FRI-UW-7909
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ANNUAL REPORT
Anadromous Fish Project

Project No. AFC-82
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Project Period: October 1, 1977 to September 30, 1978

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This project was financed with Anadromous Fish Act (P.L. 89-304) funds through U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Submitted: June 27, 1979

Approved
E. Salo for R. L. Burgner
Director

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PREFACE

Most of the past and current research conducted at the Big Beef Creek Research Station has utilized the experimental streams (controlled-flow spawning channels) that were installed in 1967 and 1968 (for a detailed description of this facility see Beall 1972; Schroder 1973; Koski 1975).

At first we employed these structures to answer questions that had a direct bearing on the design and management of spawning channels. For example, we attempted to determine the gravel composition that would maximize egg-to-fry survival in our channels (Koski 1975), the number of adults that should be placed into such structures (Schroder 1973) and whether fry production could be increased in spawning channels by allowing separate waves of adults to utilize the same spawning areas (Schroder 1977).

These investigations prompted the two major research objectives of our current proposal. First, we wanted to test the management techniques that our previous studies had suggested would maximize fry production in spawning channels. Second, we felt that the success of any salmon enhancement program (e.g., hatcheries, egg boxes, and incubation channels, stream improvement, and spawning channels) depended on its ability to meet the biological requirements of the organism - whether these were physiological, behavioral, and/or genetic. Consequently, we proposed a series of experiments that were specifically designed to examine the ethological and physiological responses of salmon to an array of controlled environmental challenges.

So far our attempts to maximize fry production in the spawning channels have met with mixed success. Egg-to-fry survival has decreased from approximately 50% in 1976 to about 13% in 1978. This decline appears to be associated with a deteriorating incubation environment. The amount of fines (material $\leq$ 3.2 mm in diameter) within the spawning bed of each channel have increased and water flows have changed because of cracks and splits in the wooden walls that separate the experimental streams from one another. Consequently, until the channels can be cleaned and repaired it will be impossible to appraise the techniques we have developed to maximize fry production.

Moreover, in 1977 not enough fish returned to the stream to fill the spawning channels. This may have been caused by poor egg-to-fry survival in the stream[1] and/or the apparently high fishing pressures

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[1]Sixty to seventy percent of the fish returning to our stream after November 1st (late run) spend 3 years in the ocean before they mature (i.e., they are 4-yr-olds). In 1973, (the brood year that would produce 4-yr-old fish in 1977) none of the late run fish was placed in the spawning channels. Consequently, part of the decrease in the number of adult salmon returning to Big Beef Creek in 1977 may have been caused by the poor incubation conditions existing in the stream.

imposed on the chum salmon stocks utilizing Big Beef Creek. During the fall and early winter of that year it was common to see one or two boats blocking the mouth and estuary of the stream with gill nets.

Because the egg-to-fry survival rate in the spawning channels was decreasing and fishing pressure was at best uncertain, the channels were not used as a production facility in 1978. Instead, a small hatchery (supplied with artesian water) located next to the spawning channels was used to incubate approximately 2 million eggs. So far, over 1.5 million chum salmon smolts have been released from the hatchery this spring (1979) and an additional 1/4 million will be liberated before June.

Even though these circumstances prevented us from fulfilling our first research objective, we have been able to use the channels to investigate adult behavior. For the past three years, the effects of intrasexual competition and epigamic selection (the two components of sexual selection) on spawning chum salmon have been investigated. In conjunction with that study, we also measured the influences of parental age and size at maturity on the growth rates and survival of progeny.

The above investigations on the effects of sexual selection have now been completed and a manuscript describing the entire study is currently being prepared. After it is finished it will be submitted as the final report for this three-year project. Part I of this current report summarizes a small portion of the work that dealt with the effects of intrasexual competition on males. Part II was prepared by Mr. Gary Duker and is a summary of his attempt to determine whether female chum salmon exhibit a preference for particular types of spawning gravels. A complete description of this study can be found in his thesis (Duker 1977) which was submitted to the National Marine Fisheries Service (NMFS) in the fall of 1977.

ABSTRACT

The annual report for 1977-78 is in two parts. The first describes research on the determination of genetic contributions made by subdominant chum salmon males in spawning acts. Through the use of protein electrophoresis, it was found that subdominant (satellite) males fertilize as much as 46% of the eggs deposited by a female in a single spawning. The second part is a report on the process of nest selection by female chum salmon. While selection for downstream position within test cells proved to be significant, gravel size was the dominant environmental factor used by females in the selection of nest sites. The importance of vision and olfaction in the expression of normal selection behavior was demonstrated in a series of experiments based on sensory occlusion.

PART ONE: USE OF PROTEIN ELECTROPHORESIS TO EXAMINE THE GAMETIC CONTRIBUTION OF SATELLITE MALES

Recently, we completed a three-year investigation that relied upon behavioral observations to determine whether mate selection in chum salmon populations varied or remained constant under a variety of sex ratios (Schroder, in preparation). The social behavior of the adult fish was thoroughly examined and it was found that the basic behavioral patterns of each sex were distinctly different.

Females establish territories and dig a series of three to six discrete nests. As each nest is completed, the female releases a portion of her eggs, while one or more males simultaneously ejaculate milt. At the completion of each spawning act, the female immediately begins to cover her eggs with gravel, and in the process she may start a new nest slightly upstream from her most recent spawning site. Generally, females are substrate-oriented because the majority of their attention is directed toward nest construction, egg burial, and finally, to the collective burial of all their eggs under one large mound of gravel.

Males, on the other hand, do not establish permanent territories or help in nest or mound construction. They are mobile and will attempt to spawn with as many females as possible. Aggression is common, and unlike females, prolonged ritualistic fights occur among rivals. These agonistic interactions often occur directly over the nest site of a female and thus effectively stop other males from courting and spawning with her.

When large differences exist among males in their ability to obtain mates the "have nots" are expected to evolve alternative mating strategies designed to circumvent the effects of intrasexual competition and/or female choice (Howard 1978). In breeding populations of salmon and trout, subdominant males have adopted the mating (behavioral) strategy of positioning themselves slightly downstream from a courting pair. These males continuously try to approach the female and spawn with her. Fish of this type have been referred to as "satellite," "accessory," or "secondary" males and if there are more than two of them, they usually lie in a semicircle (the open end facing the current, just downstream from the dominant or alpha male). Dominance hierarchies exist among satellite males with the strongest animals having the closest access to the pair (Kuznetsov 1928; Shapovalov and Taft 1954; Hanson and Smith 1967; McCart 1970; Schroder 1973).

A question that has long intrigued students of trout and salmon reproductive behavior (e.g., Jones and King 1952; Hanson and Smith 1967; McCart 1970) is whether satellite males fertilize any eggs during the spawning acts they participate in. We estimated the gametic contributions of alpha and satellite males during particular spawnings by using genetic variation analyzed by protein electrophoresis. This technique has also been used to examine paternity in a variety of other animal species (e.g., see Berry and Jakobson 1973; Tilley and Hausman 1976; Cobbs 1977; McCracken and Bradbury 1977; Nelson and Hedgecock 1977).

Methods and Results

Since single gene differences can be used to determine paternity, we created situations where the alpha and satellite males that competed for a female had different allelic forms of the same protein. To do this the allozyme phenotypes (allelic forms of a protein) of the males were determined before spawning occurred. Electrophoretic examination of muscle, eye, and liver tissue obtained from chum salmon native to Big Beef Creek showed that the fish were polymorphic in five isozyme (enzyme) systems: 6-phosphogluconate dehydrogenase (6-PGDH), asparate aminotransferase (AAT), phosphomannose isomerase (PMI), isocitrate dehydrogenase (IDH), and asparate aminotransferase-3 (AAT-3) (Seeb, personal communication). Two of these isozyme systems (6-PGDH and AAT) have allozyme phenotypes that can be detected by examining muscle tissue. Consequently, genetic differences among males within these isozyme systems could be determined without killing the fish.

Sixty adult males were captured, anesthetized, and a small bit of muscle tissue (no larger than a pencil eraser) was removed from the side of each fish. After being sampled, every male was tagged and released into a section of our spawning channel where he could easily be recaptured. The muscle samples were then electrophoretically analyzed by Mr. Jim Seeb who used methods previously described by Utter et al. (1974), May (1975), and May et al. (1975). Once the allozyme phenotypes of each fish had been identified, we placed two or three males possessing different genotypes together with a female and allowed them to spawn. The mating strategy employed by each male and his location at the time of spawning were recorded so that the association between mating strategy and gametic contribution could be determined.

After the fish had spawned (with all males participating) the parental fish were killed and liver, eye, and also muscle tissue were collected and electrophoretically analyzed to identify all the allozyme phenotypes of each fish. Moreover, every egg deposited at each spawning was retrieved and incubated in a hatchery located next to the spawning channel. Six matings of this type were obtained and the zygotes collected from each spawning were kept in the hatchery until yolk absorption was completed. Because the males involved in every mating had different allozyme phenotypes (in one or two isozyme systems) it was possible to estimate the number of eggs each fertilized by examining muscle tissue samples obtained from the progeny. Consequently, 100 randomly chosen fry originating from each spawning were killed and electrophoretically examined.

Table 1, presents the results of the biochemical analyses performed on the progeny and shows, that under some circumstances, satellite males can make significant genetic contributions. Moreover, once these data were coupled with the behavioral observations made while the fish spawned, it was found that the closer and more attuned a male was to the female the more eggs he was able to fertilize.

Table 1. The estimated genetic contribution of alpha and satellite males during natural spawnings. Each number represents the estimated percentage of eggs fertilized by a male during one spawning act.

	Male rank in the social hierarchy		
Spawning	Alpha	Satellite 1	Satellite 2
1	67	33	
2	53	30	17
3	54	46	
4	100	0	
5	83	17	
6	73	27	

DISCUSSION

The interpretation of the results shown in Table 1 depended on a number of assumptions. First, that the allozyme phenotypes used to determine paternity (in this case variant forms of AAT and PMI) represented genetic variation and were not environmental or ontological artifacts. Second, that allozyme phenotypes rarely mutate into different forms; third, that genetic migration was controlled; fourth, that the allozyme markers used did not differentially affect egg-to-fry survival in any of their possible allelic combinations; fifth, that the gametes bearing the genes responsible for each allozyme phenotype were equally viable; and finally, that each male was fertile.

The genetic basis of the variant forms of AAT and PMI was established by controlled breeding experiments performed by Seeb and Wishard (1977). The neutrality of the genes responsible for each allozyine phenotype (at least from the gamete-to-fry stage) has not been formally tested, but the data presented by Seeb and Wishard (1977) clearly suggest that gametes and zygotes possessing different combinations of these genes survived equally well. Genetic migration (i.e., the intrusion of unwanted fish during a mating) was controlled by the experimental design, and because spontaneous mutation occurs so rarely (10^{-5}, Utter, personal communication) we did not consider it to be an important source of error. We tested the fertility of some of the males that participated in these matings by artificially crossing them with the female they had previously spawned with. The eggs obtained from each cross were incubated in the hatchery until they had closed their blastopore. At this time, a random sample of fifty eggs was collected from each cross and placed in Stockard's solution (85% distilled water, 6% glycerine, 5% formalin, and 4% gacial acetic acid). Since this solution clears the chorion it was possible to determine whether any of the eggs did not possess a developing embryo. The fertility of five males was examined in this manner and in every case the males were equally fertile.

PART TWO: NEST SITE SELECTION BY CHUM SALMON (*ONCORHYNCHUS KETA*)

Introduction

While some spawning bed characteristics have been associated with salmonids, little research has been directed at the nest site selection process of the female fish. The importance of this selection process is clear for the potential progeny of fish making poor spawning site choices, since they would be strongly selected against (Linström 1967).

To investigate the nest site selection process, a series of experiments was conducted in the controlled-flow spawning channel located at the University of Washington's Big Beef Creek Fish Research Station. Chum salmon, *Oncorhynchus keta*, were used as the experimental subject. The purpose of these experiments was broadly twofold:

1) to examine how gravel size influences the selection process of chum salmon; and
2) to examine how the visual and olfactory sensory modes are used by a female when she selects a spawning site.

The Influence of Gravel Substrates on Nest Site Selection

Studies on spawning salmon have revealed several potential cues that may be used by the female fish while she selects her nest sites. By controlling the influence of several potential cues (i.e., water velocity, water depth, and upwelling water), an experimental design was devised to investigate the influence of gravel size on nest site selection.

Experimental Design

Three sections of the spawning channel were partitioned into six test cells measuring 3.0 m x 6.1 m each. Each test cell was then further divided into four equally-sized test plots. To test for a gravel size preference, four "discrete" sizes of washed gravel (Fig. 1) from a common source were introduced into each test cell. Each test plot was filled with one size of gravel, and each test cell had all four sizes of gravel. The juztaposition of the gravel sizes (Fig. 2) was arranged so that the positional effects of the test plots on nest site selection could be examined statistically.

Female chum salmon are known to select and construct nests nocturnally and diurnally with or without the presence of males. Consequently, solitary females were placed in test cells during nocturnal trials and male-attended females were placed in each test cell during daylight trials. This pattern of female placement was used to prevent fish from spawning in the test cells.

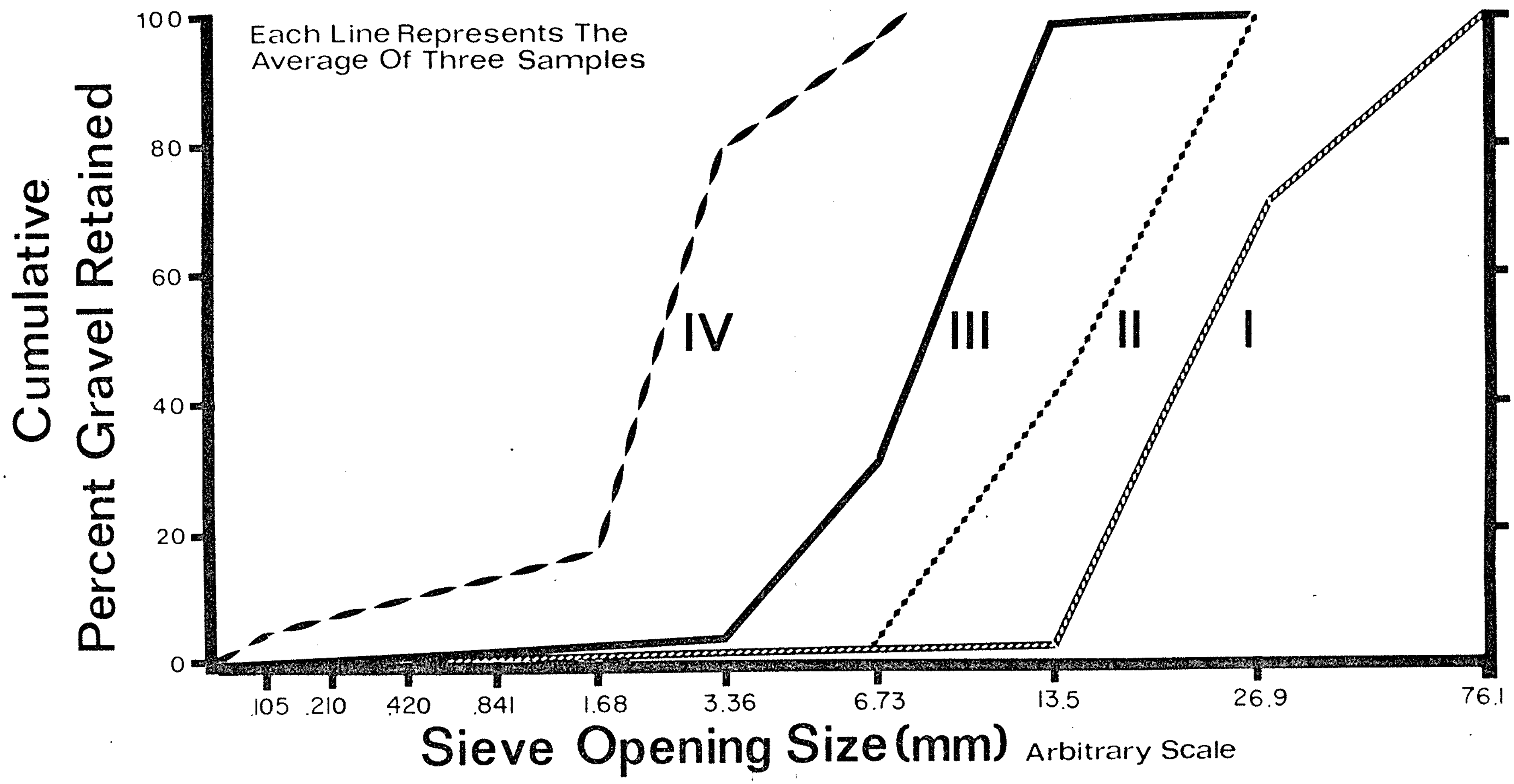

Fig. 1. The composition of the four sizes of gravel utilized in the test cells.

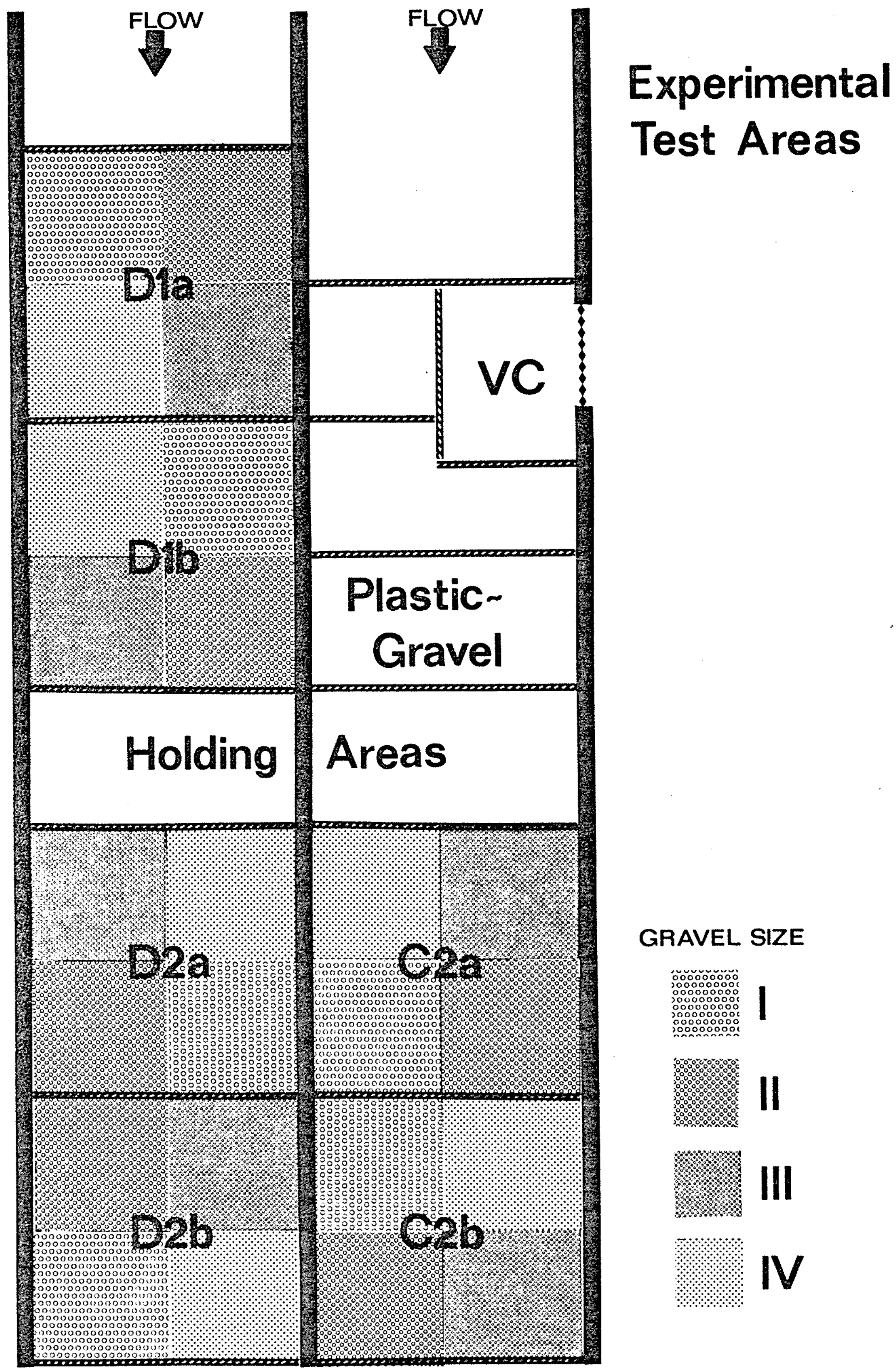

Fig. 2. Detail of experimental test areas in the Big Beef Creek spawning channel; Plastic-Gravel and VC (viewing chamber) sections were utilized in studies examining the sensory basis of the selection process.

Results and Discussion

An analysis of variance procedure was used to examine the interactions involved in the location of the selected nests (location being defined in terms of front or back position, right or left position, and gravel size for each test cell). Two sources of significance were revealed - females preferred to construct nests in the back half (downstream end) of each test cell and they showed a gravel size preference (Fig. 3). Multiple comparison of the gravel size selections revealed an obvious trend in gravel size preference; II, III, I, IV (where gravel I is the largest).

The significant selection preference for gravels II and III indicate that their compositions are the most appropriate of the four test substrates as spawning environments. However, the ultimate causation of this selection preference can only by found by studying the selective advantage provided eggs and larvae in the various gravel sizes.

The predominance of nests at the back of the test cells appeared to be related to a peculiar female behavior. Female chum salmon were frequently observed using the rear (downstream) picket for resting and as a "platform" for pushing off into a digging movement. This position could provide protection and reduce aggressive interactions or merely provide the fish with a convenient reference point.

In summary, the location of nests in the test cells can be primarily described in terms of gravel size. The position effect was significant, but the juxtaposition of gravels within the test cells was the dominant environmental stimulus for nest site selection.

THE ROLE OF SENSORY SYSTEMS IN NEST SITE SELECTION

The determination of how an organism locates suitable spawning sites requires the testing of the sensory systems of the animal in its environment. Since the array of stimuli available on the spawning ground are nearly impossible to measure and manipulate, this study resorted to an examination of the consequences of occlusion of sensory input.

Experimental Design

If a female constructed a nest during her first gravel preference trial, she was considered for use in this phase of the investigation. This willingness to construct a nest was interpreted as an indicator of the physiological state of the female, thereby all females were deemed equally motivated toward the selection of a nest site and spawning. With this assumption, the results from trials with several females could be lumped for examination.

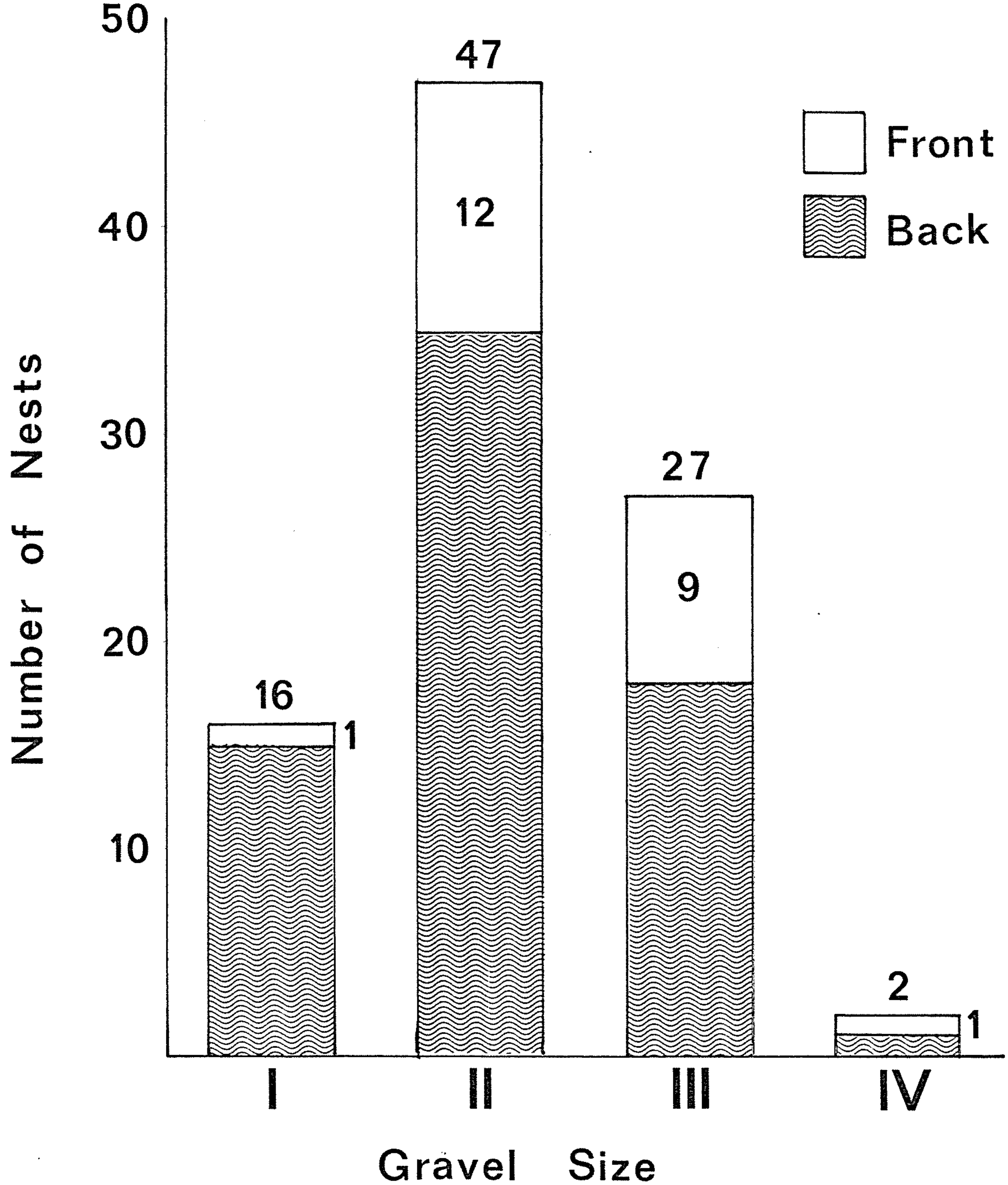

Fig. 3. The relationship between gravel size and position for nest site selections by female chum salmon.

Females with altered sensory systems were either tested in the test cells or a viewing chamber (Fig. 4) where observations were made on nest selection behavior.

Vision in Nest Site Selection

Occlusion of vision was accomplished by injecting 0.3-0.4 ml of 3% aqueous benzothonium chloride into the posterior chamber of each eye. Besides blinding females, three fish were unilaterally-blinded so that the potential orienting component of vision could be examined.

Experimental trials demonstrated an obvious area of significance; blinded females were unsuccessful in their attempts to construct nests (0 successes in 21 trials). These data are not meant to imply that the blind females were inactive and not attempting to construct nests; in reality, quite the contrary was the case.

In general, nosing and exploratory digging (activities leading to nest site selection) are initially random, which become localized once a nest site is selected (Tautz and Groot 1975). Blind fish followed the same pattern of nosing and exploratory digging; however, these activities were never observed to become localized.

Observations made in the viewing chamber on unilaterally-blinded females contributed greatly to an understanding of the orienting component of vision in chum salmon. McCart (1969) and S. Schroder (personal communication) have noted that sockeye and chum salmon, respectively, tend to alternate successive digs from one side to the other during nest preparation. In addition, McCart (1969) found the direction of turning after digging to be independent of the side on which the dig was made. On the other hand, unilaterally-blinded chum salmon females show a strong tendency to dig with the blind side toward the gravel and to turn with the untreated eye facing the nest. The eye movement during the turn was highly suggestive that the female uses reference points surrounding her nest to align her position.

The studies on bilaterally- and unilaterally-blinded fish indicate that the females do use visual reference points during nest selection and construction; and when vision is interrupted, there is a complete cessation in the normal expressions of these behaviors.

Olfaction in Nest Site Selection

Olfactory occlusion was achieved with the use of a distilled acetylated monoglyceride, MYVACET 5-07 (Health and Nutrition Division, Eastman Chemical Products, Inc.). The melted material was injected from a blunt syringe into the posterior naris of each olfactory sac. The MYVACET immediately congealed into a tough, waxy solid which was dense enough to block water passage. Subsequent dissection revealed that the MYVACET plugs overlaid the sensory epithelium completely.

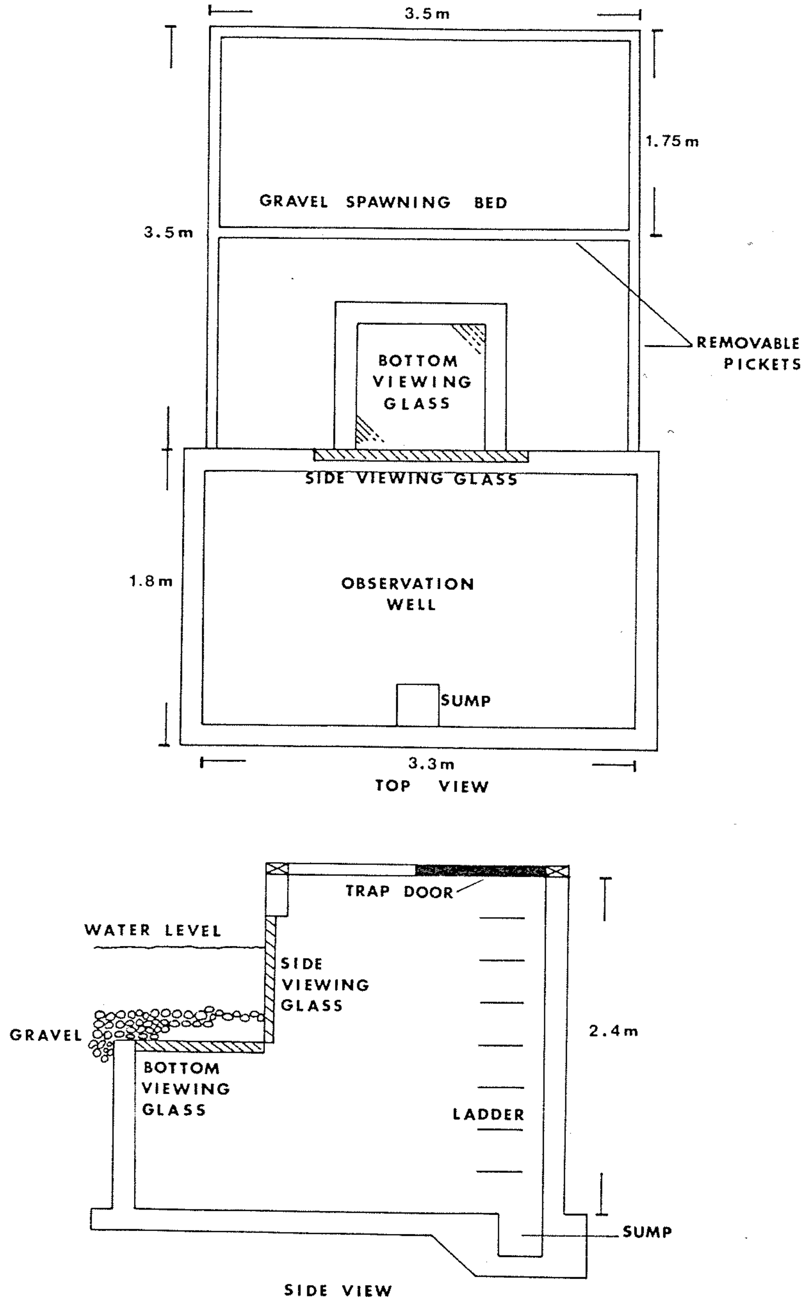

Fig. 4. Schematic views of the chamber used to house videotape and cinefilm equipment employed in producing behavioral records of spawning chum salmon.

Solitary anosmic females were lethargic and were observed to remain along the walls of the spawning channel for hours without movement. During 20 trials, no nests were observed and very little searching activity was apparent. Nest site selection and construction were only observed when females were paired with males (6 successes in 13 trials).

There appear to be several possible explanations for the behavior exhibited by anosmic chum salmon. Initially, the lethargic behavior suggests that the treated females were merely sulking because of the sensory treatment. However, this behavior was definitely not observed in females which had other sensory systems altered or in the treatment controls. Therefore, I feel that there is a more complicated relationship between olfactory occlusion and behavior.

It is conceivable that the sensory occlusion may have caused differences in behavior that transcend the loss of the sense. Peters (1971) noted the possibility that olfactory occlusion (in salmonids) may affect behavior patterns not directly associated with odor stimuli. However, several of the anosmic females were able to select and construct nests, as well as to spawn.

With the assumption of home stream recognition, the lack of activity is best explained in terms of the motivational state of the female. MacLean (1949), as quoted by Peters (1971), stated that "the olfactory sense is of great importance to lower animals and may contribute to the regulation of basic motivation needs."

It is conceivable that nest site selection can only be released when the animal is in the appropriate motivational state, with this state being dependent on the reception of certain olfactory cues. The fact that anosmic females in production sections of our spawning channel constructed nests and spawned indicates that certain fish were able to reach the necessary motivational state. Whether nest selection was the result of the maturation process of the female or the appearance and courting of a male or other unknown stimuli is impossible to interpret.

Within the constraints of this study, it is impossible to define the ultimate function of the olfactory system. Clearly, the subsequent behavior of the anosmic chum salmon suggests that olfactory cues are important in nest site selection.

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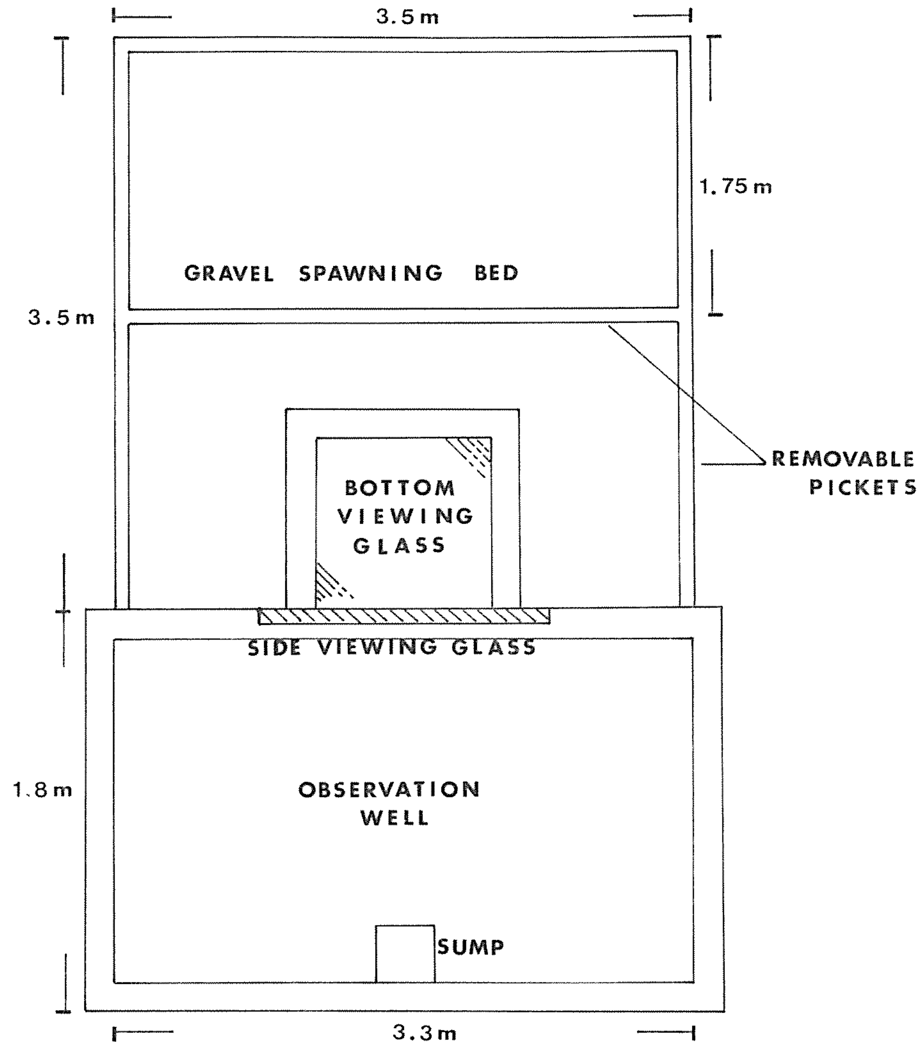
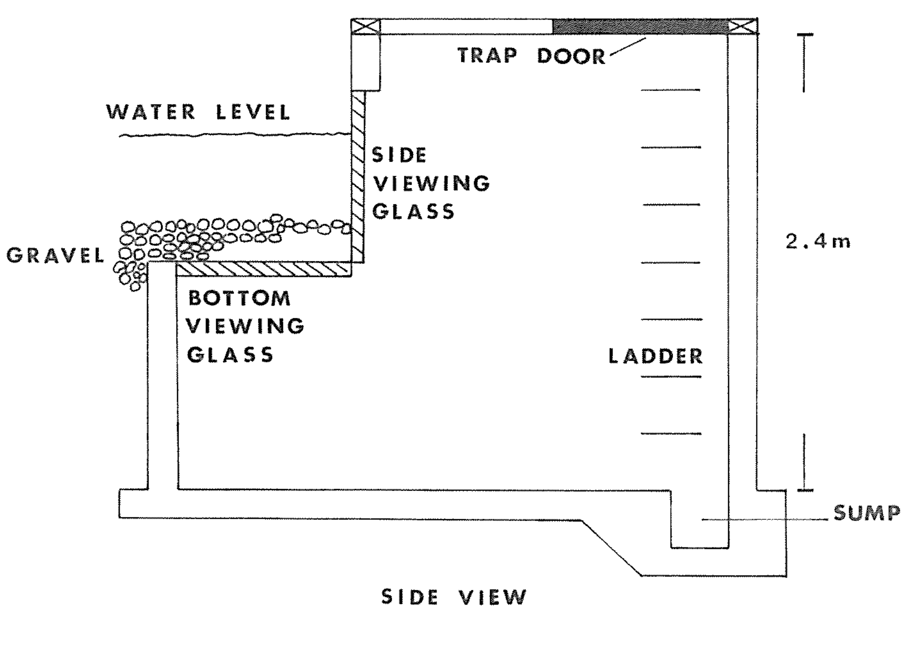


TOP VIEW



SIDE VIEW