42.7%

B

25.9%	2.5%	2.5%	34.6%
7.4%	12.3%	7.4%	7.4%

C

4.7% 7.4%	4.7% 4.9%	4.0% 1.2%	10.9% 0.0%
18.9% 56.8%	4.0% 3.7%	14.9% 2.5%	37.9% 23.5%

D

19.0% 4.9%	0.0% 1.3%	4.6% 4.9%	14.9% 12.3%
23.0% 3.7%	0.0% 2.5%	2.9% 12.4%	35.6% 58.0%

FIGURE XI

A. Positional stereotypy values in grids of the medium tank for the dominant fish before and after removal for two days. Values in upper left corner are for the before period while those in the lower right corner are for the after period.

B. Positional stereotypy values in grids of the medium tank for the subordinate fish before and after removal for two days. Values in the upper left corner are for the before period while values for the after period are in the lower right corner.

C. Positional stereotypy values in grids of the medium tank for dominant and subordinate fish. Values for dominant fish are in the upper left corner while the values for the subordinate fish are in the lower right corner.

A

57.7% 12.6%	7.3% 16.0%	6.6% 16.0%	16.1% 33.8%
5.1% 13.6%	1.6% 0.0%	0.7% 4.0%	5.1% 4.0%

B

5.1% 16.0%	5.1% 4.0%	8.0% 0.0%	40.2% 12.5%
2.1% 0.0%	1.5% 0.0%	5.1% 1.5%	32.9% 66.0%

C

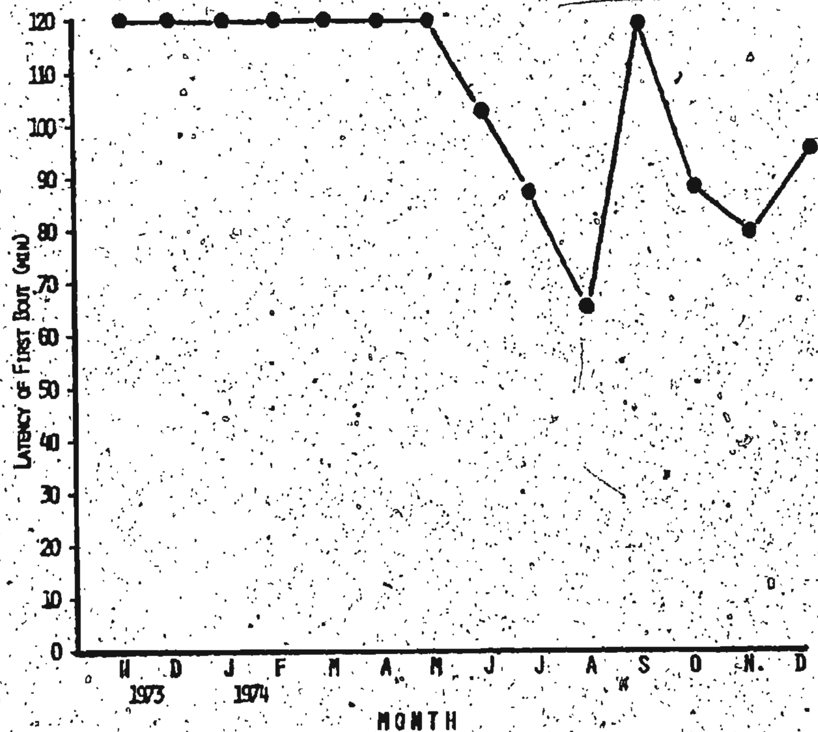
50.9% 6.8%	8.7% 5.0%	8.1% 6.8%	18.6% 36.0%
6.3% 1.9%	1.2% 1.3%	1.2% 4.3%	5.0% 37.9%

FIGURE XII

A. Monthly mean latency to first observed bout values for older fish in the aggressiveness experiment.

B. Monthly mean number of bouts per 15 minute period for older fish in the aggressiveness experiment.

A


LATENCY OF FIRST BOUT (MIN)
120
110
100
90
80
70
60
50
40
30
20
10
0
N D J F M A M J J A S O N D
1973 1974
MONTH

B

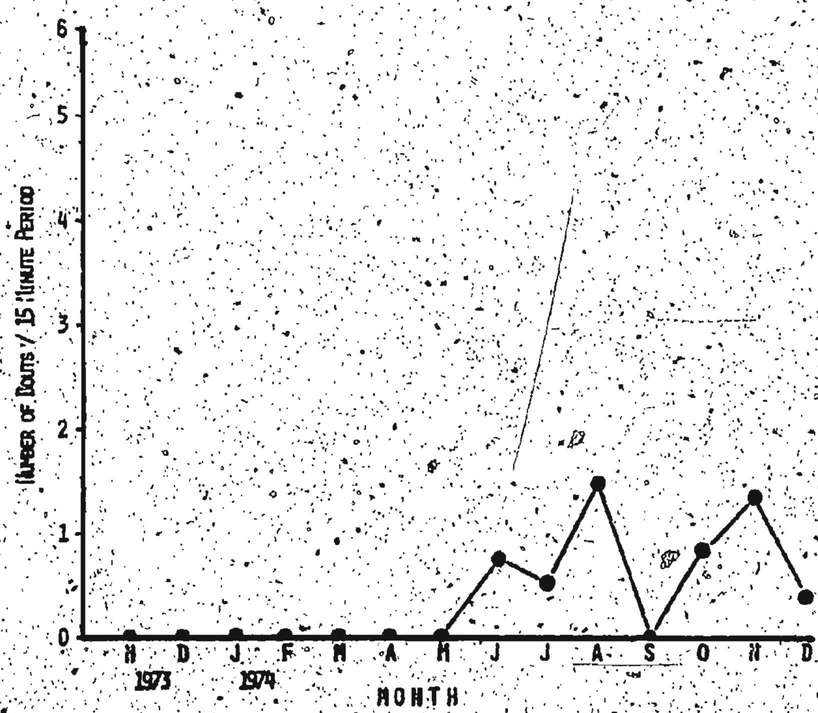

NUMBER OF BOUTS / 15 MINUTE PERIOD
6
5
4
3
2
1
0
N D J F M A M J J A S O N D
1973 1974
MONTH

FIGURE XIII

A. Monthly mean latency to first observed bout values for older fish-underyearling combination in the aggressiveness experiment.

B. Monthly mean number of bouts per 15 minute observation period values for older fish-underyearling combination in the aggressiveness experiment.

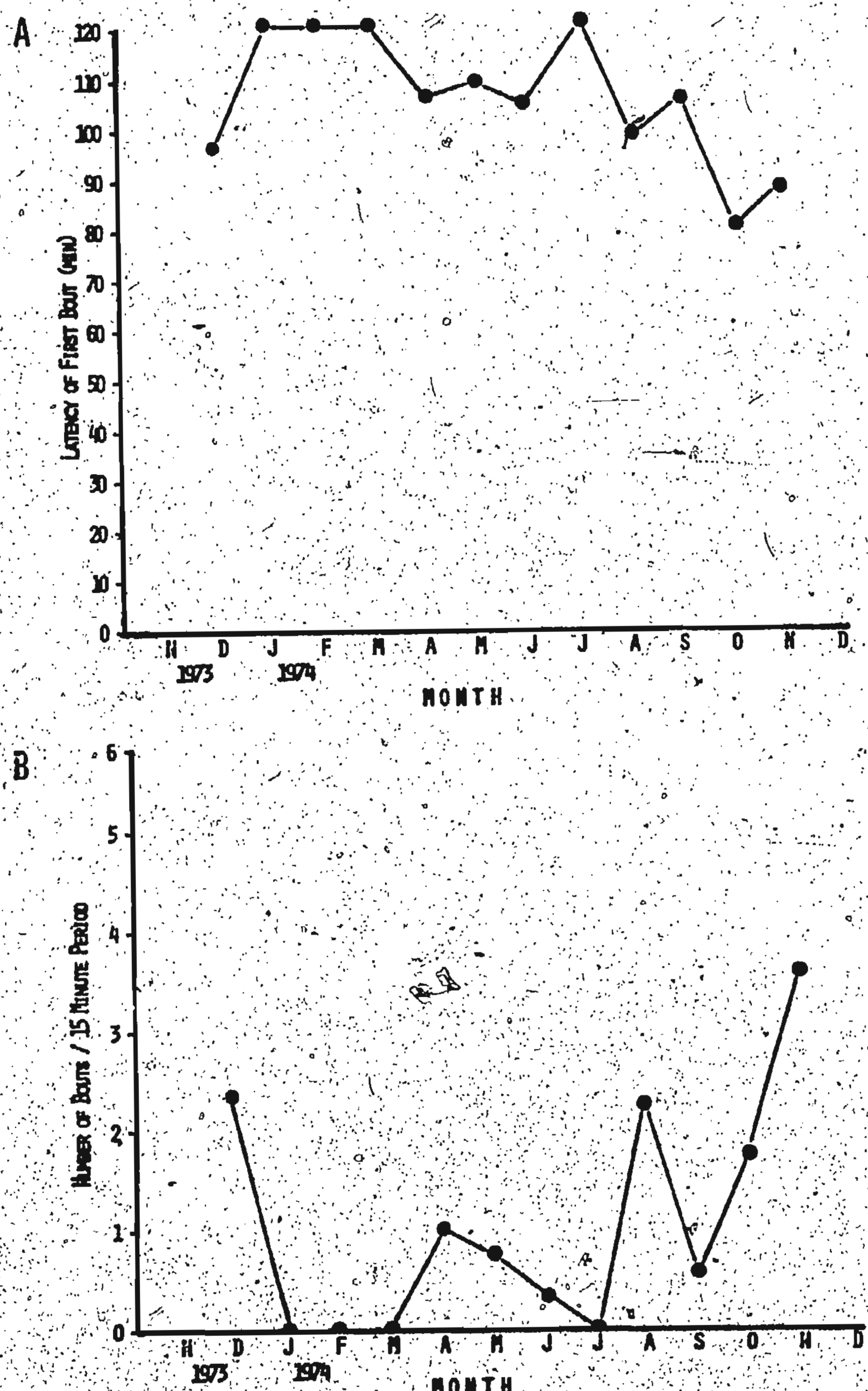
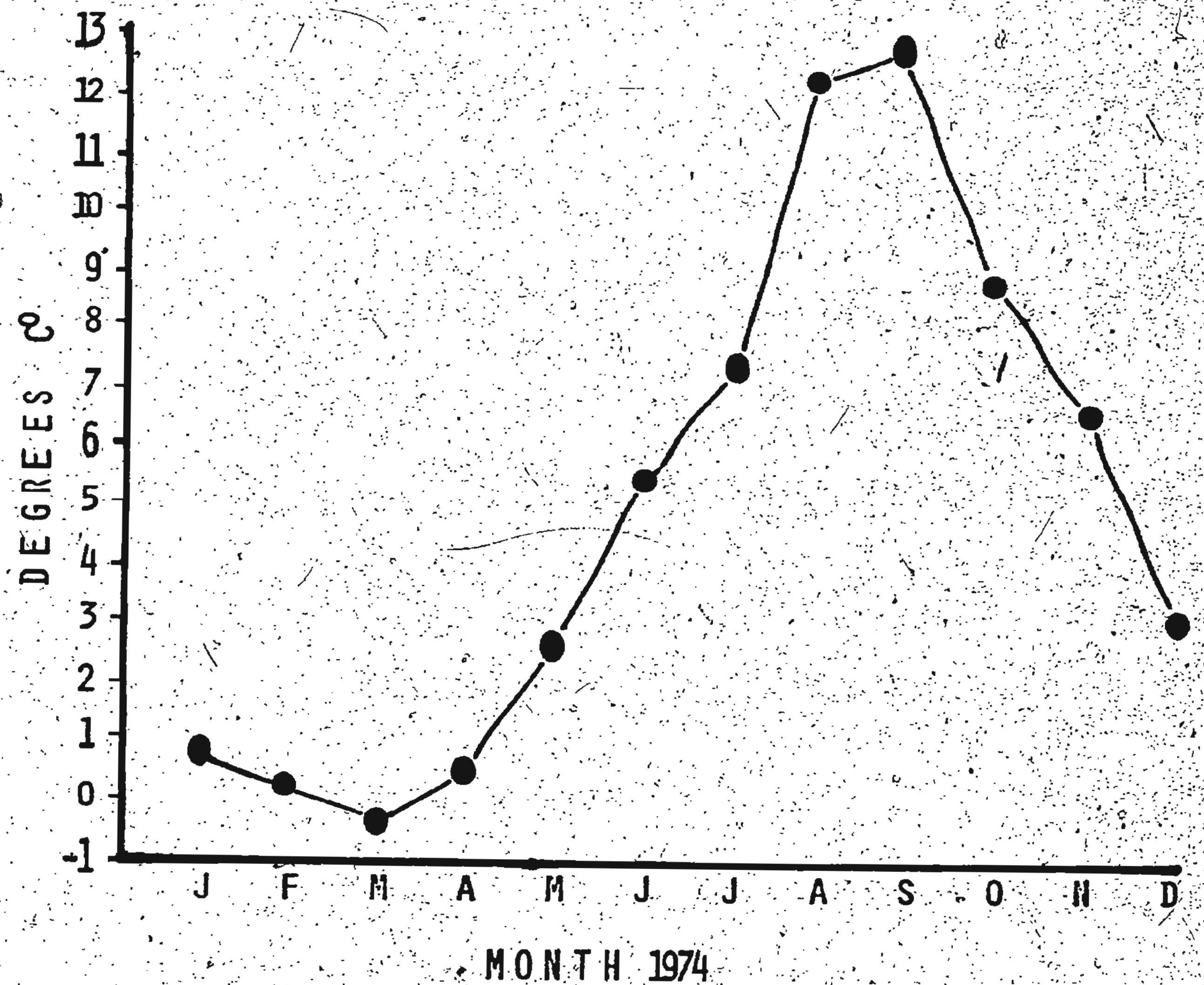

A
Latency of First Bout (min)
0
10
20
30
40
50
60
70
80
90
100
110
120
N D J F M A M J J A S O N D
1973 1974
MONTH
B
Number of Bouts / 15 Minute Period
0
1
2
3
4
5
6
N D J F M A M J J A S O N D
1973 1974
MONTH

FIGURE XIV

Monthly mean temperatures of laboratory seawater for the period January to December 1974.


DEGREES C°
13
12
11
10
9
8
7
6
5
4
3
2
1
0
-1
J F M A M J J A S O N D
MONTH 1974