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AN INTRODUCTION TO ENVIRONMENTAL ETHOLOGY: A PRELIMINARY COMPARISON OF SUBLETHAL THERMAL AND OIL STRESSES ON THE SOCIAL BEHAVIOR OF LOBSTERS, AND FISHES FROM A FRESH-WATER AND A MARINE ECOSYSTEM

By

John H. Todd, David Engstrom, Stewart Jacobson
and William O. McLarney

July 1972

PROGRESS REPORT

*Prepared for the Atomic Energy Commission
AT (11-1) - 3567.*

WOODS HOLE, MASSACHUSETTS 02543

## DISCLAIMER

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Principal Investigator: John H. Todd

Progress Report

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Approved for Distribution

John M. Hunt, Chairman
Department of Chemistry

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ABSTRACT

An environmental ethology founded upon the biological relationships linking environmental stresses, animal behavior and organization and the development of ecosystems is proposed. The concept of stress in relation to animal behavior and aquatic ecosystems has been reinterpreted. Extrinsic stresses have been separated into two categories: 1. Historical stresses, for which animals have a prior evolutionary history (e.g. thermal pollution); 2. Artificial stresses, those that have played little or no role in animal evolution (e.g. oil, chlorinated hydrocarbons, radioactive wastes) and are primarily the products of man's technologies. Experiments evaluating the impact of the two classes of stress on the social organization and behavior of fishes and lobster are described.

A comparative behavioral analysis of 3 species of fish (golden shiner, pumpkinseed sunfish, and yellow bullhead) from a freshwater ecosystem was undertaken to develop an index of behavioral complexity, a prerequisite for relating behavioral type with resistance to sublethal stresses. A comparable marine study is underway involving four species of increasing behavioral complexity as follows: killifish, Atlantic silverside, short horn sculpin and cunner. The yellow bullhead, with its highly complex social organization, was susceptible to sublethal thermal and oil stresses. Their behavior was interrupted at levels well below the lethal limits. The social behavior of the sunfish (territorial) and golden shiners (schooling) were not altered at comparable oil stress levels in preliminary experiments. The behavior of lobsters, a marine crustacea, was not significantly altered at temperatures 3 centigrade degrees below the lethal limit of 30° C. Whole kerosene and the branched-cyclic fractions of kerosene at low concentrations induced searching and feeding behavior in lobsters. The kerosene-impregnated test strips were often eaten. Other behavioral changes were detected, but they were not significant at the test concentrations. Recommendations for developing sensitive behavioral assays are made.

Short term behavioral changes may indicate longer term adaptive changes. A comparison of behavioral type relative to the appearance of resistant strains of fishes to endrin is presented. Behaviorally complex fishes may be far less able to develop resistant strains than fishes with simpler social behaviors. A scheme relating behavioral and ecological strategies in aquatic environments is suggested.

## INTRODUCTION

Our experiments are designed to help answer the following questions of importance to those concerned with the effects of man's activities on aquatic ecosystems:

1) Do sublethal stresses effect the social behavior and organization of fishes?
2) Is the kind of behavior a fish exhibits an index of its ability to withstand stress? For example, would a schooling species be able to cope with environmental perturbations that would disrupt the behavior or kill a species which is territorial?
3) Do certain kinds of social behavior predominate in certain types of ecosystems, representing different levels of stability? In other words, is there a strong correlation between behavioral type and ecotype? If such a relationship is found to exist, then ethological techniques can be used in studies designed to determine the environmental impact of pollutants on an ecosystem.

The ultimate goal of our research is to seek links between behavior and ecology that will assist us in developing the behavioral assays conducted over periods of months, which in turn, may indicate ecological trends over years and even decades.

It is too soon to know if we will be successful in our aims. This past year and a half involved setting up a new research laboratory and initiating the first series of experiments. However, we already have some indications that our approach is valid. The studies reported here indicate that:

1) Sublethal stresses can dramatically alter the behavior of some species, but not others.

2) The ability to withstand stress may be in part related to its behavioral type or level of social organization; the animals with the largest and most varied behavioral repertoires are more sensitive to at least some forms of stress.

3) The concept of a stressed ecosystem or stressed environment needs critical re-evaluation, in light of our preliminary findings which indicate that some animals within a given ecosystem may respond differently to extrinsic "historical" stress, e.g. thermal pollution, as compared to artificial stresses induced by oil pollution or chlorinated hydrocarbons. (See the following section for definitions and discussions of stress).

THE CONCEPT OF STRESS IN RELATION TO ANIMAL BEHAVIOR AND ENVIRONMENTS

The term "stressed ecosystem" is often used and discussed, but has not been subjected to a critical definition. The term, borrowed from physiology (Christian, 1956) does have valid connotations for behaviorists and ecologists who are studying the effects of natural and artificial perturbations on animal communities or ecosystems. Most authors refer to and use the term "stress", but to our knowledge it has not been appropriately defined in environmental terms.

Here we attempt to define the term from an evolutionary and environmental frame of reference. We will be concerned almost exclusively with extrinsic stresses, those imposed by man or the environment upon the behavioral ecology of a species. Intrinsic stresses: self-regulation crowding and social dynamics are only viewed here in relation to environmental change. However, extrinsic and intrinsic stresses are not easily delineated, as outside forces can have a bearing upon intrinsic pressures, and to a much more limited degree, the converse may also be true.

G. F. Gause (1942) in an article entitled "The relation of adaptability to adaptation" studied two types of stress on *Paramecium*. He subjected the *Paramecium*, fresh water ciliates, to salinities greater than they normally experienced. He compared their resistance to salinity to their resistance to quinine, a chemical substance with which his experimental animals throughout their evolution had not had to cope. He found that the acclimatization to salinity of *Paramecium* was different to that of the animals to quinine. Also, there was a "powerful capacity for the formation of adaptive modifications" to salts, whereas the ciliates showed a "relatively moderate adaptability" to the quinine solutions. It was clear from his work that the stresses were of a fundamentally different nature, and the ability of the ciliates to survive and adapt to them varied accordingly.

Slobodkin (1968) has used the term stress when he has referred to "both short-term environmental perturbations as well as permanent or unprecedented changes in the environment".

Sanders (1968) comes closest to outlining a concept of stressed environments. He makes clear discrimination between physical and biological stresses. However, he makes a strong point of the fact that the two types of stresses are interrelated, e.g. physical stress may induce biological stress. His discussion of two types of communities, which he considers abstractions, are worthy of quoting here:

> One can be called the "physically controlled community". In environments harboring this kind of community, the physical conditions fluctuate widely and the animals are exposed to severe physiological stress.
>
> In the physically controlled community the adaptations are primarily to the physical environment. Examples of such communities are those found in hypersaline bays, high arctic terrestrial environments, and deserts. The physically controlled communities are always eurytopic and are characterized by a small number of species. A similar

paucity of species occurs in environments of recent past history, such as most freshwater lakes.

The other extreme condition might be called the "biologically accommodated community". These communities are present where physical conditions are rather constant and uniform for long periods of time. Because of the historic constancy of the physical environment, physical conditions are not critical in controlling the success or failure of the species. With time, biological stress (intense competition, non-equilibrium conditions in predator-prey relationships, simple food web, etc.) is gradually mediated through biological interactions resulting in the evolution of biological accommodation. The resulting stable, complex and buffered assemblages are always characterized by a large number of stenotopic species. The deep-sea region, tropical shallow water marine regions, and tropical rain forests best represent such conditions.

There is no such thing as a "pure" physically controlled or biologically accommodated community. All communities are the result of both their physical and biological components and therefore somewhat intermediate between these extreme types. What determines the structure of any community is the relative proportions of these two parts.

## HISTORICAL AND ARTIFICIAL STRESSES

In order to obtain a crisper view of stressed environments it would seem very valuable to combine the insights of Gause with those of Sanders. From our own research, this seems necessary. We are beginning to realize that physical stresses imposed upon a community or a population are of two types, and the effects they impose upon the inhabitants may be very different. Physical stresses should be segregated into two categories: historical and artificial stresses.

### HISTORICAL STRESS

The historical stress is a "natural" one: one that animals have had to cope with throughout their evolutionary history. Historical stresses can be man-induced, as is the case with thermal effluents, or they can be natural disturbances created by atypical weather conditions or the like.

However, the picture is complicated by the fact that species vary tremendously in exposure to historical stresses throughout their evolutionary history. For example, an animal may have been exposed to extremes of heat, but not to cooling. The tarpon, *Megalops atlantica*, perhaps best illustrates this point. It can survive in artificially heated waters up to 36° C, but is very susceptible to cooling and unseasonably severe winters in Florida (Nugent, 1970).

### ARTIFICIAL STRESS

Artificial stresses are those which are exclusive to man's activities and are the products of his technologies. Animals have little or no prior experience with them, and their responses to artificial stresses may take a unique form both behaviorally and ecologically. Examples of artificial stresses are: many of the modern pesticides (particularly chlorinated hydrocarbons), radioactive compounds, oil and oil derivatives, metals in relatively high levels and numerous other byproducts of industrial and agricultural processes. The great majority of animals are experiencing artificial stresses in biologically excessive amounts only in relatively modern times. Most pollutants, with the exception of human and animal wastes and thermal discharges, are of the artificial type. At present there is no information or evidence that would permit us to predict their long-range impact on a given species; nor is it possible at present for us to predict which species will develop resistance to DDT, for example, or to pinpoint those which will succumb under the selection regimes induced by artificial stresses.

## THE IMPACT OF THE TWO MAJOR CATEGORIES OF STRESS

There is very little evidence, or research, which would enable a comparison of the effects of historical and artificial stresses on the behavior of an animal or an ecosystem although such a comparison is urgently needed. It is our intent to attempt to gather this information over the next few years.

Woodwell (1970) was struck more by broad similarities between the effects of pollutants on ecosystems. In a paper entitled "The effects of pollution on the structures and physiology of ecosystems", he argued that all pollutants cause ecosystems to regress in successional terms to simpler, less balanced states. In other words, changes in natural ecosystems exposed to stresses tend to revert to an earlier successional state. He did not differentiate between fire, a historical stress, and chronic gamma radiation, an artificial stress basically exclusive to man's activities. It is quite possible that in the broadest terms he may be right, and that the behavioral differences that we are beginning to suspect exist, may be related more to sublethal levels of stress. It is possible that when the stress is extreme enough, historical stresses would act on an animal, or an ecosystem, like an artificial stress, although the work of Gause does shed some doubt on this idea. Nevertheless, when the point is reached where the basic types of stress have a comparable impact, it is probably at the levels which result in incidences of high mortality and may not apply at the more common levels of insidious pollution. When the stress is chronic and sublethal, the difference between historical and artificial stress is most likely to be greatest.

PERSONNEL

Dr. William O. McLarney and David Engstrom investigated the effects of sublethal temperatures on the yellow bullhead, Ictalurus natalis. Dr. John Todd and Lynda Leffler studied the influence of sublethal temperatures on the behavior of two animal social groups of adult lobsters of both sexes. Stewart Jacobson was responsible for the investigations on the behavior of the golden shiner, Notemigonus crysoleucas and the pumpkinseed sunfish, Lepomis gibbosus. He also carried out the pilot study on the effects of oil stress on the three representative species from the fresh water ecosystem. Dr. John Todd conducted the work on the social behavior of the lobster and determined their responses to sublethal levels of kerosene and kerosene fractions. Joan Mitchell, newly arrived to the group, helped with the statistical analyses of the lobster behavior. Preliminary observations of the behavior of the representative animals from the marine ecosystem were carried out by John Todd.
Dr. David Boylan and Bruce Tripp prepared the kerosene fractions for the lobster study and assisted in all phases of the oil and kerosene research.

# EXPERIMENTAL APPROACHES (A)

## BEHAVIORAL DESCRIPTION AND RECORDING

Schneirla (1950) in a perceptive essay on analyzing behavior pointed out the relationship between behavioral observation and hypothesis, and described how the latter usually strongly influences the former. We attempt to overcome this bias by striving to record all the behavior in its actual temporal sequence, that we observe in our experimental groups. High quality, disciplined, direct observation is the cornerstone of sound ethological research on the dynamics of small social groups.

Our procedure is as follows: first, several months are spent recording the behavior of each species in ½ to 3/4 hour recording sessions in order to compile a relatively complete behavioral dossier for each species in the study (See Results). The methods we use are not typical of the majority of behavioral laboratories. We usually use two or three match tested observers who record simultaneously into a tape recorder. Each observer records the behavior of one, or depending on the species, two or more animals so that each animal in the community has its activities described in the sequence in which they originally occurred. These activities are verbally recorded on a stereo tape recorder. In order to insure that all the action patterns during intense bouts of activity are included, each behavioral unit, or action pattern, has a code, e.g. lunge = L; this system makes it possible for the action to be verbalized more rapidly into the tape. Each unit or sequence of units is prefaced with the number of the animal involved in the activity. After gaining experience with the system it is possible for an observer to verbally record the actions which take place in a small community in an accurate qualitative and quantitative manner.

Following the recording, the tapes are replayed and the behavior is transposed into pre- and post- unit activity distribution charts prior to detailed analyses of social behavior. The whole process, which is essential, is extremely time consuming and it is our intent to automate the transposing process if at all possible. We are looking for an electronic "ear" which will read the tape and print out the code into a temporal sequence for each individual. This printed tape could then be directly used by a computer.

## EXPERIMENTAL APPROACHES (B)

### COMPARATIVE ANALYSES OF BEHAVIOR

It is well known that various fish exhibit a wide range of behavior and behavioral sophistication, but as yet no truly comparative approach to fish behavior has been developed. In the past, several attempts, including one by the principal investigator, have been made to compare the brains of fishes with their behavior (Evans, 1931; Davis and Miller, 1967; Atema, Todd and Bardach, 1969). Also, a number of ethologists have compared the reproductive behavior of closely related species in attempts to determine phylogenetic relationships (Baerends, 1950) and to look for sexual isolating mechanisms (Liley, 1966). Breder and Rosen (1966) brought together the massive and diverse literature on the modes of reproduction in fishes and compared the different evolutionary directions fishes have followed in their sexual and parental behavior.

There are real limitations to any conclusions that might be drawn from most broad comparisons of the behavior of fishes. Only an extremely small number of fish species have been studied behaviorally, and almost nothing is known of the complete range of behavioral activities of any more than a few species of fishes. This fact has retarded the development of a comparative ethology of fishes, and has led us to consider investigating selected species, representing different levels of behavioral organization, from within a given ecosystem in order to seek a comparative approach to fish behavior.

One of the objectives of this study is to find correlations between the behavior of a fish species and the environment it inhabits. This involves comparing the behavior between fishes in a given ecosystem (See the following section on the Ecosystem Concept) and determining the various levels of behavioral organization found there. To do this, a behavioral dossier for each species is compiled. This involves observing each species for several months on a routine basis, at different periods throughout the day, until no new units, or behavioral action patterns are observed. It is then possible to make tentative comparisons of the behavioral complexity of a species--the index being the number of behavioral action patterns it exhibits.

The comparison can be extended and refined even further. It will be possible to look directly at the specificity and frequency of behaviors used by fishes at different levels of behavioral organization. For example, the schooling species from our freshwater ecosystem only rarely exhibits aggressive behaviors, and when it does, the action patterns are not precise. There are few, if any, displays or intention movements that precede aggressive interactions. The most social species on the other hand, frequently exhibit agonistic behaviors and these behaviors are usually components of long, intricate social interactions. Consequently, it has been possible for us to start establishing a scheme, illustrating different levels of behavioral organization for fishes, based upon the number and frequency of action patterns a fish exhibits. The behavioral information increases with each level of complexity. In this way we are beginning to develop a comparative behavior of fishes which is not dependent upon phylogenetic relationships, but upon the kinds and levels of social organization they exhibit.

Such a scheme could provide the foundation for linking behavior and ecology. Also, it should be possible to determine if behavioral type and the ability to withstand stress is related in any way. If it is, then there is a chance that comparative ethology can tell us something about the state of environments, and their ability to cope with various forms of stress.

## EXPERIMENTAL APPROACHES (C)

### ETHOLOGY AND THE ECOSYSTEM

Two ecosystems, one freshwater and one marine, were chosen for the study and from these two distinct environments a single species of fish has been selected, where possible, representing each level of behavioral organization. When there are several species, representing comparable levels of behavior within a given ecosystem, the one which is best known biologically and behaviorally is selected. In one case, *Ictalurus natalis*, which is not found within the experimental ecosystem, but is closely related to *Ictalurus nebulosus* which is, was substituted in the research. This was done because *Ictalurus natalis* is behaviorally comparable in most respects and has been the subject of considerable research, including a number ofstudies carried out by our group. *I. nebulosus*, the resident species, is less well known.

### ECOSYSTEM 1 -- A FRESHWATER LAKE (Figure 1)

The freshwater ecosystem is Ice House Pond, at Sippewissett, Massachusetts on Cape Cod. The lake has large populations of the schooling species, the golden shiner, *Notemigonus crysoleucas*; hierarchically organized pumpkinseed sunfish, *Lepomis gibbosus*, and bullheads, *Ictalurus nebulosus*, which exhibit complex behaviors based upon a large number of behavioral action patterns and displays, intricate means of communication and individual recognition (Todd, 1971) (Figure 1). The simplest level of behavioral organization, namely aggregations, is not represented in our freshwater study as there is no species which appropriately fits this category.

## ECOSYSTEM 1.

FRESHWATER LAKE SURROUNDED BY SCRUB-OAK FOREST.
(ICE HOUSE POND, SIPPEWISSETT,) CAPE COD.

INCREASING BEHAVIORAL COMPLEXITY ↓

| SPECIES | BEHAVIORAL TYPE | NUMBER OF BEHAVIORAL UNITS |
|---|---|---|
| GOLDEN SHINER ( *Notemigonus crysoleucas* ) FAMILY CYPRINIDAE | SCHOOLING BEHAVIOR | 36 (+5)* |
| PUMKINSEED SUNFISH ( *Lepomis gibbosus* ) FAMILY CENTRARCHIDAE | HIERARCHICAL. SEASONALLY TERRITORIAL | 51 (+10)* |
| YELLOW BULLHEAD ( *Ictalurus natalis* ) FAMILY ICTALURIDAE | INDIVIDUAL RECOGNITION COOPERATIVE GROUPS COMPLEX COMMUNICATION | 98 (+10-20)* |

ESTIMATED INCREASE IN BEHAVIORAL UNITS*
WITH FURTHER REFINEMENTS IN ANALYSIS.

Figure 1.

ECOSYSTEM 2 -- MARINE SUBTIDAL REGION (Figure 2)

The marine subtidal area selected for the study is just off Nobska Point, near Woods Hole, Massachusetts on Cape Cod. Its outer limits experience swift currents associated with tidal movements in and out of Woods Hole Channel. It's a biologically productive area, and is inhabited during the summer months by large numbers of fishes and crustacea, including lobsters. The summer residents represent a diversity of behavioral types. At the present we do not have a list of all the fishes which inhabit the area, but Figure 2 represents the animals that have been selected for study. There is no species of marine fish comparable to the bullhead in terms of behavioral complexity in the study area, perhpas because the area is too unstable (Sanders, 1969), thereby preventing or inhibiting behaviorally diverse fishes from establishing themselves.

The killifish, Fundulus majalis, is the most common aggregating species in ecosystem 2 and inhabits the area throughout most of the year. The schooling species is Menidia menidia, the Atlantic silverside. Both do well in captivity if held in large tanks or aquaria.

The short horn sculpins, Myocephalus scorpius, represent the simplest level of social organization associated with a piece of topography along the bottom of the subtidal region. Although we do not have much knowledge of their movements, it appears that they confine themselves for considerable periods to specific localities along the coast. The sculpins are not truly territorial, but defend a space around themselves. The most complex level of social organization that we have observed in the marine subtidal area is exhibited by the cunner, Tautogolabrus adspersus, which is terri-

## ECOSYSTEM 2.

### MARINE SUBTIDAL REGION, NOBSKA POINT, CAPE COD

INCREASING BEHAVIORAL COMPLEXITY ↓

| SPECIES | BEHAVIORAL TYPE |
|---|---|
| STRIPED KILLIFISH ( *Fundulus majalis* )<br>FAMILY CYPRINODONTIDAE | AGGREGATION |
| ATLANTIC SILVERSIDE ( *Menidia menidia* )<br>FAMILY ATHERINIDAE | SCHOOLING |
| SHORT HORN SCULPIN ( *Myoxocephelus scorpius* )<br>FAMILY COTTIDAE | SPACIAL DEFENSE, WITHOUT TERRITORIES |
| CUNNER ( *Tautogolabrus adspersus* )<br>FAMILY LABRIDAE | TERRITORIAL AND HIERARCHICAL |

Figure 2.

torial and hierarchical at least for part of its life history. From our very tentative early observations, this species would appear to incorporate relatively large numbers of behavioral activities within its social repertoire . Unfortunately, almost nothing is known of the social behavior and organization of this species from the marine subtidal region, and a considerable amount of description is needed before our research on ecosystem 2 will be comparable to that on the freshwater model ecosystem.

A marine crustacea, the American lobster, Homarus americanus, has been included in the study. It will not be possible to make direct comparison with the fish species in the study; however, this animal was included because of its commercial importance and abundance in the study area. The lobster is territorial and hierarchical and exhibits a considerable variety of social and feeding behaviors.

By concentrating on fishes from specific ecosystems we hope to gain some idea of the couplings between behavior and ecology, and determine how behavioral types are organized within an ecosystem and how ecosystems themselves place limits upon the social behaviors which they encompass. If links between the two levels of biological organization can be clearly delineated, then it should be possible to relate successional concepts in ecology with behavior in order to create an environmental ethology.

# EXPERIMENTAL APPROACHES (D)

## SUBLETHAL STRESSES -- THERMAL AND OIL

Small social groups of fishes and lobsters, ranging from pairs to half a dozen individuals, were housed in aquaria from 30 to 180 gallons capacity. The size of the tanks (Photos 1 & 2) were determined by each species'spatial requirements, based upon their normal feeding and social behaviors. If the aquaria were too small to allow normal social relations (determined from observations in 3,000 gallon community tanks) then larger tanks were substituted.

Communities involving all the test species from both experimental ecosystems were established in two 3,000 gallon tanks (Photo 3) until the glass windows burst on one of the systems, at which time the community observations were halted.

Both the fish and lobsters were held and observed for several weeks, and in some cases months, prior to the experiments in order to insure that a high degree of social stability within each experimental tank had been established. At this point, the animals were subjected to increasingly higher levels of heat (see Results for specific details of experimental techniques) or varying concentrations of oil for the fishes and kerosene for the lobster.

In the sublethal temperatures study, the temperatures were increased stepwise and the animals were permitted to acclimate prior to the behavioral recordings. At each level their social behavior was recorded. The controls were comparable social groups kept at a constant temperature. As well, comparisons were made between each social group's behaviors at each incre-

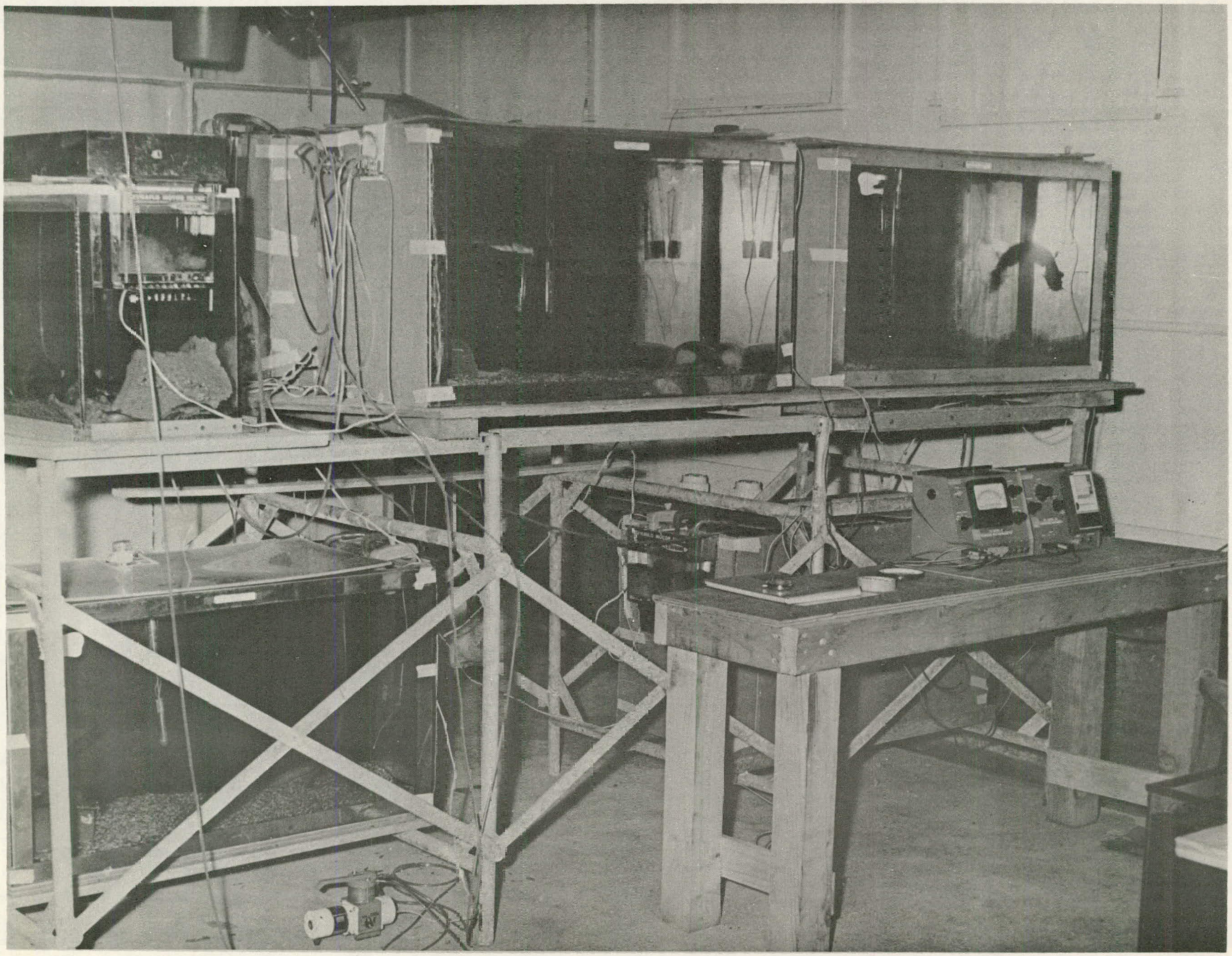


Photo 1. 55 gallon Bullhead 2 animal community tanks - thermal study.

Photo 2. 30 and 180 gallon salt water aquaria. Stable community tanks - rear, top right.

Photo 3. 3000 gallon marine community with species from ecosystem 2.

ment of thermal change. In this case, each community is acting as its own control.

The study on the effects of oil and kerosene were handled slightly differently; consequently, the methods will be described under the appropriate Results section. It should be emphasized that there are still considerable differences in the techniques used in the oil and kerosene studies, and a comparison between the different forms of stress is only broadly applicable at this time. As our knowledge of the animals and the experimental systems increases, and our ability to measure concentrations of oil and kerosene fractions is refined, then the study will be appreciably more comparative. In this respect, this first report is basically a statement of aims and methodology. The goal of determining the effects of stress on social behavior, within the ecosystem concept, is a number of years away. Although we have made a preliminary attempt to compare sublethal stresses, the emphasis of the research to date has been to develop a behavioral base-line, and to work out methods for precisely regulating and recording stresses. In the latter case, research on sublethal temperatures (a historical stress) can be much more accurately controlled than that on oil or kerosene (artificial stress). However, despite the relative straightforwardness of thermal research it was discovered after the study was well underway that the supposedly non-toxic heaters were killing fish from metal poisoning. A glass coil system was designed to supplant the heaters, and while the recirculating system was then non-toxic and accurate, the expensive HAAKE E 12 heaters ceased to function after several months and were constantly being repaired. We finally had to adopt aquarium heaters, mounted on rafts, to regulate the temperatures within the experimental systems. This arrangement, in order to be accurate, requires constant attention, and is far from ideal.

# RESULTS

## FRESH WATER LAKE: ECOSYSTEM 1

### COMPLEX SOCIAL BEHAVIOR -- THE YELLOW BULLHEAD

The social organization and behavior of the yellow bullhead, *Ictalurus natalis*, has already been described by Todd *et al*., 1967 and 1968; Bardach and Todd, 1970; and Todd, 1971. Table 1 is a behavioral dossier for this species. In terms of absolute numbers of action patterns, social displays and organization, this is behaviorally the most complex of the fishes in the study. Within a given population some of its members are territorial throughout the spring, summer and autumn seasons. Laboratory studies have strongly implied individual recognition amongst inhabitants of neighboring territories, as the basis of their social behavior. Cooperative behavior, which occurs during periods when a community has been invaded by a strange bullhead, has been described for this species (Bardach & Todd, 1970).

We have observed 98 behavioral action patterns for *I. natalis*. Interactions with their own kind are based upon displays of varying intensity, while interactions between bullheads which have not previously interacted socially (strangers) are almost always of a different character and involve action patterns exclusive to, or usually confined to, this type of interaction. The behavioral action patterns shown in Table 1 do not include activities that only occur during mating. Mating has not been described in any detail for this species.

Within a given bullhead population, large numbers of them are neither territorial nor hierarchical in their behavior. Instead, they live in dense aggregations and display little in the way of higher social behavior.

Table 1.

BEHAVIORAL DOSSIER

YELLOW BULLHEAD ( *Ictalurus natalis* )

| UNIT | RECORDING CODE |
|---|---|
| 1. APPROACH | *ap* |
| 2. ASCEND | *as* |
| 3. ATTACK | *A* |
| 4. AVOID | *av* |
| 5. BARBEL FEEL | *Baf* |
| 6. BARBEL TOUCH | *Bat* |
| 7. BARBEL TOUCH SURFACE | *Basu* |
| 8. BITE 1 | *B1* |
| 9. BITE 2 | *B2* |
| 10. BITE 3 | *B3* |
| 11. BLANCH | *bla* |
| 12. BODY THRUST | *Bt* |
| 13. BORDER TURN | *bt* |
| 14. BOTTOM BOUNCE | *Bob* |
| 15. BOTTOM CREEP | *Bcp* |
| 16. BUTT | *bu* |
| 17. CHASE | *ch* |
| 18. CIRCLE | *ci* |
| 19. COLLIDE | *C* |
| 20. COUGH | *cg* |
| 21. CREEP | *Cp* |
| 22. CREEP ATTACK | *CpA* |
| 23. CRUISE 1 | *Cr1* |
| 24. CRUISE 2 | *Cr2* |
| 25. CRUISE 3 | *Cr3* |
| 26. DARKEN | *da* |
| 27. DART | *Dt* |
| 28. DEFECATE | *Def* |
| 29. DESCEND | *ds* |
| 30. DIG | *D* |
| 31. DORSAL FIN ERECT | *dfe* |
| 32. ENTER | *E* |
| 33. EXIT | *ex* |
| 34. EXPLORE | *exp* |
| 35. EXTEND OR ERECT | *e* |
| 36. FEED | *F* |
| 37. FINS ERECT | *fe* |
| 38. FINS FOLDED | *ff* |
| 39. FLEE | *Fl* |
| 40. FOLLOW | *Fw* |
| 41. FORWARD | *Fwd* |
| 42. FRONTAL DISPLAY 1 | *FD 1* |
| 43. FRONTAL DISPLAY 2 | *FD 2* |
| 44. FRONTAL DISPLAY 3 | *FD 3* |
| 45. GULP | *G* |
| 46. HALT | *h* |
| 47. HALT APPROACH | *hap* |
| 48. HEAD PUSH | *hp* |
| 49. HEAD STAND | *hs* |
| 50. HEAD THRUST | *ht* |
| 51. HEAD WAG | *Hw* |
| 52. HORIZONTAL EYE MOVEMENT | *hem* |
| 53. HOVER | *ho* |
| 54. INGEST | *i* |
| 55. INTERTWINE | *I* |
| 56. LATERAL DISPLAY 1 | *LD 1* |
| 57. LATERAL DISPLAY 2 | *LD 2* |
| 58. LATERAL DISPLAY 3 | *LD 3* |
| 59. LEAVE | *lv* |
| 60. MOUTH DISPLAY 1 | *MD 1* |
| 61. MOUTH DISPLAY 2 | *MD 2* |
| 62. MOUTH DISPLAY 3 | *MD 3* |
| 63. MOUTH DISPLAY 4 | *MD 4* |
| 64. MOUTH FLAP | *flap* |
| 65. MOUTH FIGHT | *MF* |
| 66. MOUTH PUSH | *MP* |
| 67. MOUTH UNLOCK | *Mu* |
| 68 NIP | *N* |
| 69. NO RESPONSE | *θ* |
| 70. PUSH | *P* |
| 71. PUSH THRUST | *Pt* |
| 72. QUIVER | *Q* |
| 73. RAPID GULP | *RG* |
| 74. RESTING POSITION 1 | *RP1* |
| 75. RESTING POSITION 2 | *RP2* |
| 76. RESTING POSITION 3 | *RP3* |
| 77. RESTING POSITION 4 | *RP4* |
| 78. RESTING POSITION 5 | *RP5* |
| 79. REVERSE | *re* |
| 80. ROLL | *R* |
| 81. SCRATCH | *sc* |
| 82. SEARCH | *S* |
| 83. SPIRAL | *spir* |
| 84. SPIT | *sp* |
| 85. START | *st* |
| 86. STATIONARY AGAINST | *stag* |
| 87. STRESS PUMP 1 | *Sp1* |
| 88. STRESS PUMP 2 | *Sp2* |
| 89. STRESS PUMP 3 | *Sp3* |
| 90. SURFACE CREEP | *sucp* |
| 91. TOUCH | *T* |
| 92. TAIL BEAT | *TBt* |
| 93. TAIL THRUST | *t* |
| 94. TURN | *tu* |
| 95. VERTICAL EYE MOVEMENT | *VEM* |
| 96. WINDOW CREEP | *WC* |
| 97. WINDOW PUSH | *WP* |
| 98. YAWN | *Y* |

It has been postulated (Todd, 1971) that this behavioral duality has an adaptive function. By having two types of social behavior exhibited by the same species, the bullheads may more effectively utilize space and food resources, and thus sustain higher populations, while at the same time maintaining groups of individuals with complex social behavior. The bottom of the lake houses the territorial centers of the behaviorally diverse individuals, while the aggregating members have been observed swimming apparently without restriction throughout the waters of the lake. These observations in nature, while not the subject of detailed investigations to date, have been made by us in a variety of lakes in different parts of the country.

## THE EFFECTS OF SUBLETHAL TEMPERATURES, A HISTORICAL STRESS, ON THE SOCIAL BEHAVIOR OF THE YELLOW BULLHEAD

Two types of observations were made during the period covered by this report: description of social behavior and territorial mapping. Attempts were also made to relate feeding behavior to thermal changes, but these were inconclusive. In addition to descriptions of these experiments, we have included a statement of present and future research plans and a brief taxonomic note.

All aspects of our bullhead research have been set back by problems with equipment and experimental animals. As was previously mentioned, the circulating heaters caused metal poisoning after certain copper parts became exposed to water, resulting in a heavy mortality in our experimental animals. Fortunately, we were able to develop interim techniques of achieving satisfactory precision of temperature control using conventional 200 watt aquarium heaters. Once the trouble was determined, we were able to proceed with the investigation.

As has been mentioned, Ecosystem 1 contained only the brown bullhead, I. nebulosus, and in the earlier pilot study at the University of Michigan (McLarney and Bardach, 1969) we had used the yellow bullhead, I. natalis. After the decision had been made to switch to yellow bullheads, a source had to be located. A small supply was sent to us from the Department of Wildlife and Fisheries at the University of Michigan, which were used in the work described in the report.

Since that time we have been able to locate a substantial population of I. natalis 180 mi from Woods Hole on Frest Lake near Palmer, Massachusetts. Subsequent collections have been made from this lake.

THERMAL EFFECTS ON SOCIAL BEHAVIOR:

Emphasis during this study period was on the interactions of single species social groups of two fish. Such communities were maintained in 50 gallon tanks provided with heaters and a shelter for each fish. Each social group or community was observed at room temperature (24$^{o}$ C) and the behavior recorded daily until it was judged that the relationship between the two animals had stabilized with respect to territoriality and aggression. This process required at least 5 weeks and up to 8 weeks in some instances. Once social stability was reached, the temperature was raised in one degree increments. Each day of behavioral recording was followed by one day of gradually increasing temperature, so that each community was observed every other day. The animals were fed prior to each recording bout, so that some activity was induced. Fifteen minutes after the introduction of food, behavioral recording commenced and continued for 30 minutes.

Our approach to behavioral observations, in which we attempt to record all the behavior which occurs in a given period of time, rather than concentrating on selected units, provides us with an index of overall activity. Figure 3 illustrates the activity of pairs of bullheads at temperatures from 24° to 35° C. The combined number of ascents, descents and turns by the two fish was used as a measure of relative activity.

At first, the animals behaved as one might expect; they corroborated the statement of Fry (1947) that temperature affects activity through metabolism. Activity increased directly with temperature up to 29° C. However, at 30° C and 31° C, activity declined abruptly, to rise again at 32° and above. Decline in activity in fishes is often associated with physiological stress. However, at 30-31° C, except after severe bouts of agonistic behavior, none of the experimental animals exhibited any of the behavior characteristic of stress in bullheads. Stress was observed independently of social interactions at 34-35° C . This may be responsible for the decline in activity at 35°.

Frequency of agonistic behavior (Figure 4) is often found to be related to the overall level of activity, simply because active animals come into contact more frequently than relatively inactive ones. This effect was seen in the pilot study, but in the present study, the total amounts of agonistic behavior observed did not differ discernibly between

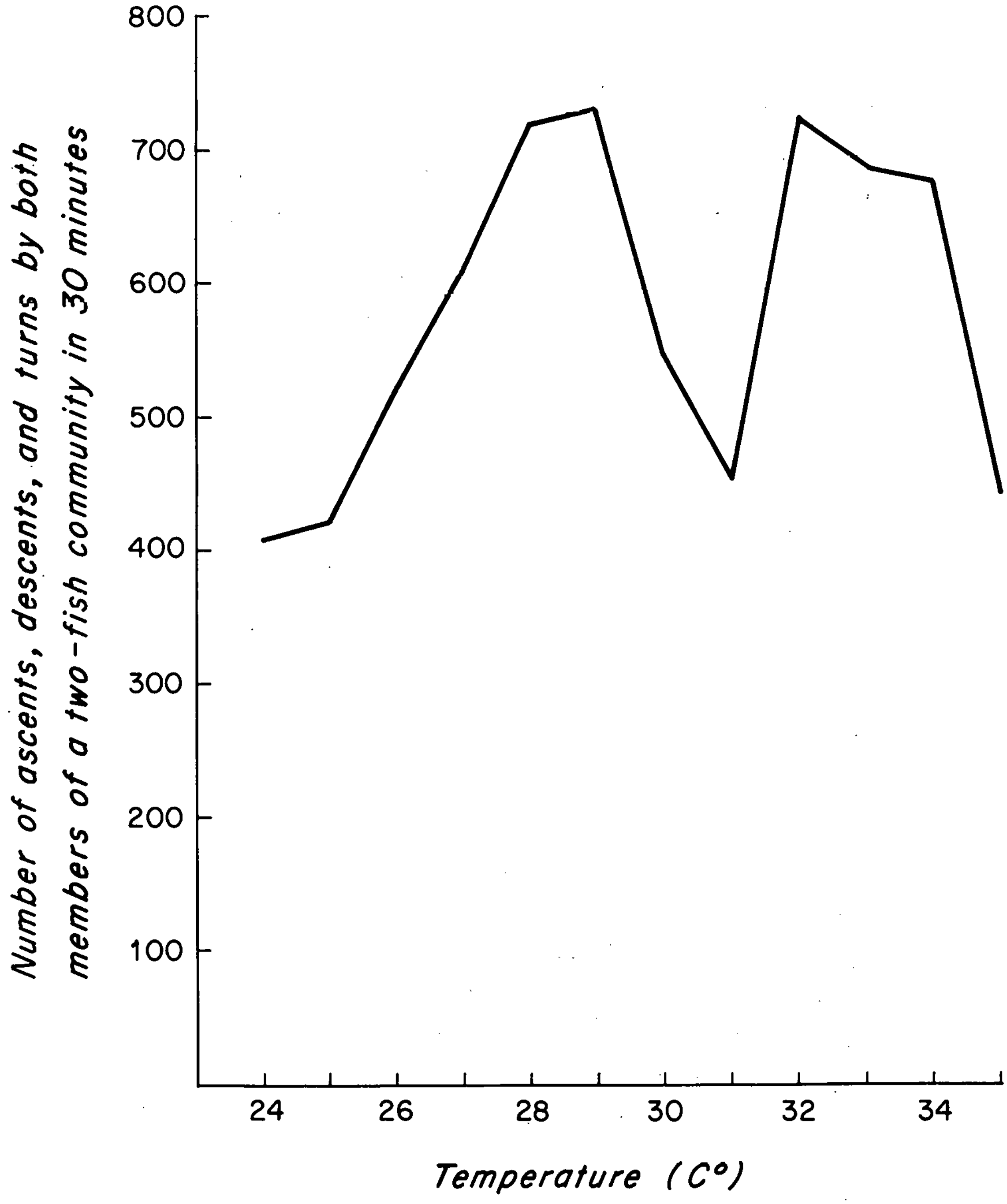



Figure 3. Relative Activity

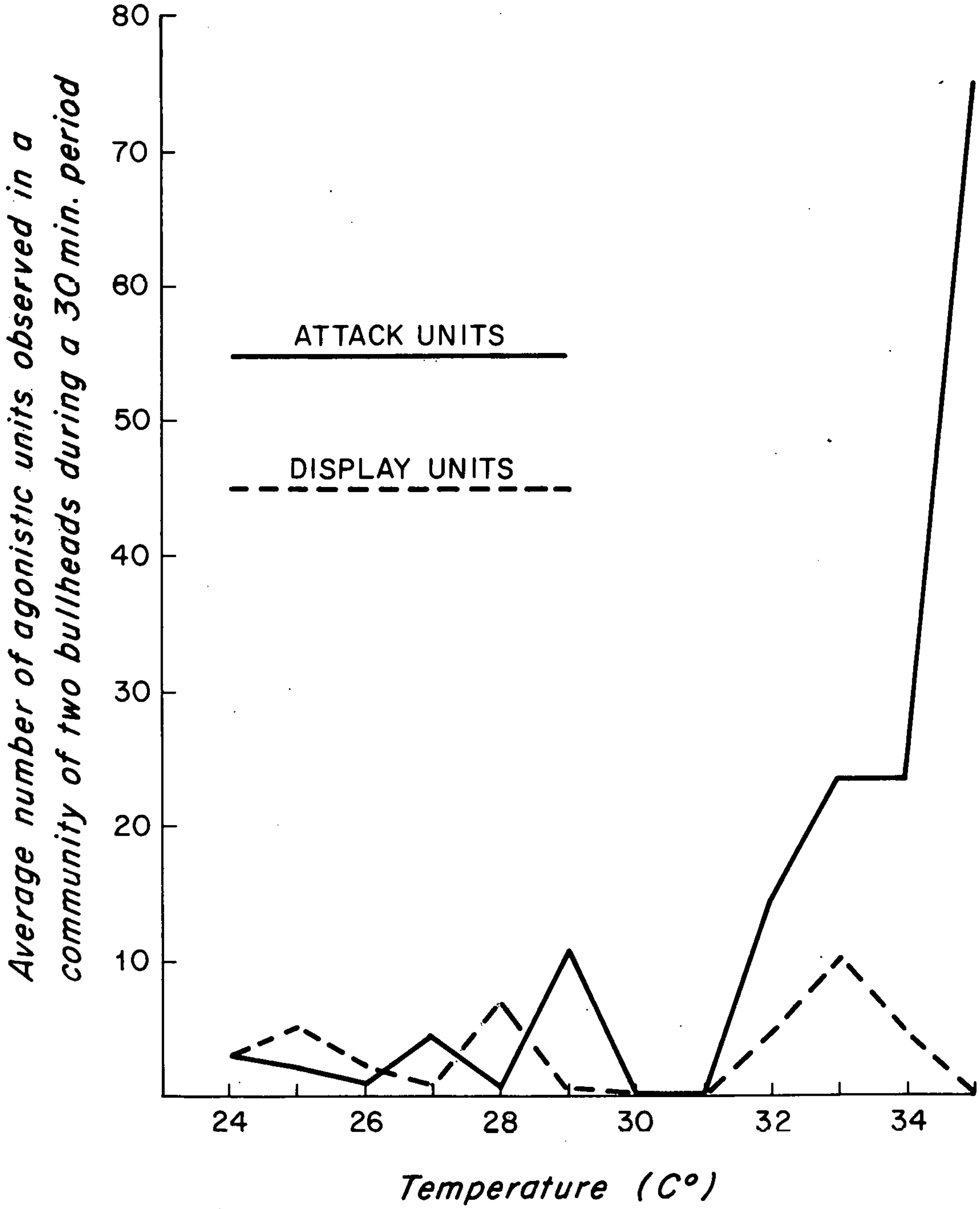



Figure 4. Agonistic Behavior

24° and 29° C. (The peak seen at 29° C is attributable almost entirely to an extraordinary amount of fighting in one of the study tanks.) At 30° and 31° C, however, a remarkable thing happened: agonistic behavior ceased entirely in all the study communities. Above 31° C, it increased very rapidly.

In the pilot study, a qualitative change in agonistic behavior was observed as well as a quantitative one. At about 30°-31° C, the "display" units ("mouth display","lateral display", etc.) which function as threats or warnings, but result in no physical damage, disappeared completely, while there was a great increase in attack units ("nip", "bite", etc.) which do cause injury. Further, the dominant fish was for the first time seen to seek out and deliberately attack the submissive animal, rather than engaging in agonistic behavior only when the two chanced to come into contact with each other. In the present study, the second effect was observed again. The display units never disappeared as they did in the pilot study, but above 31° C attack units were seen far more frequently.

The increase in intensity of aggression above 31° C is perhaps even more dramatically illustrated by the frequency of "bite", the most damaging of the attack units (Figure 5). Recognition of tankmates was probably disrupted.

The effectiveness of attacks at the highest temperatures studied may have been vitiated somewhat by an apparent lessening of stamina, so that bites and the like could not be sustained so long or executed as vigorously as before. Nevertheless, severe damage was inflicted. Although the upper LD 50 temperature for I. natalis from Michigan appears to be around 39° C, we were not able to take any pairs past 35° C; one member of the pair was always killed by its tankmate at or below this temperature.

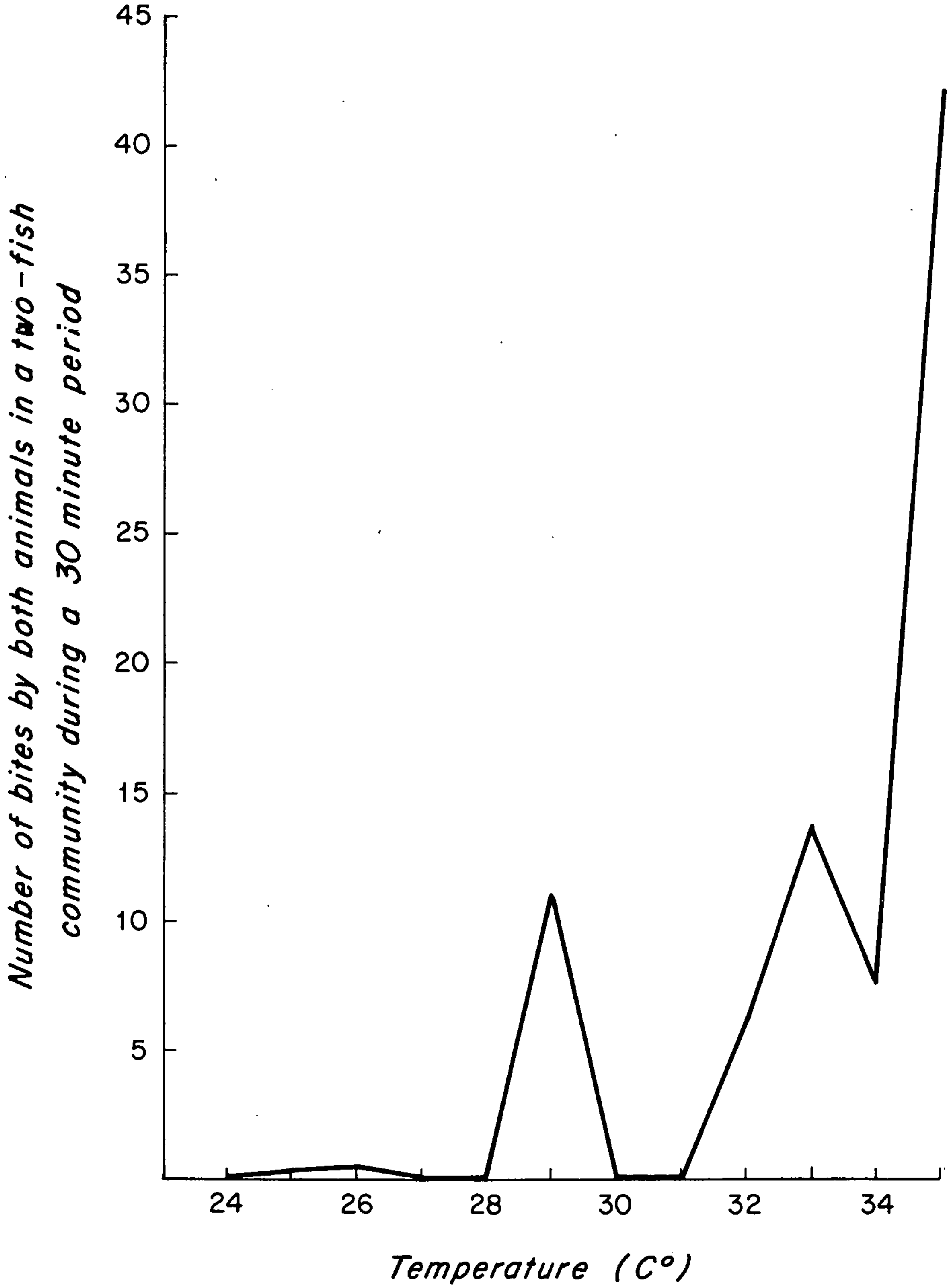



Figure 5. Overt Attacks.

In one community we observed cannibalistic behavior toward a living but severely injured submissive fish.

TERRITORIAL MAPPING

The same communities were used in territorial mapping as in the behavioral observations, but the results are less clear-cut. To aid in this phase of the study, a grid was marked on the front glass of each tank, dividing it into top and bottom halves and into four parts along the horizontal axis. As the investigator could easily distinguish front from back halves of the tank, each tank was effectively divided into 16 sectors. Prior to beginning observations, the animals were fed as described for the behavioral observations.

Each fish in a community was observed for 15 minutes daily, and the number of entries into each sector recorded, along with the location of any aggressive behavior and the location and duration of resting periods. The data has not yet been subjected to any statistical analysis, but from inspection, one could classify each of the 16 sectors on any given day as controlled by the dominant fish, controlled by the submissive fish, contested by the two fish, or seldom entered by either fish. Table 2 shows the results of these observations for two of our experimental communities.

There appears to be a decrease in social stability with temperature up to about $27^{o}$-$28^{o}$, and again above $31^{o}$ C, where there is a substantial increase in the number of sectors described as contested. Between $28^{o}$ and $30^{o}$ C, or approximately the range where activity and agonistic behavior declined in the behavioral observations, territorial stability was remarkable; no appreciable change was observed in any of the communities.

Table 2. Territorial Mapping.

TERRITORIAL STATUS OF 16 SECTORS OF A 50 GALLON

AQUARIUM OCCUPIED BY 2 YELLOW BULLHEADS AT INCREASING TEMPERATURES

COMMUNITY 3

| Temperature (° C) | Controlled by dominant fish | Controlled by submissive fish | Contested | Seldom entered by either fish |
|---|---|---|---|---|
| 24 | 3 | 1 | 0 | 12 |
| 25 | 3 | 1 | 0 | 12 |
| 26 | 3 | 3 | 1 | 9 |
| 27 | 4 | 4 | 1 | 7 |
| 28 | 3 | 4 | 1 | 8 |
| 29 | 3 | 4 | 0 | 9 |
| 30 | 3 | 4 | 0 | 9 |
| 31 | 3 | 3 | 0 | 10 |
| 32 | 3 | 4 | 0 | 9 |
| 33 | 0 | 0 | 8 | 8 |
| 34 | 4 | 0 | 8 | 4 |
| 35 | Submissive animal died | | | |

COMMUNITY 4

| Temperature (° C) | Controlled by dominant fish | Controlled by submissive fish | Contested | Seldom entered by either fish |
|---|---|---|---|---|
| 24* | 0 | 9 | 5 | 2 |
| 25 | 8 | 1 | 3 | 4 |
| 26 | 6 | 2 | 2 | 6 |
| 27 | 11 | 2 | 1 | 2 |
| 28 | 7 | 5 | 0 | 4 |
| 29 | 8 | 4 | 0 | 4 |
| 30 | 8 | 3 | 1 | 4 |
| 31 | 5 | 0 | 9 | 2 |
| 32 | 3 | 0 | 6 | 7 |
| 33 | Too much activity to record | | | |
| 34 | 4 | 1 | 7 | 4 |
| 35 | 5 | 0 | 10 | 1 |

* It is believed that observations of this community were begun prematurely, hence the great change between 24° and 25° C.

PHYSIOLOGICAL IMPLICATIONS OF THE BEHAVIORAL AND TERRITORIAL STUDIES

Perhaps the most interesting aspect of our studies to date is that while the behavioral changes observed in the pilot study are not in all respects the same as those observed at Woods Hole (which may be due to the fact that the pilot study was conducted during the winter, whereas the bulk of our observations here were made during the summer) in all cases a major shift in patterns of agonistic behavior occurred around 30°-31° C. It has recently come to our attention that this temperature range is also associated with anomalies in such physical properties of water as the index of refraction, thermal conductivity, isothermal compressibility, and adiabatic compressibility (Drost-Hansen, 1967). Thorhaug (1969) has demonstrated similar abrupt changes at the same temperature range in the bioelectric potential of the membrane system of <u>Valonia</u>, a marine alga.

Although, as mentioned above, no behavioral indications of physiological stress were observed in bullheads at 30°-31° C, it would appear that some sort of physiological changes must be involved in the behavioral changes we have observed. Perhaps over a long period of time these changes would be damaging in themselves. As a preliminary test, we have set up two tanks in which single bullheads are held at 31° C. As of this writing, these fish have been thus maintained for over two weeks and are behaving and feeding normally and appear healthy.

FEEDING BEHAVIOR

Whenever the animals are fed prior to recording, the time taken by each fish to become alerted to the food (as indicated by extended barbels and searching behavior) and to actually feed is recorded. In the pilot study, a drastic disruption of feeding behavior was observed between 30° and 35° C. Alert time was not altered, but the efficiency of the bullheads in finding and ingesting the food pellets was much less. No such effect was observed in the present study, and the fish fed normally at all temperatures studied.

TAXONOMIC NOTE

A by-product of our work has been a potential contribution to the taxonomy of the genus _Ictalurus_. _I natalis_ and _I. nebulosus_, which are often found in the same bodies of water, are very difficult to distinguish by sight. The key characteristics cited for the two species involve ray counts which are difficult to make in the field, particularly at night when the trapping of bullhead is most effective. Other characteristics cited are rather subjective, and the matter is further complicated by the fact that some overlap in meristic characters occurs.

In the course of handling many bullheads of both species, we have observed that _I. nebulosus_, when captured, usually produces sounds by stridulation, using the pectoral fins. _I. natalis_ never does this. It is possible that this observation could serve as the basis for a behavioral key character. We plan to examine as many bullheads of both species as possible to determine the usefulness of this observation.

PRESENT AND FUTURE STUDIES

In addition to holding yellow bullheads at 31° C, as described above, we are presently attempting to obtain enough replicates of the behavioral and territorial studies to permit statistical analysis. When this is accomplished, we will begin observations on two fish communities held at constant temperatures selected from the range used in our experiments to date. After that, we will commence the studies of larger communities and communities housing all three species from ecotype 1.

# THE EFFECTS OF OIL, AN ARTIFICIAL STRESS, ON THE BEHAVIOR OF THE YELLOW BULLHEAD, ICTALURUS NATALIS

A pilot study on the effects of oil on the social organization and feeding behavior of the yellow bullhead has just been completed. Social groups comprising two individuals were studied. The fishes were housed during the pilot study in 20 gallon aquaria. In the present research they are kept in 55 gallon tanks which are comparable to those used in the thermal studies. Each aquaria is supplied with aeration, silica sand and shelters, made of halved flower pots and bricks. Recording techniques were comparable to those in the sublethal temperatures study.

## THE OIL EXTRACT

An aqueous extract of Kuwait crude oil was prepared by gently stirring overnight 100 ml of oil with 15 liters of aged tapwater in a manner comparable to Boylan and Tripp (1971) for seawater extracts of oils. Initial tests had shown that small volumes (50-200 ml) of the oil extract had no detectable effect on any of the three species of fish from Ecosystem 1, the freshwater lake. Therefore, 4 liters of oil extract were added in the experiments involving all three species. This volume was estimated to produce an initial concentration of oil components of less than 1 part per million. Adsorption to various surfaces including the fish, undoubtedly occurred, resulting in a decreased concentration of oil in the static system.

## FINDINGS

Two groups of bullheads were used in the pilot investigation. Feeding was unaffected by the oil throughout the study. However, bullheads, unlike the other two species from the freshwater ecosystem, showed marked changes in their social behavior following the addition of the oil extract. Addition of 4 liters of tap water as a control did not cause detectable changes in behavior.

Figure 6 illustrates changes in activity and in the social actions "mouth displays", "mouth fights" and "chasing" for the first of the bullhead experimental communities comprising two fish. The larger fish was dominant throughout most of the aquarium. The subordinate was not harassed in one of the corners, which it defended. Prior to the introduction of the oil extract, the subordinate showed low intensity mouth displays when the dominant approached and passed his barbels over the subordinate's body.

Upon introduction of the oil, the behavior in the small community changed. When the dominant approached, the subordinate responded with high intensity mouth displays. This behavior led to attacks which were followed by mouth fights, indicating a breakdown in normal social relations. It is possible that individual recognition was interrupted, as the action patterns were more characteristic of encounters between strangers. This possibility will be tested further. The behavior "mouth fighting" had not been recorded in the community for some time, and only initially when the two fish were first placed in the same aquaria.

The changes in behavior that we noted did not follow immediately upon the introduction of oil; in fact, there was a lag time of between 24 and 72 hours before maximal changes occurred. The social behavior returned to "normal" about a week following the addition of the oil extract. Perhaps this reestablishment of earlier social relations coincided with decreasing

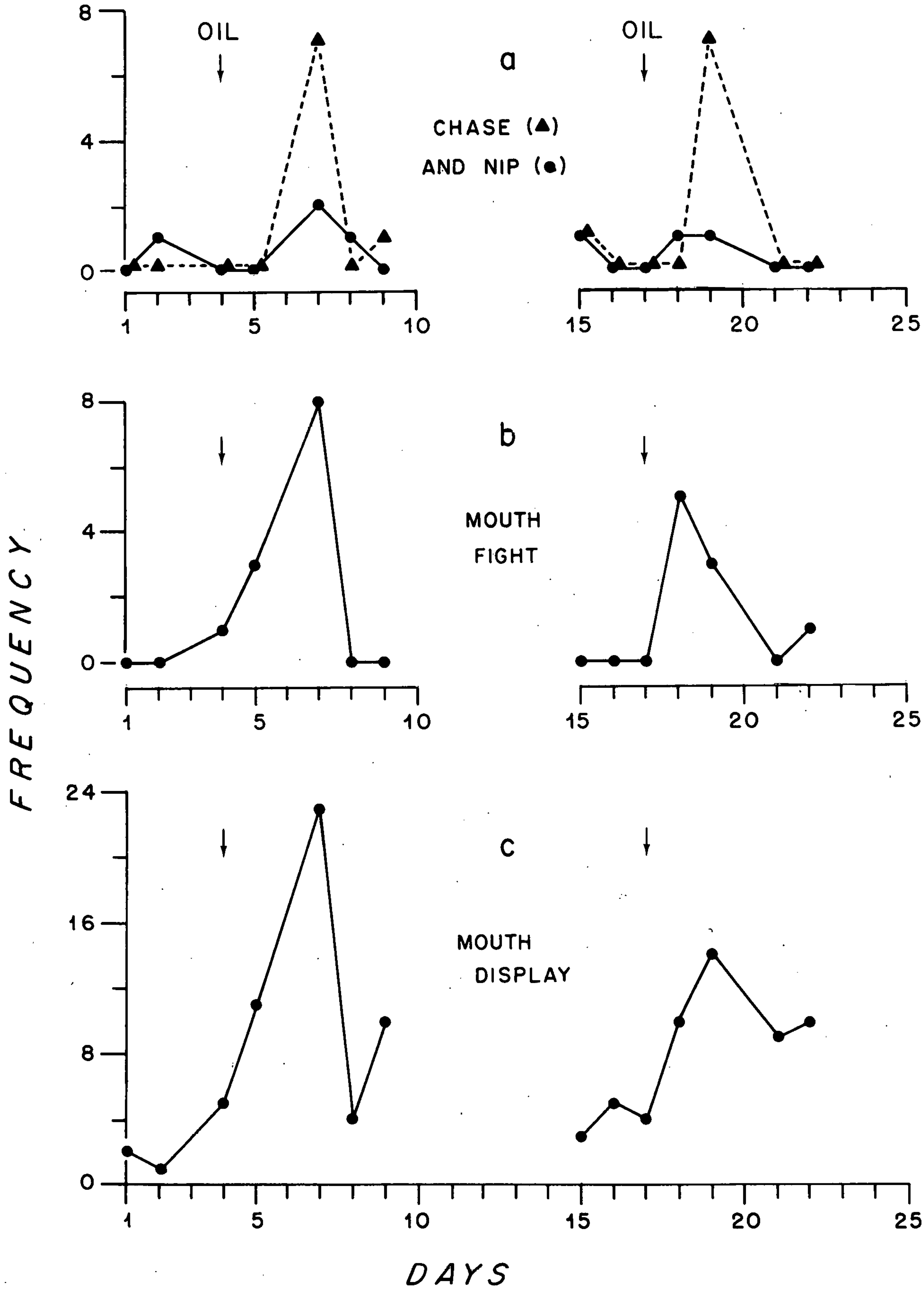



Figure 6. Agonistic behavior between two Bullheads exposed to an aqueous extract of oil.

concentrations of oil components.

One week later, 4 liters of oil extract was again added and the resulting behavior closely monitored. There were comparable behavioral alterations following the second introduction of oil into the community (Figure 6).

The second bullhead experimental group, upon exposure to oil, exhibited changes in a similar direction, namely towards disruption of the normal social relations. Most predominant were increases in the frequency of chasing and nipping by the dominant fish.

It was apparent from the pilot study on the effects of oil extracts on the social behavior of yellow bullheads, that low concentrations of the water soluble fractions of oil dramatically alters the behavior of this species. The behavioral changes appear to be comparable in many respects to those observed in the thermal studies. It is hoped that further research will elucidate the differences and similarities of the effects of historical and artificial stresses on the social behavior of bullheads.

ECOSYSTEM 1: FRESHWATER LAKE (Cont.)

HIERARCHICALLY AND TERRITORIALLY ORGANIZED

BEHAVIORAL TYPE PUMPKINSEED SUNFISH: *LEPOMIS GIBBOSUS*

During most of the year, pumpkinseeds remain in mixed sex groups. These groups seem to be hierarchically structured, which is often most predominantly expressed during feeding. In our experimental communities, the fish feed in order of size, with the largest feeding prior to the smaller individuals.

Nesting males maintain territories from May to September (Miller, 1964).

In 20 and 55 gallon aquaria, groups of two or three *L. gibbosus* form hierarchies in which one individual is dominant and nips and chases subordinate tank mates. These hierarchies are usually quite stable over time, and our observations are in agreement with Miller, 1964 for *L. gibbosus* and Greenberg, 1947 for *L. cyanellus*.

In addition to overt behavior, pumpkinseeds possess another means of signalling status within an hierarchy. Dominant fish are characterized by a specific color pattern, the operculum (gill tab) is black and edged with red. The body color is bright green and gold. The subordinates, in contrast, have pale opercula and dark vertical bars overlying a subdued body color. This is most noticeable in subordinates lowest on the social order, in communities comprising three or more individuals.

When two comparable pumpkinseeds are introduced, they normally fight, initially displaying and then circling and tail thrusting. These behaviors are almost invariably followed by biting. Eventually one fish begins to avoid its opponent and loses its intense coloration, which is replaced by the barred pattern. The winner then chases and nips the loser.

BEHAVIORAL DOSSIER

Table 3 lists the behavioral action patterns we have observed for the pumpkinseed sunfish, Lepomis gibbosus. There are 51 units in their social and feeding repertoires, apart from those exclusive to premating and reproductive behavior, which have not yet been observed in the laboratory. This species in intraspecific social interactions display to indicate status and to settle contacts without damaging contacts. Nevertheless, fights do occur and some physical damage can result to the loser. The displays of the sunfish are possibly less precise than those of the bullheads and there are far fewer action patterns incorporated into their social encounters. Also, there seems to be less clear distinction between different degrees of lateral, frontal and mouth displays. The behavioral dossier with 51 units suggests that there is less information in their social behavior, and that the level of behavioral complexity is well below that of the bullhead. We assume that the simpler behaviors and fewer signalling units are characteristic of an intermediate level of social evolution. It would appear that less information is required to sustain a hierarchical community compared with one based upon recognition of individuals, cooperative behavior and density dependent behavior. Our environmental ethology hypothesis would indicate that the pumpkinseed sunfish, with an intermediate level of social organization,would be less vulnerable to social disruption that a species like the bullhead from the same ecosystem exhibiting more complex behavior.

Table 3.

BEHAVIORAL DOSSIER

PUMPKINSEED SUNFISH ( *Lepomis gibbosus* )

| UNIT | RECORDING CODE | UNIT | RECORDING CODE |
|---|---|---|---|
| 1. APPROACH | *ap* | 27. HEAD DOWN | *hdn* |
| 2. ASCEND | *as* | 28. HOVER | *ho* |
| 3. ATTACK | *A* | 29. JERK | *J* |
| 4. AVOID | *av* | 30. LATERAL DISPLAY | *LD* |
| 5. BARRED | *bar* | 31. LEAN | *ln* |
| 6. BITE | *B* | 32. MOUTH LOCK | *ML* |
| 7. BLANCH | *bla* | 33. MOUTH UNLOCK | *Mu* |
| 8. CARROUSEL | *car* | 34. NIP | *N* |
| 9. CHASE | *ch* | 35. OPERCULUM BLANCHED | *obla* |
| 10. CHEW | *cw* | 36. OPERCULUM DARKENED | *odk* |
| 11. CRUISING 1 | *Cr 1* | 37. OPERCULUM ERECT | *Op* |
| 12. CRUISING 2 | *Cr 2* | 38. PECTORAL FLAPPING | *Pec* |
| 13. CRUISING 3 | *Cr 3* | 39. PUSH | *P* |
| 14. DARKEN | *da* | 40. REST | *R* |
| 15. DART | *Dt* | 41. REVERSE | *re* |
| 16. DESCEND | *ds* | 42. RUSH | *ru* |
| 17. DORSAL FIN ERECT | *dfe* | 43. SCRATCH | *sc* |
| 18. DORSAL FIN DOWN | *dfd* | 44. SIDLE | *Sde* |
| 19. ENTER | *E* | 45. SPIT | *sp* |
| 20. EYE BAR | *eb* | 46. SURFACE GULP | *sur* |
| 21. EXIT | *ex* | 47. TAIL BEAT | *TBt* |
| 22. FEED | *F* | 48. TAIL THRUST | *t* |
| 23. FIX | *fix* | 49. TOUCH | *To* |
| 24. FLEE | *Fl* | 50. TURN | *tu* |
| 25. INGEST | *i* | 51. YAWN | *Y* |
| 26. HALTING | *h* | | |

## THE EFFECTS OF A HISTORICAL AND ARTIFICIAL STRESS ON THE BEHAVIOR OF THE PUMPKINSEED SUNFISH, *LEPOMIS GIBBOSUS*

### SUBLETHAL TEMPERATURES: THE HISTORICAL STRESS

The study of the effects of sublethal temperatures on the social behavior of pumpkinseed sunfish are presently underway. We do not yet know if there is social disruption at high sublethal temperatures comparable to that found for the bullheads.

### OIL: THE ARTIFICIAL STRESS

The methods and concentrations of oil were identical to that used in the bullhead study on water soluble oil fractions. Feeding was not affected, and unlike the bullheads, there were no clear cut alterations in social behavior or organization at the test concentrations. However, we do not feel that the original pilot experiments in the small aquaria were necessarily valid, as there was a fairly high level of ambient social stress created by the small tanks. We are now using larger aquaria and our behavioral assays will be far more sensitive in the future.

## ECOSYSTEM 1: FRESHWATER LAKE (Cont.)

### SCHOOLING BEHAVIORAL TYPE:GOLDEN SHINER, NOTEMIGONUS CRYSOLEUCAS

We have observed schools of golden shiner in Ecosystem 1 and other nearby lakes from April to October. However, their reproductive and spawning behavior have not been observed in this study.

Hubbs and Cooper, 1936, summarized briefly the spawning behavior of this species.

> "As far as known, no one has given a detailed description of the act of spawning. The eggs, which are adhesive and stick to plants, are scattered over beds of rooted aquatic plants, according to some authors, throughout masses of filamentous algae according to others."

It would seem from the sparse literature on the behavior of this species that their sexual behavior may not involve nest building or the intricate courtship activities of pumpkinseeds or bullheads, or the elaborate parental care of bullheads noted by Breder (1936) and Atema (personal communication).

The golden shiner exhibits the simplest social behavior of the test fishes from Ecosystem 1. Their non-reproductive social behavior has not been previously described. In 20 and 55 gallon aquaria groups of 2 to 4 shiners aggregate, but maintain irregular spacing. Greater regularity of spacing has been observed in wild, lake populations. In the laboratory, golden shiner social groups seem to be comparatively anonymous, since introduction of a strange conspecific does not elicit any marked change in the behavior of the residents.

In our observations, highly aggressive behavior has not been recorded, although non-injurious aggressive-appearing behavior has been observed and consists of gentle nipping or nip-pushing and avoiding by the other fish. It may be that hierarchies do form in shiner aggregations, but we have yet to discover this phenomenon. There are no obvious signals identifying dominant or subordinate individuals, and all members of the group are subject to nudging and nipping on occasion. In none of the shiner communities has any individual been subject to the degree of aggression and punishment resembling that observed in pumpkinseed communities.

BEHAVIORAL DOSSIER

Of the freshwater fishes in the study, the golden shiner had by far the simplest behaviors. Only 36 units were observed (Table 4) and a number of them, particularly the agonistic units, occurred only infrequently. The behavior of this fish species is probably typical of most schooling species which inhabit small lakes. The bulk of their time is spent resting in close proximity, and darting from place to place within the aquaria. Rarely do they align themselves into tight formations, even in the large 3,000 gallon observation tanks. They do aggregate, though, rather than distribute themselves throughout the aquaria, no matter how large. It can be seen from the behavioral unit list (Table 4) that this schooling species lacks most of the social behaviors characteristic of higher levels of social organization in fishes.

Table 4.

# BEHAVIORAL DOSSIER

## GOLDEN SHINER (*Notemigonus crysoleucas*)

| UNIT | RECORDING CODE | UNIT | RECORDING CODE |
|---|---|---|---|
| 1. APPROACH | *ap* | 19. HOVER | *ho* |
| 2. ASCEND | *as* | 20. INGEST | *i* |
| 3. AVOID | *av* | 21. NIBBLE PUSH | *Np* |
| 4. CHASE | *ch* | 22. NIP | *N* |
| 5. CHEW | *cw* | 23. NOSE | *no* |
| 6. CRUISE 1 | *Cr1* | 24. NUDGE | *nud* |
| 7. CRUISE 2 | *Cr2* | 25. REST | *R* |
| 8. CRUISE 3 | *Cr3* | 26. REVERSE | *re* |
| 9. DART | *Dt* | 27. SCRATCH | *sc* |
| 10. DESCEND | *ds* | 28. SPIT | *sp* |
| 11. DORSAL FIN ERECT | *dfe* | 29. STATIONARY IN WATER | *Sta* |
| 12. DORSAL FIN DOWN | *dfd* | 30. SURFACE GULP | *sur* |
| 13. ENTER | *E* | 31. TAIL BEAT | *TBt* |
| 14. EXIT | *ex* | 32. TAIL THRUST | *t* |
| 15. FEED | *F* | 33. TOUCH | *T* |
| 16. FINS ERECT | *fe* | 34. TURN | *tu* |
| 17. FLEE | *Fl* | 35. WINDOW PUSH | *WP* |
| 18. HALT | *h* | 36. YAWN | *Y* |

# THE EFFECTS OF A HISTORICAL AND ARTIFICIAL STRESS ON THE BEHAVIOR OF THE GOLDEN SHINER, NOTEMIGONUS CRYSOLEUCAS

## SUBLETHAL TEMPERATURES: THE HISTORICAL STRESS

Like the pumpkinseed sunfish research, the study of the effects of sublethal temperatures on the social behavior of the golden shiner has not been completed, and it would be premature to make any preliminary statements, even though we have not yet found any qualitative behavioral changes associated with high temperatures.

## OIL: THE ARTIFICIAL STRESS

The methods, recording techniques and concentrations of the water soluble fractions of oil were identical to those used in the bullhead study. 20 gallon aquaria were used in the pilot study, although these small tanks have now been replaced with larger aquaria.

Feeding was not affected by the initial concentrations of the water soluble fractions of oil and the addition of the same amount of oil into the static system a week later did not affect feeding or any other observable behavior. Unlike the bullheads, there were no changes in social behavior or organization at the test concentrations.

This is our first evidence, albeit very preliminary and tentative, that fishes with the smallest and simplest behavioral repertoires are also the least prone to disruption by at least one type of pollutant. Sublethal thermal and oil stresses, on the other hand, induce dramatic changes in the social behavior of the behaviorally complex yellow bullhead.

The ongoing research on the selected species from Ecosystem 1 is intended to refine and extend the very preliminary pilot studies described in this report. Our analysis of the influence of sublethal temperatures on the social behavior of bullheads has recently been completed and the data is now undergoing statistical treatment. Further, a paper tentatively titled "The Impact of Sublethal Thermal Stresses on the Social Behavior of the Yellow Bullhead, Ictalurus natalis" (Engstrom, McLarney and Todd) is now in preparation. Comparable thermal studies on the remaining two freshwater species will be completed in 1972.

ECOSYSTEM 2: MARINE SUBTIDAL REGION

THE FISHES

Aggregating Behavioral Type:
Killifish - Fundulus majalis

Schooling Behavioral Type:
Atlantic Silverside - Menidia menidia

Spatial Defense Without Territories Behavioral Type:
Short Horn Sculpin - Myoxocephelus scorpius

Territorial and Hierarchical Behavioral Type:
Cunner - Tautogolabrus adspersus.

We have not completed the behavioral dossiers for any of the marine fishes in the study. The failure of the two, 3,000 gallon observation tanks has temporarily halted this phase of the research and no funds are presently available (approximately $8,000) to make these tanks operational. We intend to make some observations on the behavior of these four species in their natural habitat this coming summer, and to supplement these observations with recordings of their behavior in inexpensive outdoor pools.

## THE AMERICAN LOBSTER - *HOMARUS AMERICANUS*

The lobster, *Homarus americanus*, has been included in this study because of its economic importance as a fishery on the east coast of Canada and the New England states. We have been able to make a rough, preliminary assessment of the impact of a historical stress (sublethal temperatures) and an artificial stress (kerosene and its fractions) on the social and feeding behavior of the lobsters.

It is unfortunate that at this time the lobster research does not lend itself to our overall scheme of relating behavioral systems with ecosystems, as a direct comparison between the behavior of fishes and a single crustacean species cannot readily be made at this time. Our primary index of comparison between the fish species, the behavioral dossier, cannot be equated directly with the dossier of the lobster. The lobsters during the course of this study incorporated 89 action patterns into their behaviors, while the fish species (*Lepomis gibbosus*) with a similar level of social organization had only 51 action patterns in its repertoire. The differences between the two, which are reflected in the indexes, are primarily due to the lobster's higher number of external appendages.

In our opinion, it would be interesting and important for some investigator to initiate a comparative study of crustacea to look for correlations between the levels of social organization exhibited by the various kinds of crustacea, and their ability to withstand the two different classes of stress. Perhaps this study would be more difficult than our comparative fish study, as there are fewer crustacean species available within any inshore marine ecosystem. Each ecosystem may lack crustacea representative of one or several of the major categories of behavioral organization. However, since we have not explored this question in any depth, the advisability of a comparative crustacea study remains an open question.

BEHAVIOR

The lobster, until very recently, has been almost totally neglected by ethologists. Templeman (1934), and Atema and Engstrom (1971), have published brief descriptions of the sexual behavior of the lobster. Less than a year ago a Fisheries Research Board of Canada Technical Report by Scrivener (1971) entitled "Agonistic Behavior of the American Lobster, Homarus americanus (Milne-Edwards)" appeared. Scrivener compiled an ethogram of agonistic behaviors for this species based upon what he called "16 stereotyped action patterns". The experimental animals were placed in aquaria, separated by partitions and allowed to interact for 15 minutes after the partitions were listed. Although Scrivener did not look at their behavior in a "normal" or community social situations, he did provide a valuable analysis of how lobsters fight, what determines the outcome of conflicts, and the role of sex apart from reproduction, in agonistic interactions.

He found that there was a direct relationship between body size, and the probability that the largest animals win in combat, irrespective of sex. However, it was also ascertained that males were more aggressive in combat, compared with females. Our research substantiates both of these findings.

Scrivener also developed a scheme of behavioral sequence pathways for the lobster based upon his conflict resolution observations. Since his observations were made outside of a typical social conflict situation, it is difficult to evaluate the relevance of these pathways for the lobster in "real life" interactions. Clearly, winner and losers behave differently, but the critical regulating factors of dominance, territoriality, shelter, etc. were omitted from consideration in the experimental situation. Our impression, from observing small mixed-sex social groups has been that the dynamics of lobster communities, like their fish counterparts, are highly tuned and very sensitive to a variety of intrinsic and extrinsic influences; consequently they would not be readily amenable to description under the 3 or 4 basic activity chains outlined by Scrivener. What his activity chains perhaps illustrate, is a few of the strategies available to fighting lobsters. This might be equivalent to describing human aggression exclusively on the basis of boxing matches.

BEHAVIORAL DOSSIER AND SOCIAL BEHAVIOR

In order to compile a behavioral dossier for the lobster, we observed their social and feeding interactions in 30, 180, and 3,000 gallon observation tanks. The large majority of the observations were made in 180 gallon aquaria within which we tried to simulate some of the elements of their natural habitat. Shelters, retreats and brick wall barriers were made available to the inhabitants. The bottom of the tanks were covered to a depth of several inches with oyster chips and gravel. The oyster chips acted to buffer the seawater. Also, there were small pebbles and stones, and small numbers of a variety of marine organisms, including molluscs and killifishes, in several of the communities. Both open and semi-closed seawater systems were used depending upon the season of the year. During the winter and spring, heated semi-closed systems were employed and 1/3 of the volume of water was changed weekly. Air was added to keep dissolved oxygen close to the saturation point. Three to five lobsters were resident in each of the experimental communities.

In this report, we only overview some of the major characteristics of the behavior of Homarus, and describe briefly the pilot experiments on the influences of sublethal temperatures and kerosene and its fractions on their feeding, social behavior and organization. Several months ago a detailed analysis of behavioral development in lobster larvae and juveniles was initiated. This research, not reported here, is intended to provide a solid foundation for future research on the influences of environmental stresses on what we suspect will be the more sensitive stages in the life history of Homarus. This latter investigation is intended to explore the biological bases for aggression and cannibalism in young lobsters.

The behavioral dossier of the American lobster, Homarus americanus, is illustrated in Table 5. Units exclusive to sexual or courtship behavior are not included. A total of 89 behavioral action patterns were observed throughout the study, although more recently, Dr. Atema (personal communication) has extended this list even further on the basis of his research on the influences of the female sex pheromone on the behavior of other lobsters.

The majority of the behavioral activities of Homarus appear within a given behavioral context--e.g. units used in social behavior are not often found in feeding or other behaviors. Twenty-one out of the 89 behavioral activities, or action patterns, are of a general nature and can occur within a variety of behavioral contexts.

The breakdown of units associated with broad behavioral categories are as follows:

| | |
|---|---|
| SOCIAL.................... | 39 behavioral units |
| FEEDING................... | 26 behavioral units |
| GENERAL................... | 21 behavioral units |
| BODY CARE.................. | 5 behavioral units (This number will increase with further recording refinements.) |
| STRESS BEHAVIORS........... | 3 behavioral units |
| TOTAL.......... | 94 |

Five of the behavioral units, "antennule frequency in beats/minute", "antennule twitch", "grasp", "jump" and "lunge" were components of both social and feeding behaviors.

## Table 5.

BEHAVIORAL DOSSIER

AMERICAN LOBSTER (HOMARUS AMERICANUS)

| | UNIT | RECORDING CODE | PRINCIPAL CONTEXT(S) |
|---|---|---|---|
| 1. | AGITATE | A | STRESS |
| 2. | AMBULATORY SWAY | Am S | FEEDING |
| 3. | AMBULATORY GATHER (GRAVEL) | AGG | SOCIAL |
| 4. | ANTENNAE SWAY | A Sw | GENERAL |
| 5. | ANTENNAE SWEEP | S W | SOCIAL |
| 6. | ANTENNAE TOUCH | T | SOCIAL |
| 7. | ANTENNAE WAVE | AW | SOCIAL |
| 8. | ANTENNULE FREQUENCY | AF (beats / min) | FEEDING, SOCIAL |
| 9. | ANTENNULE TWITCH | A T | STRESS, FEEDING |
| 10. | APPROACH : LOBSTER | A L | SOCIAL |
| 11. | APPROACH : STIMULUS | A S | FEEDING |
| 12. | APPROACH : OBJECT | A O | GENERAL |
| 13. | ARCHED POSE | A P | SOCIAL |
| 14. | BOB | Bo | GENERAL |
| 15. | BACK TO | Ba t | GENERAL |
| 16. | BULLDOZE | B | SOCIAL |
| 17. | CARRY | Ca | FEEDING |
| 18. | CHASE | Ch | SOCIAL |
| 19. | CHEW | C | FEEDING |
| 20. | CLAW JABBING | C J | SOCIAL |
| 21. | CLAWS CLOSED | C C | GENERAL |
| 22. | CLIMB UP ON TANK | Clb | GENERAL |
| 23. | CLING | Cg | GENERAL |
| 24. | CROSSED CLAWS | Cr C | GENERAL |
| 25. | CROUCH | Cro | SOCIAL |
| 26. | CRUSH | Cr | FEEDING |
| 27. | DROP | D | FEEDING |
| 28. | DROP DOWN (OVER FOOD) | D D | FEEDING |
| 29. | EXOPODITE WAVE | E W | GENERAL |
| 30. | EXOPODITE WAVE (RAPID) | E W (R) | FEEDING |
| 31. | FACE OFF | F O | SOCIAL |
| 32. | FLEE | Fl | SOCIAL |
| 33. | FLOP DOWN ON STIMULUS/FOOD | Fd | FEEDING |
| 34. | FLOP DOWN ON SUBSTRATE | F S | SOCIAL |
| 35. | FOLD CLAWS | F C | SOCIAL |
| 36. | GRASP | Gr | FEEDING, SOCIAL |
| 37. | GRAVEL PUSHING | G P | GENERAL |
| 38. | GROOM | G | BODY CARE |
| 39. | INGEST | I | FEEDING |
| 40. | JERK BODY | J B | STRESS |
| 41. | JUMP | J | FEEDING, SOCIAL |
| 42. | LOBSTER RESTING IN VERTICAL POSITION ON TANK | L R V | GENERAL |
| 43. | LUNGE | L | FEEDING, SOCIAL |
| 44. | LUNGE AT LOBSTER AND HIT | L L H | SOCIAL |
| 45. | LUNGE AT LOBSTER AND MISS | L L M | SOCIAL |

| | UNIT | RECORDING CODE | PRINCIPAL CONTEXT(S) |
|---|---|---|---|
| 46. | MAXILLIPED (3) GRIND | M G | FEEDING |
| 47. | MAXILLIPED (3) STROKE | M St | BODY CARE |
| 48. | MAXILLIPED (3) SWAY | M | FEEDING |
| 49. | OPEN CLAW STANCE | O C S | SOCIAL |
| 50. | OPEN CLAWS | O C | SOCIAL |
| 51. | PICK UP (3rd MAXILLIPED) | P-3 | FEEDING |
| 52. | PICK UP (1st AMBULATORY) | P-1 | FEEDING |
| 53. | PICK UP (CHELA) | P-C | FEEDING |
| 54. | PIVOT | Pi | GENERAL |
| 55. | PUSHING | Pu | SOCIAL |
| 56. | RAKE (AMBULATORY) | R | FEEDING |
| 57. | RAISE UP | Ra U | SOCIAL |
| 58. | RAISE UP ON CLAWS | R Uc | SOCIAL |
| 59. | RAPID SWIM | R S | SOCIAL |
| 60. | REAR UP | R U | SOCIAL |
| 61. | REST ON CLAWS | R C | GENERAL |
| 62. | REVERSE | Re | GENERAL |
| 63. | REVERSE AVOIDANCE | Ra | SOCIAL |
| 64. | REVERSE CLIMB ON TANK | R Cl | GENERAL |
| 65. | ROLL OVER | R O | SOCIAL |
| 66. | RUN | R N | SOCIAL |
| 67. | SIDE WALK | S W | SOCIAL |
| 68. | SINGLE CLAW LUNGE | S C.L | SOCIAL |
| 69. | SIT ON | S O | GENERAL |
| 70. | SPIT OUT | Sp O | FEEDING |
| 71. | STILL | S | GENERAL |
| 72. | STOP | Stp | GENERAL |
| 73. | STROKE ANTENNAE | S A | BODY CARE |
| 74. | STROKE ANTENNULE | S A T | BODY CARE |
| 75. | STROKE ANTENNULE WITH AMBULATORY LEG | S A L | BODY CARE |
| 76. | STRUT | St | SOCIAL |
| 77. | SWIMMERET BEAT MOVING GRAVEL | S B G | GENERAL |
| 78. | SWIMMERET WAVE BEAT | S W B | GENERAL |
| 79. | TAIL CURLED UNDER | T C U | SOCIAL |
| 80. | TAIL FLIP | T F | SOCIAL |
| 81. | TAIL SPREAD | T S | SOCIAL |
| 82. | TAIL UP | T U | SOCIAL |
| 83. | TOUCH 3rd MAXILLIPED | T 3 M | FEEDING |
| 84. | TOUCH AMBULATORY LEG | T A L | FEEDING |
| 85. | TOUCH ANTENNAE | T A | SOCIAL |
| 86. | UPRIGHT STANCE | U S | SOCIAL |
| 87. | WALK | W | GENERAL |
| 88. | WALK CLOSE TO STIMULUS | W C | FEEDING |
| 89. | WALK OVER | W O | FEEDING |

ABSENT FROM THIS LIST ARE THE BEHAVIORAL ACTIVITIES EXCLUSIVE TO COURTSHIP AND MATING.

The fact that almost half of the behavioral activities are associated with social organization suggests that Homarus is a relatively complex animal in behavioral terms. In the experimental communities containing 3 - 5 animals, a dominance order was always established within a few days and tended to remain relatively stable over time, at least for periods up to several months.

The introduction of new lobsters into a stable community did in some cases alter dominance relationships, particularly when the introduced animal was large enough to secure for itself a territory at the expense of the more subordinate residents. The dynamics of "unstable social communities" resulting from the introduction of new residents of both sexes has not yet been detailed. Such a study is needed, though, to help determine if Homarus is a species primarily adapted to shifting social relations and constant change in community structure, or if they are normally residents of more stable social communities, for at least part of the year. Direct field observations of marked animals would also help to determine if stability were a characteristic of lobster communities. We suspect, from the very little information we have gathered, that their social dynamics are based upon simultaneously stable and unstable elements. The larger, most dominant animals comprise the stable element in lobster communities, with smaller animals constantly seeking a territory and a "place", as they shift or travel from locality to locality on the ocean floor. Seasonal migrations commonly reported by lobster fishermen would not be part of this phenomenon.

TERRITORIALITY

The lobsters in the experimental communities were territorial, with the most dominant having the darkest and usually most remote, shelter. Territories were established through conflict and were maintained by constant agonistic exchanges. Subordinates, in order of rank, also established territories if there were available shelters. The lowest ranked individuals either occupied territories vacant at the front of the tanks or, if suitable shelters were not available, they rested on top of blocks and stones in the upper waters of the tank. In these exposed locations they remained motionless, and during daylight hours were relatively immune from attack by dominants, unless the carrying capacity of the community had been exceeded. When this happened (usually when there were five or more animals in the community) the lowest ranked individuals were removed.

HOME RANGE

Associated with territoriality is the phenomenon of home ranges and in the experimental communities the more dominant animals also maintained and defended the largest home ranges or areas within the tank they regularly patrolled and explored. In most cases, only the alpha lobster had a range that extended throughout a large portion of the community. Subordinates rarely travelled far beyond their shelter entrance. Home ranges are defended, but not with the vigor or intensity associated with conflicts in the immediate area of the shelter or burrow.

BURROWING AND ENVIRONMENTAL MANIPULATION

Dominant or highly ranked lobsters constantly manipulate their environment by moving stones, bricks, gravel about in their area of shelter.

Cobb (1969) has described their burrowing behavior.

In the small experimental communities, almost all of the shelter excavation and substrate manipulation was confined to the most dominant animal. The next in rank showed the same kinds of behavior, but far less frequently. It would seem possible to determine dominance in a community almost exclusively on the basis of shelter and substrate manipulation activity.

FEEDING

Feeding in the experimental communities was, to a large degree, under dominance control. The subordinates, because of their limited ranges, were less able to move about in search of the food which was dropped into the tanks. Consequently, the dominants, with more searching behaviors in their repertoires, were able to locate first and ingest most of the food. The subordinates usually fed after the dominant had returned to its shelter with chunks of food, usually chopped up bits of fish. It was necessary for us to insure that all animals fed, so food chunks were placed directly in front of the shelters of the animals lowest in rank. In nature, under food limiting conditions, it is quite conceivable that feeding might be restricted to those animals closest to the top of the hierarchy.

DOMINANCE AND MOLTING

The influence of dominance on molting in Homarus and the impact of the molting animal on the social structure was not investigated, due primarily to the fact that very few molts took place within the experimental communities. From the few observations on molting that were made, it would appear that the quality of the shelter, and therefore dominance, is a major variable in community regulation. The newly molted animals, which are unable to defend themselves, must have a shelter which can protect them while they are soft-bodied. Good hiding shelters were only inhabited by the most highly ranked individuals, and molting in the communities occurred only twice and was confined to dominant animals. During the same period, there were a number of molts by animals housed in individual aquaria nearby.

SEX AND COMMUNITY SOCIAL STRUCTURE

The role of sex in social interaction of pairs of lobsters has been discussed by Scrivener (1971), and our investigation of the effects of sublethal temperatures on lobster social behavior involving 40 half-hour pair interactions by 8 animals indicated that females employ less overtly aggressive strategies in encounters with their own sex, as compared with the males. There were, however, no qualitative differences between male-male and male-female encounters. (See RESULTS under SUB-LETHAL TEMPERATURES.

A single male-female conflict resolution series was carried out during the pilot studies. Both the male and female were dominant prior to their being placed in the experimental tank and the female was slightly larger with a carapace of 0.3 cm longer than the male's. Their first two interactions are shown in figure 13. The figure depicts how closely matched they were in the two initial half hour conflict periods. The male (subordinate) claw jabbed with a greater frequency at the same time as it tail flipped. This suggests that he was equally motivated towards flight and attack behaviors. The female was the victor, but the male did not assume subordinate status until the end of the fourth encounter. At this time he remained crouched close to the substrate with his claws held closed, indicating that dominance relations had finally been established.

Whether this atypically long series of agonistic exchanges before rank was established was a consequence of their past experiences (both had a history of being winners in conflicts) or whether sex recognition and sexuality were the major variable here is not yet known. It would seem though, that the sex of a lobster may not be the overriding factor in status determination. Since females carrry their eggs externally many months before hatching, a comparable degree of aggressiveness and shelter-related behavior between the sexes might be highly adaptive for this species.

## THE EFFECTS OF A HISTORICAL AND ARTIFICIAL STRESS ON THE BEHAVIOR OF THE LOBSTER, *HOMARUS AMERICANUS*

In our introductory investigations on the effects of a historical and artificial stress on the behavior of lobsters, two very different kinds of behavioral assays were employed and the assays are not directly comparable. In the early stages of the research we were evaluating several assay possibilities in order to find the most meaningful and sensitive approaches for an environmental ethology.

In the thermal stress study, pairs of animals, normally separated by a screen barrier, were used in conflict resolution encounters. The barriers were removed and the agonistic interactions at the different sublethal temperatures were recorded and compared. This approach assumes that aggressive social exchanges are fundamental to lobster social organization, and if these exchanges are qualitatively altered in a meaningful way, that this could represent an alteration or breakdown in normal social relations. Scrivener (1971) used a comparable approach.

The conflict resolution method has the advantage of enabling the investigator to gather large amounts of data in a relatively short period of time. It is, however, a behaviorally artificial test condition and in our view is not sensitive or meaningful enough to be adopted as a behavioral assay.

Consequently, for the artificial stress study in which kerosene and its fractions were the pollutants, we adopted a biologically more complete technique. Stable, multi-animal communities, with some habitat complexity built in, were the basis of the assay. Relatively normal social relations could be established and maintained within the communities, and any breakdown in these relations due to extrinsic stresses could be detected by detailed ethological recording techniques. The experimental tanks in the "community" method were 6 times greater in volume than the 30 gallon conflict resolution systems, and it was much easier to control for major variables such as pH and oxygen within the larger communities.

The stable community approach to studying stress has several major drawbacks: it is more expensive, requires much more space, and takes far longer to carry out. Also, it is more difficult to compile significant amounts of data, because of the long periods of time required to create stability within the communities used in subsequent stress experiments. Despite the drawbacks, the "stable community" assay is much more preferable and in our future research, if space can be found, we intend to confine the research to this type of assay.

## SUBLETHAL TEMPERATURES--THE HISTORICAL STRESS

Eight pairs of animals were housed in 30 gallon glass fronted aquaria and were separated by a porous plastic partition which permitted an exchange of water between the two sides. Subsand filters were placed under a bed of oyster chips and gravel, and each tank was supplied with air. The water was slowly replaced with fresh thermally adjusted sea water three times weekly. The light in the observation area was reduced to a minimum and supplemented with red lights to aid the observers. Two hundred watt aquarium heaters encased in glass were used for temperature control.

The barriers were lifted for half an hour and two observers simultaneously recorded the activities of each lobster.

Three temperatures were used throughout the study. We initially determined the lethal temperatures for the lobster (30-31° C) and selected 27° C, 3 centigrade degrees below the lethal limit, as the "high stress" level. The baseline temperature was 21° C, the temperature of the tanks in the laboratory, without the addition of any heat. An intermediate temperature, 24.5° C was chosen. This represented the upper thermal range normally enountered by lobsters during late summer off Cape Cod.

Each series of recordings began at room temperature and then heat was added until the temperature was slowly raised to the next level. When the temperature was stable at 24.5° C the animals were allowed to acclimate for at least 24 hours before interactions commenced. Finally, the temperatures were slowly raised to 27° C and held for at least a day before the final set of recordings. At each temperature, a number of the animals were switched from tank to tank and an overall total of 30 half hour conflict resolution encounters comprised the sublethal temperatures pilot study. The lobsters were fed on mussels and herring three times a week throughout the experimental period.

FINDINGS

The results of the experiment are reported in Tables 6 and 7. Table 6 represents a summary of key agonistic action patterns or behavioral units observed for dominant and subordinate animals in male - male and female-female encounters at 21° C, 24.5° C and 27° C. The sixteen action patterns were selected for analysis on the basis of their being indicators of aggressive and dominance related activities, or conversely, subordinate and avoidance actions critical to the behavioral pathways of lobsters during conflicts.

Table 7 is a further interpretation of the information shown in Table 6. The means, plus or minus two times the standard error of the ranges, have been tabulated to help overview the significance of the behavioral differences we observed.

While the study is not intended to be in any way definitive or complete, it was apparent that no fundamental changes in behavior were observed at the highest sublethal temperature (27° C), and the strategies and action pattern sequences remained constant at the three test temperatures. The only marked changes in behavior which were detected were an increase in grooming in many of the dominant males and in subordinate and dominant females at 27° C. This increase is probably indicative of a mild stress. Another unit, body jerk, was observed once in a dominant male at room temp-

## Table 6.

**TEMPERATURE 21° C**

| UNIT | Dominant Male n | $\bar{x}$ | s.e. | Range | Subordinate Male n | $\bar{x}$ | s.e. | Range | Dominant Female n | $\bar{x}$ | s.e. | Range | Subordinate Female n | $\bar{x}$ | s.e. | Range |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. antennae sweep | 10 | 13.5 | 5.7 | 0 - 57 | 10 | 1.6 | 0.8 | 0 - 7 | 5 | 11.8 | 4.0 | 2 - 20 | 5 | 4.0 | 2.1 | 0 - 9 |
| 2. antennae touch | 10 | 81.5 | 20.1 | 21 - 203 | 10 | 30.9 | 7.1 | 1 - 59 | 5 | 67.8 | 9.1 | 46 - 101 | 5 | 25.6 | 15.6 | 1 - 86 |
| 3. approach lobster | 10 | 19.5 | 2.9 | 10 - 40 | 10 | 0.5 | 0.2 | 0 - 2 | 5 | 6.4 | 3.3 | 3 - 18 | 5 | 0.2 | 0.2 | 0 - 1 |
| 4. body jerk | 10 | 0.1 | 0.1 | 0 - 1 | 10 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| 5. claw jabbing | 10 | 21.0 | 5.8 | 5 - 62 | 10 | 0 | 0 | 0 | 5 | 7.6 | 4.1 | 0 - 23 | 5 | 2.0 | 2.0 | 0 - 10 |
| 6. gravel pushing | 10 | 2.0 | 1.4 | 0 - 14 | 10 | 0 | 0 | 0 | 5 | 1.6 | 0.8 | 0 - 4 | 5 | 0 | 0 | 0 |
| 7. grooming | 10 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| 8. lunge & hit | 10 | 8.7 | 1.8 | 0 - 22 | 10 | 0 | 0 | 0 | 5 | 0.8 | 0.6 | 0 - 3 | 5 | 0 | 0 | 0 |
| 9. lunge & miss | 10 | 19.4 | 2.5 | 8 - 31 | 10 | 0.3 | 0.2 | 0 - 2 | 5 | 1.8 | 1.1 | 0 - 5 | 5 | 0.2 | 0.2 | 0 - 1 |
| 10. push by lobster | 10 | 12.2 | 4.4 | 0 - 40 | 10 | 0.8 | 0.6 | 0 - 6 | 5 | 12.4 | 2.8 | 6 - 21 | 5 | 1.0 | 0.6 | 0 - 3 |
| 11. rear-up | 10 | 8.7 | 1.5 | 3 - 17 | 10 | 1.3 | 0.5 | 0 - 5 | 5 | 14.4 | 3.8 | 8 - 29 | 5 | 6.2 | 2.1 | 1 - 13 |
| 12. rest on wall | 10 | 0 | 0 | 0 | 10 | 4.6 | 1.7 | 0 - 16 | 5 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| 13. reverse avoidance | 10 | 0 | 0 | 0 | 10 | 21.1 | 3.1 | 4 - 35 | 5 | 0 | 0 | 0 | 5 | 2.0 | 1.1 | 0 - 6 |
| 14. still | 10 | 4.9 | 0.9 | 1 - 10 | 10 | 12.8 | 1.4 | 3 - 20 | 5 | 5.8 | 1.7 | 1 - 10 | 5 | 23.2 | 3.0 | 14 - 33 |
| 15. stroke antennule | 10 | 8.9 | 1.8 | 0 - 19 | 10 | 2.8 | 1.7 | 0 - 18 | 5 | 8 | 0.7 | 6 - 10 | 5 | 10.0 | 3.3 | 3 - 22 |
| 16. tail flip | 10 | 0.5 | 0.4 | 0 - 2 | 10 | 28.7 | 7.2 | 2 - 58 | 5 | 0 | 0 | 0 | 5 | 2.8 | 2.1 | 0 - 11 |

**TEMPERATURE 24.5°**

| UNIT | Dominant Male n | $\bar{x}$ | s.e. | Range | Subordinate Male n | $\bar{x}$ | s.e. | Range | Dominant Female n | $\bar{x}$ | s.e. | Range | Subordinate Female n | $\bar{x}$ | s.e. | Range |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. antennae sweep | 4 | 12.5 | 4.2 | 5 - 24 | 4 | 0 | 0 | 0 | 2 | 19.0 | 1.0 | 18 - 20 | 2 | 0 | 0 | 0 |
| 2. antennae touch | 4 | 155.2 | 56.5 | 25 - 284 | 4 | 12.5 | 3.2 | 7 - 21 | 2 | 56.0 | 24.1 | 32 - 80 | 2 | 13.5 | 0.5 | 13 - 14 |
| 3. approach lobster | 4 | 18.7 | 2.9 | 12 - 24 | 4 | 0 | 0 | 0 | 2 | 10.0 | 6.0 | 4 - 16 | 2 | 0 | 0 | 0 |
| 4. body jerk | 4 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 5. claw jabbing | 4 | 28.5 | 1.9 | 24 - 33 | 4 | 2.0 | 1.2 | 0 - 5 | 2 | 9.0 | 6.0 | 3 - 15 | 2 | 0 | 0 | 0 |
| 6. gravel pushing | 4 | 1.2 | 1.0 | 1 - 4 | 4 | 0.2 | 0.3 | 0 - 1 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 7. grooming | 4 | 3.5 | 0.3 | 3 - 4 | 4 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 8. lunge & hit | 4 | 8.2 | 3.4 | 2 - 15 | 4 | 0.2 | 0.3 | 0 - 1 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 9. lunge & miss | 4 | 13.5 | 3.8 | 5 - 23 | 4 | 1.2 | 1.3 | 0 - 5 | 2 | 3.5 | 0.5 | 3 - 4 | 2 | 0 | 0 | 0 |
| 10. push by lobster | 4 | 9.7 | 3.4 | 6 - 20 | 4 | 1.5 | 1.2 | 0 - 6 | 2 | 5.5 | 0.5 | 5 - 6 | 2 | 0 | 0 | 0 |
| 11. rear-up | 4 | 5.7 | 0.6 | 4 - 7 | 4 | 1.2 | 0.5 | 0 - 2 | 2 | 12.5 | 6.5 | 6 - 19 | 2 | 2 | 1 | 1 - 3 |
| 12. rest on wall | 4 | 0 | 0 | 0 | 4 | 1.0 | 0.7 | 0 - 3 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 13. reverse avoidance | 4 | 0 | 0 | 0 | 4 | 22.5 | 1.6 | 18 - 25 | 2 | 0 | 0 | 0 | 2 | 7 | 0 | 1 - 13 |
| 14. still | 4 | 7.2 | 1.8 | 2 - 10 | 4 | 19.2 | 2.6 | 16 - 27 | 2 | 3.5 | 2.5 | 1 - 6 | 2 | 29.5 | 6.5 | 23 - 36 |
| 15. stroke antennule | 4 | 13.7 | 1.3 | 11 - 16 | 4 | 2.7 | 1.0 | 0 - 5 | 2 | 9.5 | 3.5 | 6 - 13 | 2 | 10.5 | 10.5 | 0 - 21 |
| 16. tail flip | 4 | 0 | 0 | 0 | 4 | 15.5 | 6.4 | 4 - 33 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |

**TEMPERATURE 27°**

| UNIT | Dominant Male n | $\bar{x}$ | s.e. | Range | Subordinate Male n | $\bar{x}$ | s.e. | Range | Dominant Female n | $\bar{x}$ | s.e. | Range | Subordinate Female n | $\bar{x}$ | s.e. | Range |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. antennae sweep | 2 | 4.0 | 4.0 | 0 - 8 | 2 | 0 | 0 | 0 | 3 | 24.6 | 15.2 | 7 - 55 | 3 | 0.3 | 0.3 | 0 - 1 |
| 2. antennae touch | 2 | 57.5 | 67.7 | 0 - 135 | 2 | 2.5 | 2.5 | 0 - 5 | 3 | 49.6 | 9.7 | 40 - 69 | 3 | 33.3 | 10.4 | 16 - 52 |
| 3. approach lobster | 2 | 7.5 | 7.5 | 0 - 15 | 2 | 0 | 0 | 0 | 3 | 5.6 | 1.8 | 3 - 9 | 3 | 0 | 0 | 0 |
| 4. body jerk | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 3 | 1.6 | 0.3 | 1 - 2 | 3 | 0.3 | 0.3 | 0 - 1 |
| 5. claw jabbing | 2 | 9.5 | 9.5 | 0 - 19 | 2 | 2.0 | 2.0 | 0 - 4 | 3 | 11.0 | 1.0 | 10 - 13 | 3 | 2.0 | 2.0 | 0 - 6 |
| 6. gravel pushing | 2 | 3 | 3.0 | 0 - 6 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| 7. grooming | 2 | 9.5 | 9.5 | 0 - 19 | 2 | 0 | 0 | 0 | 3 | 0.6 | 0.7 | 0 - 2 | 3 | 4.6 | [illegible] | 0 - 14 |
| 8. lunge & hit | 2 | 5.5 | 5.5 | 0 - 11 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| 9. lunge & miss | 2 | 6.0 | 6.0 | 0 - 12 | 2 | 0.5 | 0.5 | 0 - 1 | 3 | 3.6 | 1.2 | 2 - 6 | 3 | 0 | 0 | 0 |
| 10. push by lobster | 2 | 3.5 | 3.5 | 0 - 7 | 2 | 0.5 | 0.5 | 0 - 1 | 3 | 11.6 | 1.7 | 10 - 15 | 3 | 0.6 | 0.3 | 0 - 1 |
| 11. rear-up | 2 | 2.5 | 2.5 | 0 - 5 | 2 | 1.0 | 1.0 | 0 - 2 | 3 | 12.0 | 2.3 | 8 - 16 | 3 | 1.0 | 0.5 | 0 - 2 |
| 12. rest on wall | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| 13. reverse avoidance | 2 | 0 | 0 | 0 | 2 | 7.0 | 7.0 | 0 - 14 | 3 | 0 | 0 | 0 | 3 | 3.3 | 2.4 | 0 - 8 |
| 14. still | 2 | 9.5 | 3.5 | 6 - 13 | 2 | 13.5 | 2.5 | 11 - 16 | 3 | 8.0 | 2.7 | 4 - 13 | 3 | 17.3 | 4.4 | 9 - 24 |
| 15. stroke antennule | 2 | 7.5 | 7.5 | 0 - 15 | 2 | 4.0 | 1.0 | 3 - 5 | 3 | 18.6 | 4.3 | 10-24 | 3 | 24.0 | 6.8 | 11 - 34 |
| 16. tail flip | 2 | 0 | 0 | 0 | 2 | 0.5 | 0.5 | 0 - 1 | 3 | 0 | 0 | 0 | 3 | 2.3 | 1.3 | 1 - 5 |

SOCIAL INTERACTIONS OF LOBSTERS AT 21°, 24.5° and 27° C

# Table 7.

SOCIAL INTERACTIONS OF LOBSTERS

($\bar{x}$ ± 2 x s.e.)

| UNIT | 21° C DOMINANT ♂ | 21° C SUBORDINATE ♂ | 21° C DOMINANT ♀ | 21° C SUBORDINATE ♀ | 24.5° DOMINANT ♂ | 24.5° SUBORDINATE ♂ | 24.5° DOMINANT ♀ | 24.5° SUBORDINATE ♀ | 27° C DOMINANT ♂ | 27° C SUBORDINATE ♂ | 27° C DOMINANT ♀ | 27° C SUBORDINATE ♀ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. antennae sweep | 2.1-24.9 | .1-3.0 | 3.9-19.7 | 0 - 8.1 | 4.2-20.8 | 0 | 17.0-21.0 | 0 | 4.0-12.0 | 0 | 0-55.1 | 0-1.0 |
| 2. antennae touch | 41.4-121.6 | 16.8-45.0 | 50.0-86.1 | 0-56.9 | 42.1-268.3 | 6.0-19.0 | 7.9-104.1 | 12.5-14.5 | 0-202.9 | 0-7.5 | 30.3-68.9 | 12.4-54.2 |
| 3. approach lobster | 13.7-25.3 | 0-0.9 | 0-12.9 | 0-0.6 | 13.0-25.9 | 0 | 0-22.0 | 0 | 0-22.5 | 0 | 2.1-9.1 | 0 |
| 4. body jerk | 0-0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0-2.3 | 0-1.0 |
| 5. claw jabbing | 9.5-32.5 | 0 | 0-15.8 | 0-6 | 24.7-32.3 | 0-4.4 | 3.0-21.0 | 0 | 0-28.6 | 2.0-6.0 | 9.0-13.0 | 0-6.0 |
| 6. gravel pushing | 0-4.8 | 0 | 0-3.2 | 1.5-7.1 | 0-3.1 | 0-0.7 | 0 | 0 | 3.0-9.0 | 0 | 0 | 0 |
| 7. grooming | 0 | 0 | 0 | 0 | 2.9-4.1 | 0 | 0 | 0 | 0-28.6 | 0 | 0-1.9 | 0-14.0 |
| 8. lunge & hit | 5.1-12.3 | 0 | 0-2.0 | 0 | 1.5-14.9 | 0-0.7 | 0 | 0 | 0-16.5 | 0 | 0 | 0 |
| 9. lunge & miss | 14.3-24.5 | 0-0.7 | 0-4.0 | 0-0.6 | 6.0-21.0 | 0-3.7 | 2.5-4.5 | 0 | 6.0-18.0 | 0-1.5 | 1.2-6.0 | 0 |
| 10. push by lobster | 3.4-21.0 | 0-2.0 | 0-17.9 | 0 | 2.9-16.5 | 0-3.9 | 4.5-6.5 | 0 | 3.5-10.5 | 0-1.5 | 8.3-14.9 | 0-1.3 |
| 11. rear-up | 5.7-11.7 | 0.2-2.4 | 6.9-21.9 | 2.1-10.3 | 4.4-7.0 | 0.2-2.2 | 0-25.5 | 0-4.0 | 0-7.5 | 1.0-3.0 | 7.4-16.6 | 0-2.2 |
| 12. rest on wall | 0 | 1.2-8.0 | 0 | 0 | 0 | 0-2.7 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13. reverse avoidance | 0 | 14.9-27.3 | 0 | 0-4.3 | 0 | 19.4-25.6 | 0 | 0-19.0 | 0 | 0-21.0 | 0 | 0-8.1 |
| 14. still | 3.0-6.8 | 9.9-15.7 | 2.4-9.2 | 17.2-29.2 | 3.6-10.8 | 14.0-24.4 | 0-8.5 | 16.5-42.5 | 2.5-16.5 | 8.5-18.5 | 2.7-11.3 | 8.5-26.1 |
| 15. stroke antennule | 5.3-12.5 | 0-6.3 | 6.6-9.4 | 3.7-16.7 | 11.1-16.3 | 0.6-4.8 | 2.5-16.5 | 0-31.6 | 0-22.5 | 2.0-6.0 | 10.1-28.3 | 10.4-39.6 |
| 16. tail flip | 0-1.2 | 14.4-43.0 | 0 | 0 | 0 | 2.6-28.4 | 0 | 7.0-7.0 | 0 | 0-1.5 | 0 | 0-4.9 |

erature. It appeared again in both dominants and subordinate females at $27^{\circ}$ C. This action, violent and reminiscent of a spasm, is probably associated with stress, although the significance of this behavior is not yet understood.

The pilot investigation indicated that the overall modes of interacting during the establishment of dominance and stable social relations did not vary significantly with increased temperatures, even at a level of thermal stress 3 centigrade degrees below their lethal limits. For the lobster, it is quite likely that high sublethal temperatures up to $27^{\circ}$ C do not disrupt their social behavior and organization. Stable community assays are needed to substantiate these findings.

CONFLICT RESOLUTION

The frequency of key action patterns during male - male, female - female and male - female encounters are illustrated in figures 7 through 13. They show the strategies employed by both the dominants and subordinates during agonistic bouts. Each figure depicts two selected encounters and therefore is not representative of all the interactions we observed at each temperature. They are included here only to demonstrate the different kinds and frequency of action patterns or behavioral units used by dominants and subordinates in conflict resolution encounters.

Figures 7, 8 and 9 depict male - male encounters at each temperature. With the exception of units associated with avoidance and flight, the subordinates are behaviorally far less active, while the dominants are very aggressive throughout the half-hour interactions. The behavior of the subordinates is almost always in response to action sequences initiated by the

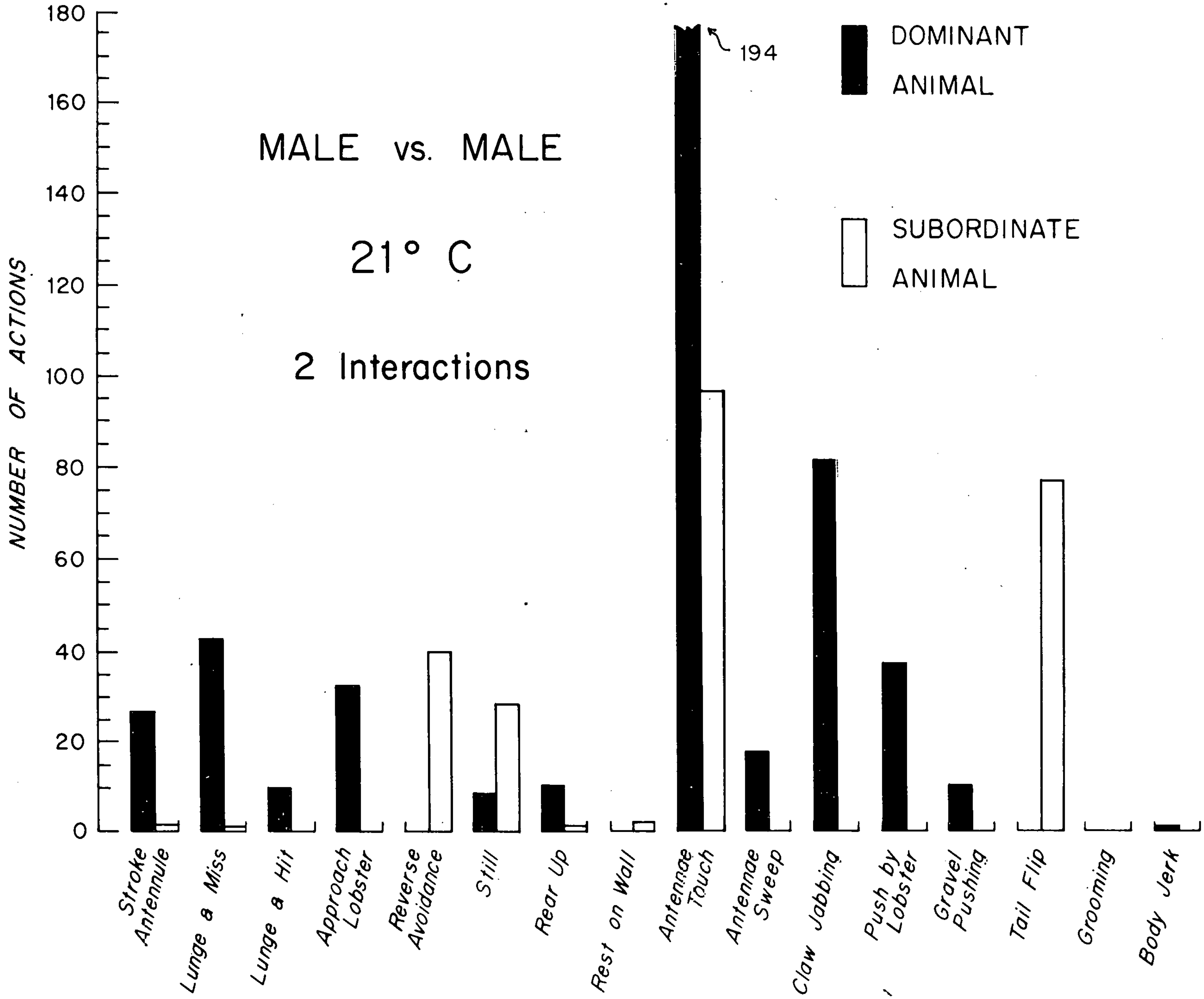
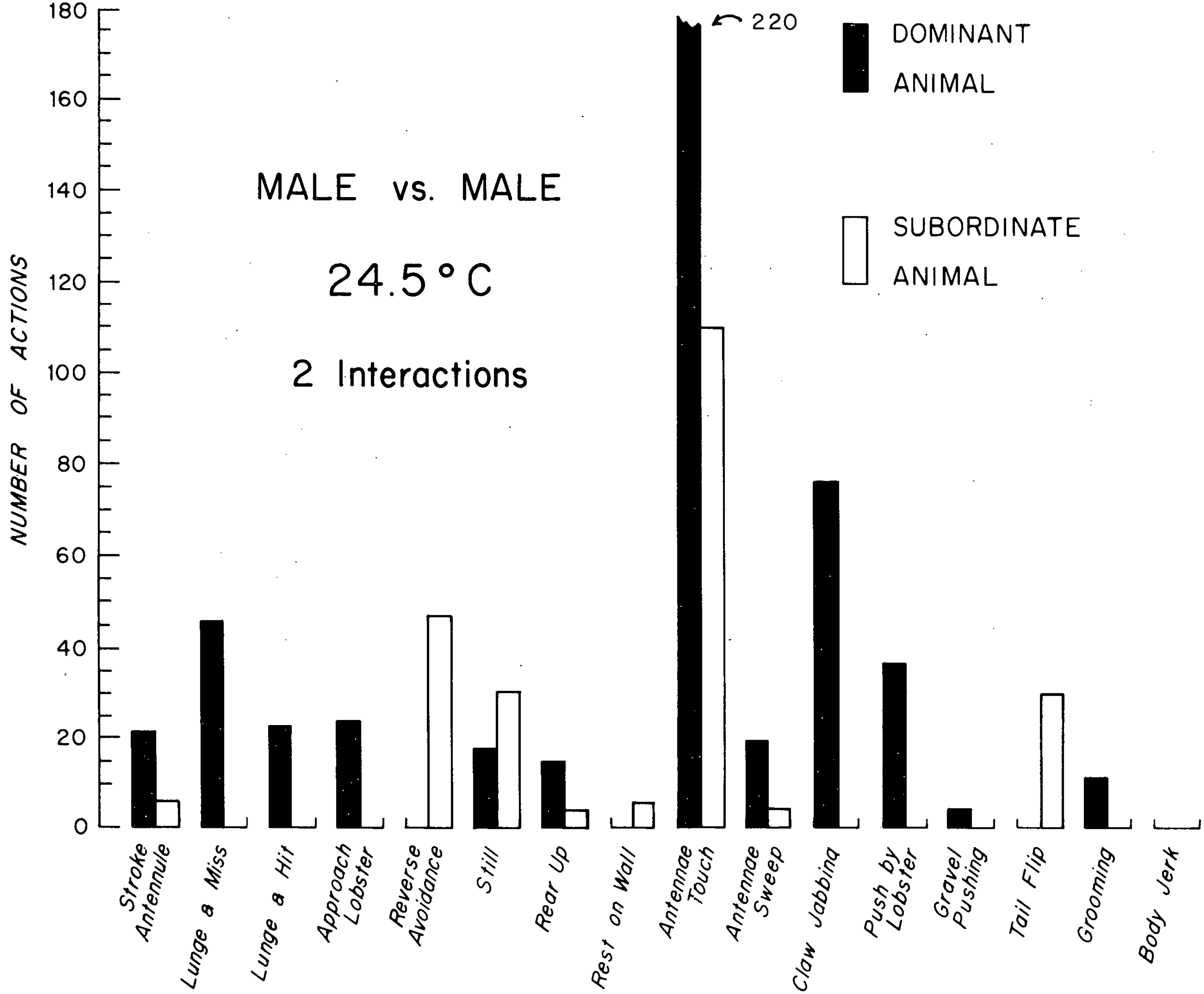

MALE vs. MALE
21° C
2 Interactions
NUMBER OF ACTIONS
180
160
140
120
100
80
60
40
20
0
194
DOMINANT ANIMAL
SUBORDINATE ANIMAL
Stroke Antennule
Lunge & Miss
Lunge & Hit
Approach Lobster
Reverse Avoidance
Still
Rear Up
Rest on Wall
Antennae Touch
Antennae Sweep
Claw Jabbing
Push by Lobster
Gravel Pushing
Tail Flip
Grooming
Body Jerk

Figure 7.



NUMBER OF ACTIONS
0
20
40
60
80
100
120
140
160
180
220
MALE vs. MALE
24.5°C
2 Interactions
DOMINANT ANIMAL
SUBORDINATE ANIMAL
Stroke Antennule
Lunge a Miss
Lunge a Hit
Approach Lobster
Reverse Avoidance
Still
Rear Up
Rest on Wall
Antennae Touch
Antennae Sweep
Claw Jabbing
Push by Lobster
Gravel Pushing
Tail Flip
Grooming
Body Jerk


Figure 8.

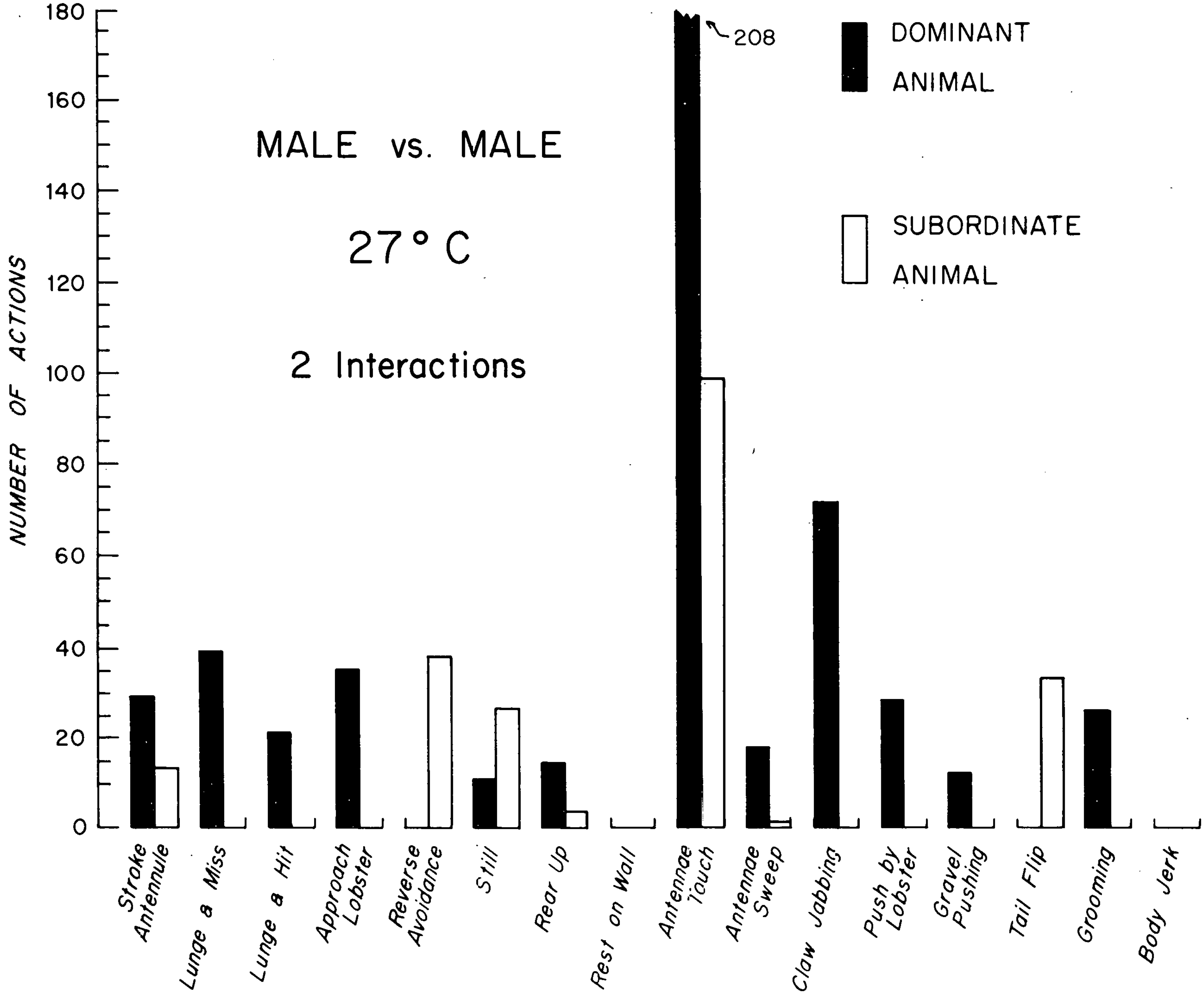

MALE vs. MALE
27° C
2 Interactions
DOMINANT ANIMAL
SUBORDINATE ANIMAL
208
NUMBER OF ACTIONS
0
20
40
60
80
100
120
140
160
180
Stroke Antennule
Lunge a Miss
Lunge a Hit
Approach Lobster
Reverse Avoidance
Still
Rear Up
Rest on Wall
Antennae Touch
Antennae Sweep
Claw Jabbing
Push by Lobster
Gravel Pushing
Tail Flip
Grooming
Body Jerk

Figure 9.

dominants.

Figures 10, 11 and 12 portray comparable female encounters. The female encounters during conflict resolution involve fewer activities and the action patterns tend to be less overt. Pushing, antennule sweeping and antennule stroking are predominant in female encounters, while claw jabbing and lunging were more characteristic of males. The exception to this tendency on the part of each sex to use slightly different conflict strategies, was the females at 27° C. The frequency of claw jabbing at this temperature was equivalent to that of the males.

Figure 13 illustrates the previously described male - female encounters.

The study indicates that there are sexual differences during the establishment of dominance, but these differences are of a quantitative, rather than a fundamental, nature.

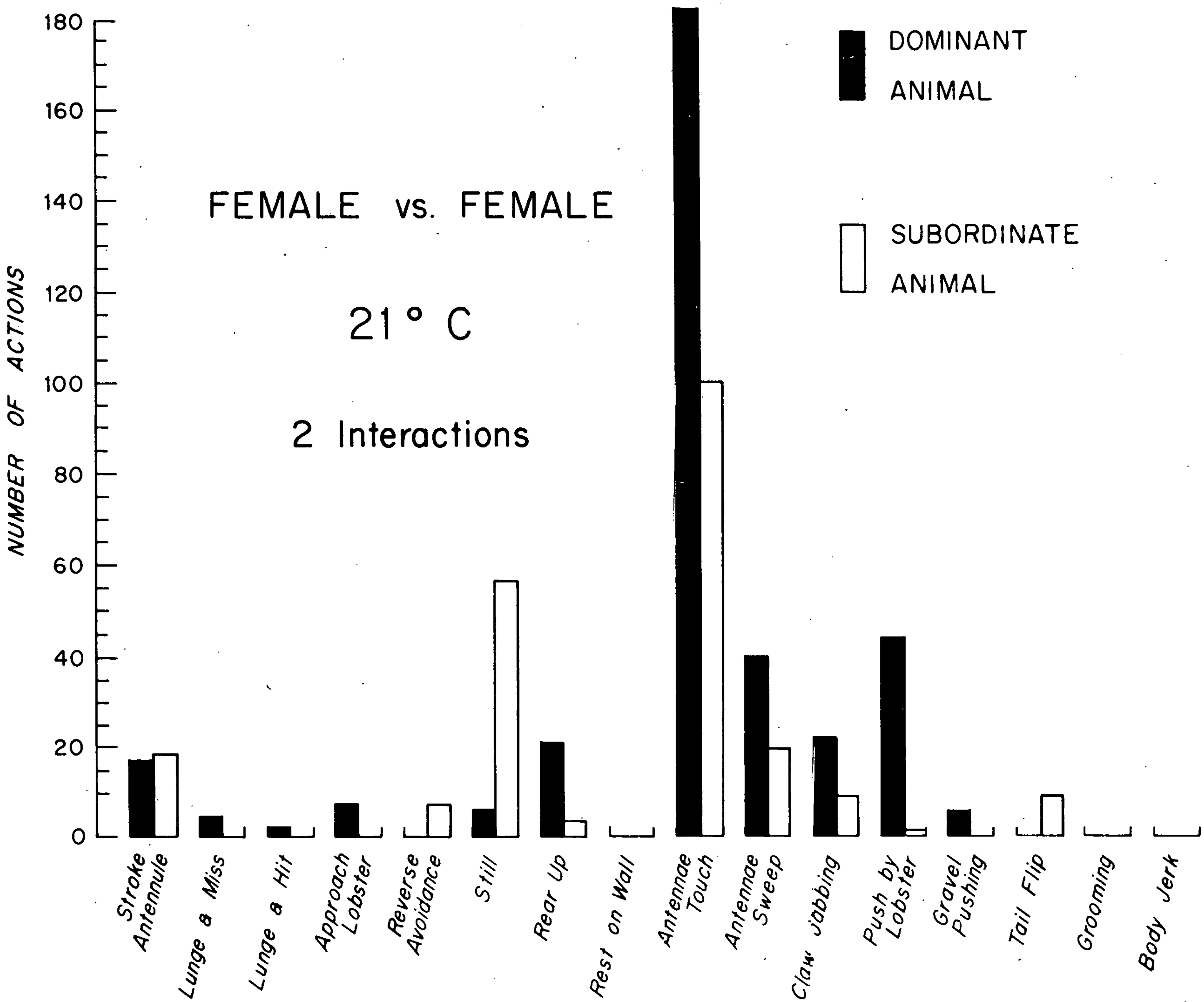

FEMALE vs. FEMALE
21° C
2 Interactions
DOMINANT ANIMAL
SUBORDINATE ANIMAL
NUMBER OF ACTIONS
0
20
40
60
80
100
120
140
160
180
Stroke Antennule
Lunge a Miss
Lunge a Hit
Approach Lobster
Reverse Avoidance
Still
Rear Up
Rest on Wall
Antennae Touch
Antennae Sweep
Claw Jabbing
Push by Lobster
Gravel Pushing
Tail Flip
Grooming
Body Jerk

Figure 10.

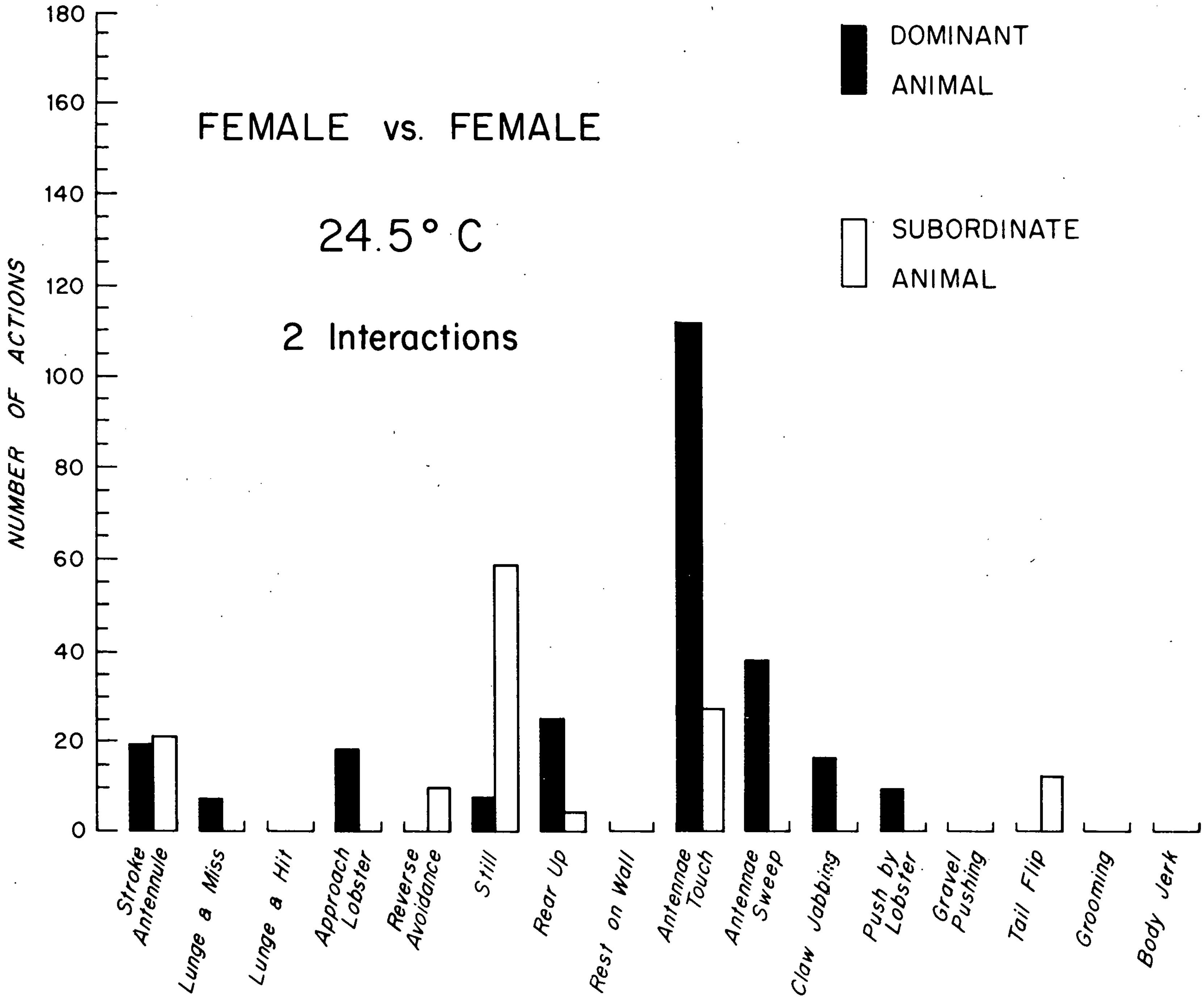
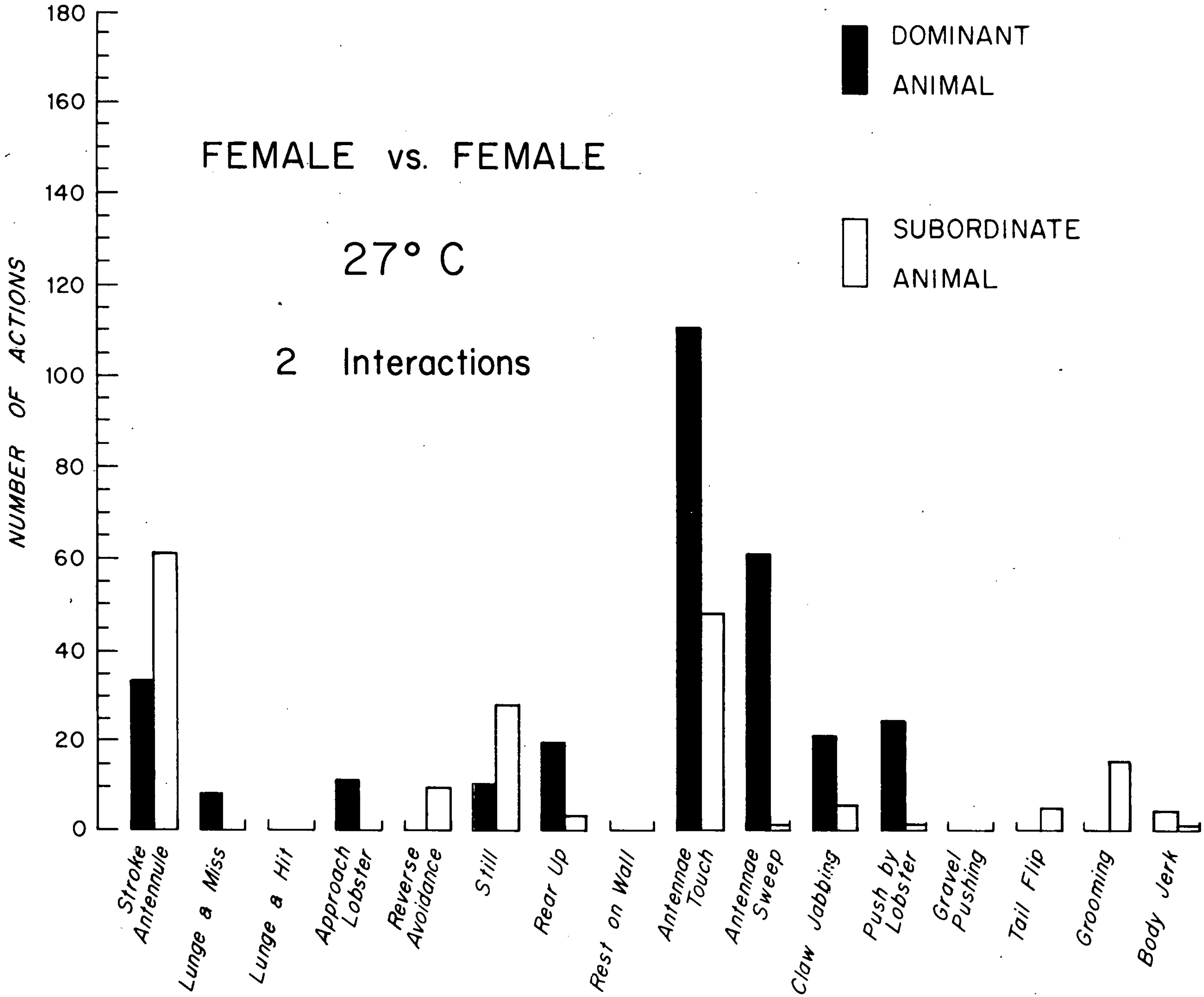

FEMALE vs. FEMALE
24.5° C
2 Interactions
DOMINANT ANIMAL
SUBORDINATE ANIMAL
NUMBER OF ACTIONS
180
160
140
120
100
80
60
40
20
0
Stroke Antennule
Lunge a Miss
Lunge a Hit
Approach Lobster
Reverse Avoidance
Still
Rear Up
Rest on Wall
Antennae Touch
Antennae Sweep
Claw Jabbing
Push by Lobster
Gravel Pushing
Tail Flip
Grooming
Body Jerk

Figure 11.



FEMALE vs. FEMALE
27° C
2 Interactions
DOMINANT ANIMAL
SUBORDINATE ANIMAL
NUMBER OF ACTIONS
180
160
140
120
100
80
60
40
20
0
Stroke Antennule
Lunge & Miss
Lunge & Hit
Approach Lobster
Reverse Avoidance
Still
Rear Up
Rest on Wall
Antennae Touch
Antennae Sweep
Claw Jabbing
Push by Lobster
Gravel Pushing
Tail Flip
Grooming
Body Jerk


Figure 12.

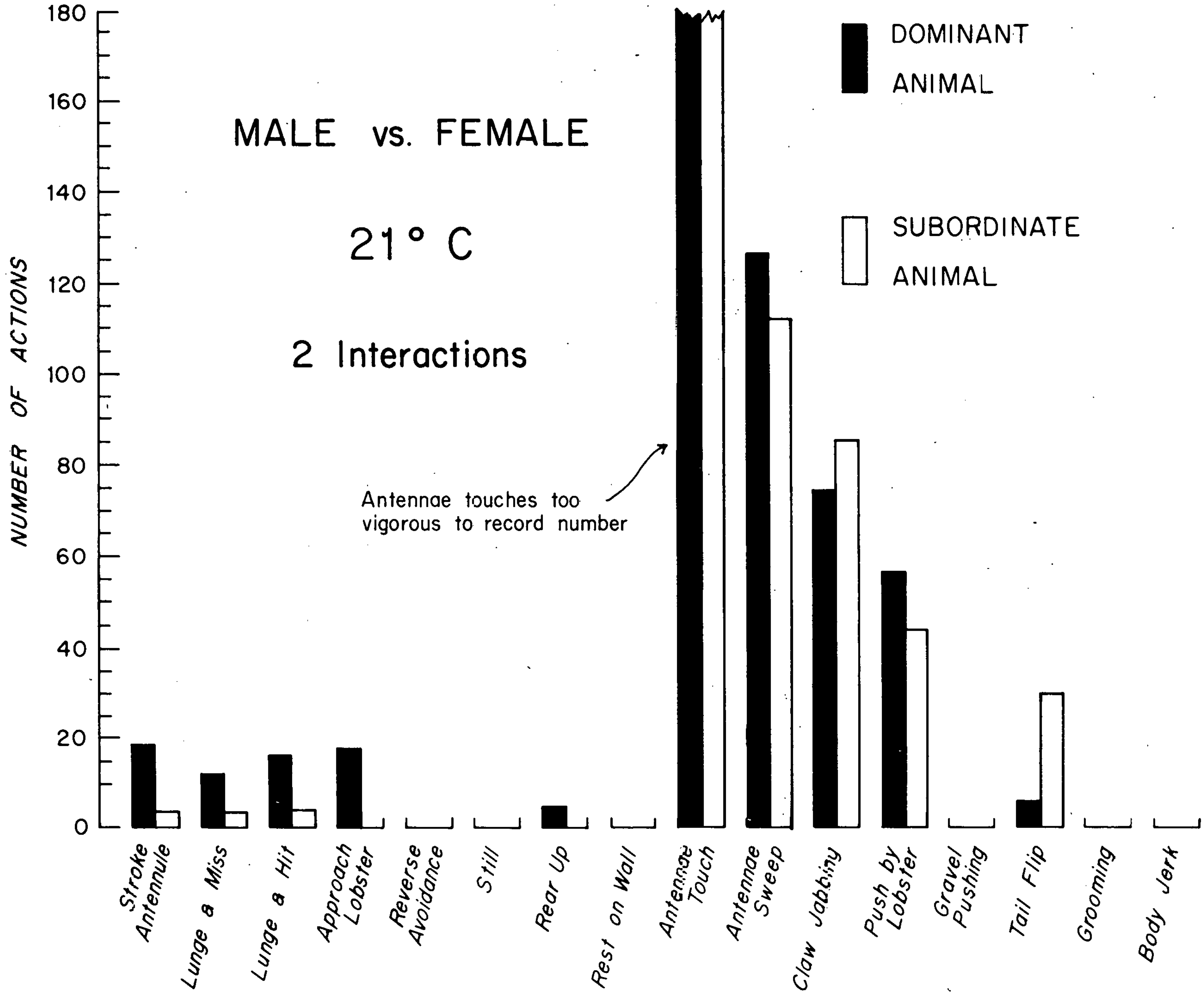

MALE vs. FEMALE
21° C
2 Interactions
DOMINANT ANIMAL
SUBORDINATE ANIMAL
NUMBER OF ACTIONS
180
160
140
120
100
80
60
40
20
0
Antennae touches too vigorous to record number
Stroke Antennule
Lunge & Miss
Lunge & Hit
Approach Lobster
Reverse Avoidance
Still
Rear Up
Rest on Wall
Antennae Touch
Antennae Sweep
Claw Jabbing
Push by Lobster
Gravel Pushing
Tail Flip
Grooming
Body Jerk

Figure 13.

## WHOLE KEROSENE AND KEROSENE FRACTIONS--THE ARTIFICIAL STRESS

The stable community behavioral assay was developed during the kerosene study. Three to five lobsters were housed together in 180 gallon observation tanks set up to simulate some of the characteristics of their natural environment. (See introduction to the section on stress-related behavior of lobsters.) The preliminary study was based upon five communities and only a single concentration of whole kerosene, and kerosene fractions. The concentrations used during the study were perhaps so low that the term stress is perhaps inaccurate. It was originally planned to increase the concentrations of the test material up to the lethal limit in a manner comparable to the freshwater pilot study with fish. However, we were forced to terminate the investigation prematurely in order to relocate our laboratory. At the present we do not have any information on the concentrations of kerosene which are lethal to Homarus and we suspect that our test levels of the pollutants were many orders of magnitude below the lethal limits.

### THE POLLUTANT

Whole kerosene, and straight-chain, branched-cyclic and polar aromatic fractions were prepared by Boylan and Tripp. Twenty microliters of material was placed upon a cleaned asbestos strip and subsequently the strip was lowered into the community and the responses of the animals were recorded. Two strips were used in each trial for a total concentration at the outset of 40 microliters of the pollutant per trial.

An attempt was made to determine the concentrations of kerosene and kerosene fractions in the experimental community at the end of the trial periods without success. Dr. Boylan, the organic chemist in the group, also tried to determine the quantity of the test materials on the strips after the trial period, but he did not feel that the measurements were reliable enough for us to compute the concentrations that actually influenced the lobsters. In any event, the levels of whole kerosene and kerosene fractions which came into contact with, and influenced the behavior of, lobsters was extremely low, probably in the parts per billion range.

RECORDING

At the beginning of each trial period, 3 blank strips (cleaned but no test material) were dropped into the center of the community tank and the responses of the lobsters to the blanks were recorded for 15 minutes. The dominant would, on occasion, patrol its home range after the strips were introduced; even less frequently, one of the lobsters would lunge at the moving strip as it floated towards the bottom of the tank. At no time during the experiments were the blank strips eaten.

After the 15 minute control period, two strips containing a total of 40 μl of test materials were lowered into the tank and the behavior in the community was recorded for a half-hour. At the end of the trial period, all the strips were removed.

Each community was exposed to a particular kerosene fraction, or whole kerosene, only once. The communities were fed normally during the "rest" period of several days between trials of the different test materials.

One interesting benefit of using the stable community approach for stress and lobster research was that the communities, when not feeding, were quite inactive during the periods of the day when they were being observed. As a consequence, there were relatively few behavioral activities during the control period. Some of the behaviors that were observed could, therefore, be directly attributable to the influence of the whole kerosene or a given fraction. Twenty-eight social units, 5 body care units and 21 feeding units were analyzed.

FINDINGS

We found that lobsters respond to kerosene and its fractions at the test concentrations, but no disruption or alteration of the community structure was observed during our preliminary trials. Table 8 illustrates the impact of whole kerosene and its fractions on the body care and feeding behaviors. Table 9 depicts the effects of the same materials on the community social behavior. The number of communities is represented by n, and the means and ranges are based upon the actual number of times a given unit appeared within a community. There is no distinction as to which resident exhibited the behavior, even though the most dominant animals were the most active.

The most significant changes in behavior were those associated with feeding. Whole kerosene and the branched-cyclic fractions induced searching and feeding behavior leading to ingestions of the test strips. The branched-cyclic fractions were more attractive than whole kerosene, perhaps because of the presence of the polar aromatic fraction in the whole kerosene. The polar aromatics induced searching behavior at a distance, but were repulsive to lobsters at close range. In one instance, a lobster did pick up a polar aromatic strip, which it chewed briefly then spat out. The straight chain fraction did not have any influence upon feeding behavior.

# Table 8.

SOCIAL INTERACTIONS OF LOBSTERS

| | Straight Chain | | | | Branched-Cyclic | | | | Polar Aromatic | | | | Whole Kerosene | | | | ($\bar{x}$ ± 2 x s.e.) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UNIT | n | $\bar{x}$ | s.e. | Range | n | $\bar{x}$ | s.e. | Range | n | $\bar{x}$ | s.e. | Range | n | $\bar{x}$ | s.e. | Range | Straight | Branched Cyclic | Polar Aromatic | Whole |
| **Body Care** | | | | | | | | | | | | | | | | | | | | |
| Agitate | 3 | .3 | 0.3 | 0 - 1 | 4 | | | | 4 | 1.5 | 0.7 | 0 - 3 | 5 | 0.4 | 0.3 | 0 - 1 | 0 - 0.9 | | 0.1 - 2.9 | 0 - 1.0 |
| Antennule stroke | 3 | .3 | 0.3 | 0 - 1 | 4 | 3.3 | 1.1 | 1 - 6 | 4 | 0.8 | 0.3 | 0 - 1 | 5 | | | | 0 - 0.9 | 1.1 - 5.5 | 0.2 - 1.4 | |
| Antennae twitch | 3 | 1.0 | 1.0 | 0 - 3 | 4 | | | | | | | | 5 | 1.6 | 0.8 | 0 - 5 | 0 - 3.0 | | | 0 - 3.2 |
| Groom | 3 | 1.0 | 0 | 1 | 4 | 3.8 | 1.8 | 1 - 9 | 4 | 5.5 | 2.5 | 3 - 13 | 5 | 2.6 | 2.7 | 1 - 11 | 1.0 - 1.0 | 0.2 - 7.4 | 0.5 - 10.5 | 0 - 8.0 |
| Swimmeret beat | 3 | 0 | 0 | 0 | 4 | | | 0 | 4 | | | | 5 | | | | | | | |
| **Feeding** | | | | | | | | | | | | | | | | | | | | |
| Anten. Freq. | 3 | | | | 4 | | | | 4 | | | | 5 | | | | | | | |
| Ambul. sway | 3 | 1.6 | 1.7 | 0 - 5 | 4 | 2.8 | 1.2 | 1 - 6 | 4 | 4.0 | 1.7 | 1 - 9 | 5 | 4.8 | 1.3 | 3 - 10 | 0 - 5.0 | 0.4 - 5.2 | 0.6 - 7.4 | 2.2 - 7.4 |
| Approach | 3 | 1 | 0.6 | 0 - 2 | 4 | 1.8 | 0.3 | 1 - 2 | 4 | 0.5 | 0.3 | 0 - 1 | 5 | 1.6 | 1.9 | 0 - 4 | 0 - 2.2 | 1.2 - 2.4 | 0 - 1.1 | 0 - 5.4 |
| Carry | 3 | | | | 4 | | | | 4 | | | | 5 | 0.8 | 0.6 | 0 - 3 | | | | 0 - 2.0 |
| Chew | 3 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 5 | 1.2 | 0.6 | 0 - 3 | | 0 - 0.9 | | 0 - 2.4 |
| Drop | 3 | | | | 4 | 1.0 | 0 | 1 | 4 | 0.3 | 0.3 | 0 - 1 | 5 | 0.8 | 0.2 | 0 - 2 | | 1.0 - 1.0 | 0 - 0.9 | 0.4 - 1.2 |
| Drop down on | 3 | | | | 4 | 1.0 | 0.4 | 0 - 2 | 4 | | | | 5 | 0.2 | 0.2 | 0 - 1 | | 0.2 - 1.8 | | 0 - 0.6 |
| Exopodite wave | 3 | 1.6 | 1.2 | 0 - 4 | 4 | 2.8 | 0.8 | 1 - 4 | 4 | 1.5 | 0.7 | 0 - 3 | 5 | 3.2 | 1.5 | 0 - 7 | 0 - 4.0 | 1.2 - 4.4 | 0.1 - 2.9 | 0.2 - 6.2 |
| Ingest | 3 | | | | 4 | 1.5 | 0.5 | 1 - 3 | 4 | | | | 5 | 1.0 | 0.5 | 0 - 3 | | 0.5 - 2.5 | | 0 - 2.0 |
| Jump | 3 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 5 | | | | | 0 - 0.9 | | |
| Lunge at | 3 | | | | 4 | | | | 4 | | | | 5 | | | | | | | |
| 3rd. Maxilliped sway | 3 | | | | 4 | 1.3 | 0.8 | 0 - 3 | 4 | 0.5 | 0.5 | 0 - 2 | 5 | 0.4 | 0.3 | 0 - 1 | | 0 - 2.9 | 0 - 1.5 | 0 - 1.0 |
| 3rd. Max. grind | 3 | | | | 4 | | | | 4 | | | | 5 | 0.8 | 0.2 | 0 - 1 | | | | 0.4 - 1.2 |
| Pick up | 3 | 0.3 | 0.3 | 0 - 1 | 4 | 1.5 | 0.3 | 1 - 2 | 4 | 0.8 | 0.8 | 0 - 3 | 5 | 1.6 | 0.4 | 1 - 3 | 0 - 0.9 | 0.9 - 2.1 | 0 - 2.4 | 0.8 - 2.4 |
| Rake | 3 | | | | 4 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 5 | 0.2 | 0.2 | 0 - 1 | | | 0 - 0.9 | 0 - 0.6 |
| Sit on | 3 | 0.7 | 0.7 | 0 - 2 | 4 | | | | 4 | | | | 5 | | | | 0.3 - 1.1 | | | |
| Spit out | 3 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 4 | | | | 5 | 0.2 | 0.2 | 0 - 1 | 0.1 - 0.5 | | | 0 - 0.6 |
| Touch antennae | 3 | 0.7 | 0.7 | 0 - 2 | 4 | | | 0 | 4 | | | | 5 | 0.2 | 0.2 | 0 - 1 | 0.3 - 1.1 | | | 0 - 0.6 |
| Touch 1st amb. legs or chelopeds | 3 | 2.0 | 2.0 | 0 - 6 | 4 | 1.0 | 0.6 | 0 - 2 | 4 | 0.5 | 0.3 | 0 - 1 | 5 | 3.2 | 2.7 | 0 - 13 | 0.8 - 3.2 | 0.2 - 1.0 | 0 - 1.1 | 0 - 8.6 |
| Walk close to stimuli | 3 | 0.7 | 0.7 | 0 - 2 | 4 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 5 | 1.0 | 0.6 | 0 - 3 | 0.3 - 1.1 | 0 - 0.9 | | 0 - 2.2 |
| Walk over stimuli | 3 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 4 | 2.3 | 1.4 | 0 - 6 | 5 | 0.8 | 0.2 | 0 - 1 | | 0 - 0.9 | 0 - 5.1 | 0.4 - 1.2 |

# Table 9.

SOCIAL INTERACTIONS OF LOBSTERS

| UNIT | Straight Chain | | | | Branched-Cyclic | | | | Polar Aromatic | | | | Whole Kerosene | | | | ($\bar{x} \pm 2 \times$ s.e.) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | $\bar{x}$ | s.e. | Range | n | $\bar{x}$ | s.e. | Range | n | $\bar{x}$ | s.e. | Range | n | $\bar{x}$ | s.e. | Range | Straight | Branched Cyclic | Polar Aromatic | Whole |
| **Social** | | | | | | | | | | | | | | | | | | | | |
| Antennae wave | 3 | 0.3 | 0.3 | 0 - 1 | 4 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 5 | | | | 0 - 0.9 | 0 - 0.9 | | |
| Approach lobster | 3 | 2.6 | 1.5 | 0 - 5 | 4 | 1.3 | 0.8 | 0 - 3 | 4 | | | | 5 | 3.6 | 1.8 | 1 - 10 | 0 - 5.6 | 0 - 2.9 | | 0 - 7.2 |
| Arched pose | 3 | 0.3 | 0.3 | 0 - 1 | 4 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 5 | 1.8 | 0.5 | 1 - 3 | 0 - 0.9 | 0 - 0.9 | | 0.8 - 2.8 |
| Bulldoze | 3 | | | | 4 | | | | 4 | | | | 5 | | | | | | | |
| Chase | 3 | 0.3 | 0.3 | 0 - 1 | 4 | 0.3 | 0.3 | 0 - 1 | 4 | 0.5 | 0 | 0 - 2 | 5 | 1.6 | 1.1 | 0 - 6 | 0 - 0.9 | 0 - 0.9 | 0.5 - 0.5 | 0 - 3.8 |
| Crouch | 3 | | | | 4 | | | | 4 | | | | 5 | 0.2 | 0.2 | 0 - 1 | | | | 0 - 0.6 |
| Face off | 3 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 4 | | | | 5 | 0.4 | 0.3 | 0 - 1 | 0 - 0.9 | | | 0 - 1.0 |
| Flee | 3 | 0.3 | 0.3 | 0 - 1 | 4 | 0.3 | 0.3 | 0 - 1 | 4 | 0.3 | 0.3 | 0 - 1 | 5 | 0.8 | 0.6 | 0 - 3 | 0 - 0.9 | 0 - 0.9 | 0 - 0.9 | 0 - 2.0 |
| Flop down | 3 | | | | 4 | 0.8 | 0.3 | 0 - 1 | 4 | 0.3 | 0.3 | 0 - 1 | 5 | 0.4 | 0.2 | 0 - 2 | | 0.2 - 1.4 | 0 - 0.9 | 0 - 0.8 |
| Fold claws | 3 | 0.7 | 0.3 | 0 - 1 | 4 | 0.5 | 0.3 | 0 - 1 | 4 | | | | 5 | 0.4 | 0.3 | 0 - 1 | 0.1 - 1.3 | 0 - 1.1 | | 0 - 1.0 |
| Lunge at Lobster | 3 | | | | 4 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 5 | | | | | | 0 - 0.9 | |
| Open Claw | 3 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 4 | 0.3 | 0.3 | 0 - 1 | 5 | | | | | 0 - 0.9 | 0 - 0.9 | |
| Open Claw stance | 3 | | | | 4 | | | | 4 | | | | 5 | 0.6 | 0.6 | 0 - 3 | | | | 0 - 1.8 |
| Raise up | 3 | | | | 4 | 0.5 | 0 | 0 - 2 | 4 | 0.3 | 0.3 | 0 - 1 | 5 | 0.4 | 0.3 | 0 - 1 | | 0.5 - 0.5 | 0 - 0.9 | 0 - 1.0 |
| Raise up on claws | 3 | | | | 4 | | | | 4 | | | | 5 | 0.2 | 0.2 | 0 - 1 | | | | 0 - 0.6 |
| Rapid swim | 3 | | | | 4 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 5 | | | | | | 0 - 0.9 | |
| Rear up | 3 | 2.3 | 1.2 | 0 - 4 | 4 | 2.3 | 0.6 | 1 - 4 | 4 | 0.5 | 0.3 | 0 - 1 | 5 | 2.0 | 0.6 | 1 - 4 | 0 - 4.7 | 1.1 - 3.5 | 0 - 1.1 | 0.8 - 3.2 |
| Reverse | 3 | | | | 4 | | | | 4 | | | | 5 | 0.6 | 0.3 | 0 - 1 | | | | 0 - 1.2 |
| Roll over | 3 | | | | 4 | | | | 4 | | | | 5 | | | | | | | |
| Run | 3 | | | | 4 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 5 | | | | | | 0 - 0.9 | |
| Side walk | 3 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 5 | | | | | 0 - 0.9 | | |
| Still | 3 | 4.3 | 3.4 | 0 - 11 | 4 | 6.3 | 2.1 | 3 - 12 | 4 | 9.0 | 2.7 | 4 - 15 | 5 | 7.8 | 3.5 | 2 - 21 | 0 - 11.1 | 3.9 - 10.5 | 3.6 - 14.4 | 0.8 - 14.8 |
| Strut | 3 | | | | 4 | | | | 4 | | | | 5 | | | | | | | |
| Tail curled under | 3 | | | | 4 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 5 | 0.2 | 0.2 | 0 - 1 | | | 0 - 0.9 | 0 - 0.6 |
| Tail flip | 3 | | | | 4 | | | | 4 | | | | 5 | 0.2 | 0.2 | 0 - 1 | | | | 0 - 0.6 |
| Tail up | 3 | | | | 4 | 0.3 | 0.3 | 0 - 1 | 4 | | | | 5 | | | | | 0 - 0.9 | | |
| Touch antennae | 3 | 0.7 | 0.7 | 0 - 2 | 4 | | | | 4 | | | | 5 | 0.2 | 0.2 | 0 - 1 | 0 - 2.1 | | | 0 - 0.6 |
| Upright stance | 3 | | | | 4 | | | | 4 | | | | 5 | | | | | | | |

The impact of the kerosene pollutants on body care and social behaviors was less clear, and significant differences are not indicated in the data. To the observers it seemed that the polar aromatic and branched-cyclic fractions and whole kerosene produced detectable increases in grooming behavior and agitate, a stress-related behavior. The latter was particularly obvious when the polar aromatics were the test substances. Further trials, particularly at higher concentrations, are needed to test the significance of these observations.

No pronounced changes in social behavior or organization were observed during the study. Nevertheless, whole kerosene and many of the fractions influenced the behavior of the lobsters. The greatest array of behaviors occurred during the whole kerosene trials, while the fewest were associated with the straight chain components of kerosene.

POSTSCRIPT

Kerosene and kerosene fractions were used in this study because lobster fishermen have the habit of using kerosene-soaked bricks as bait in lobster traps. If lobsters feed on oil related products, as we have found, then there is some possibility of their becoming contaminated with oil as their habitats become increasingly polluted. However, the most important finding is that these animals are extremely sensitive to kerosene and there is the distinct possibility that lobsters could be attracted to oil spills. At close range their social organization and behavior might, as a consequence, be disrupted.

With this thought in mind, we intend to study in the future not kerosene, but the water soluble fractions of oil as described earlier in this report. We intend to standardize our artificial stress research to the stable community behavioral assay and the water soluble components of crude oil in order to provide a more meaningful and coordinated appraoch to a comparative ethology of artificial stresses in marine environments.

## DISCUSSION

The limitations and shortcomings of the preliminary research reported here have been indicated where appropriate throughout the text. For the past year and a half, we have been seeking ways of shaping a comparative ethology of fishes based upon levels of complexity and information, rather than on phylogenetic relationships. One of the purposes of this work is to see if there are relationships between behavioral systems and ecosystems. We have also been looking for biologically significant ways of behaviorally studying the effects of stress upon a variety of aquatic animals, representing different levels of behavioral complexity. Concurrently, we have been investigating the possibility that there are two fundamentally different kinds of environmental stresses, designated "historical" or "artificial" depending upon whether they have been part of the evolutionary history of marine or freshwater animals, or are "new" and have only appeared in significant amounts since the advent of man's industrial and technological activities. In our view, there has been some measure of success towards shedding light on these questions--in building a foundation that will enable us to probe into the relationships between environmental stress and animal behavior and determine their ecological and evolutionary meaning. We want to know if behavioral studies can predict the fate of aquatic environments under stress, and if they can tell us which aquatic animals are most likely to be threatened with extinction.

In the discussion we would like to explore briefly some of the ideas and concepts which have evolved from our work. Perhaps some of them may have a bearing on the ability of biologists to predict the fate of freshwater and marine environments stressed as a result of man's activities.

## BEHAVIORAL SYSTEMS AS INDICATORS OF ADAPTABILITY TO STRESS

Environmental managers and conservationists would like to know which organisms within a given ecosystem are most prone to being deleteriously affected by pollutants. No general theory presently exists which would explain whether extinction, or adaptation, will be in store for a plant or animal after continued exposure to sublethal levels of pollutants. It is unlikely that a general theory will ever be formulated which will be complete enough to provide a clear picture of tomorrow's world. The multiplicity of avenues open to organisms adapting to changing environments is probably great.

Nevertheless, some animals may carry in their behavior a record of their past evolutionary history and also provide us with clues as to the stability and complexity of the environments within which they evolved. For the fishes, the largest group of vertebrates with some 26,000 living species, we suspect that a comparative ethology could tell us not only their environmental history, but also something about their ability to withstand and adapt to changes in the future.

The evidence for this opinion is fragmentary; however, the research reported here indicates that there may be a definite correlation between behavioral complexity and a fish's ability to withstand stress. The most complex animal in the study, the yellow bullhead, has a social system based upon an apparently large and subtle array of communication signals, and its behavior is disrupted and altered at levels of stress considerably below the stress level that kills them. The simplest fish behaviorally, the golden shiner, is less prone to disruption under stress, suggesting that selection in its case has been towards physiological toughness rather than towards behavioral sophistication and complexity.

If there is selection and evolution in two somewhat diverse and mutually exclusive directions (towards physiological toughness on the one hand, or behavioral diversity on the other), then we may have a handle on one of the elementary links in what could become a predictive environmental ethology. But, physiological toughness has to be measured in some way and then related to the behavior of an animal. There is no proof that the kind of short term behavioral changes we have observed will have a long term impact which can be described in successional or evolutionary terms. It can be deduced that if an animal like the bullhead is disrupted socially under chronic exposure to a sublethal stress, then it would not have available to it the necessary communication signals or social organization to reproduce the species. This assumption is logical and the spectre of waning populations under polluted conditions is no doubt real, though the case is far from settled.

If our theory is correct, however, and behavior is inversely related to resistance to environmental perturbations, then evidence other than our behavior assays should agree with the relationships between behavior and stress that we have established.

Fortunately, information does exist that sheds some light on the relationships between short term behavioral changes and longer term adaptive changes. Since the widespread used of the chlorinated hydrocarbons beginning in the late 1940's, many environments have inadvertently become experimental grounds for the development of resistant strains of animals under chronic exposure to artificial stresses. The theory would predict that the behaviorally most simple animals would be most likely to develop resistance to stress, while the most complex animal would be the least likely to make the necessary physiological and genetic adjustments.

There is an abundant literature on insect resistance but, to our knowledge, no attempts have been made by entomologists to relate insect behavioral systems, environmental complexity and diversity with the development of resistance. A survey of the fish literature on resistance turned up some information with a direct bearing on the question we had posed. Ferguson and his associates (1964, 1965, 1966) had been looking at resistance in fishes and--fortunately for us--the fishes he studied were either the same as those in our freshwater model ecosystem or closely related. They found evidence for the emergence of resistant strains of yellow bullheads, the green sunfish (a close relative to the pumpkinseed sunfish) and the golden shiner. He also gathered data on _Gambusia_, the mosquito fish. We have observed the behavior of _Gambusia_ and have placed it at the bottom of the ladder of behavioral complexity and diversity. (See Figure 15).

Endrin, a very toxic chlorinated hydrocarbon, was the stress in this case and after more than a decade of exposure, the resistant strains that had survived and developed were tested to determine the degree to which they had become resistant. From these findings it became possible for us to relate behavioral type with the development of resistant strains. Figure 14 depicts possible relationships between behavioral complexity and resistance. With an increase in behavioral complexity, there is a dramatic decrease in the ability of a species to develop resistance. The yellow bullhead resistant strain can only cope with 75 ppb of endrin, while the golden shiner resistant strain can withstand up to 1,000 ppb. The simplest animal behaviorally is the mosquito fish and the resistant strains of this species can tolerate up to 1,500 ppb of the potent insecticide. With the exception of the mosquito fish, the species in this study reproduce only once annually.

The studies of Ferguson on resistant strains in fishes are a measure of one important kind of "physiological toughness", and they support the contention that behavioral complexity and diversity, as measured by the number of different behaviors a fish exhibits, is inversely related to the ability of a given species to withstand one of the major classes of stress. These findings provide us with a time-link between our behavioral assays and long term adaptability. Other measures of physiological resistance to stresses will be sought over the next few years and related to the behavior we observe in our experimental ecosystems.

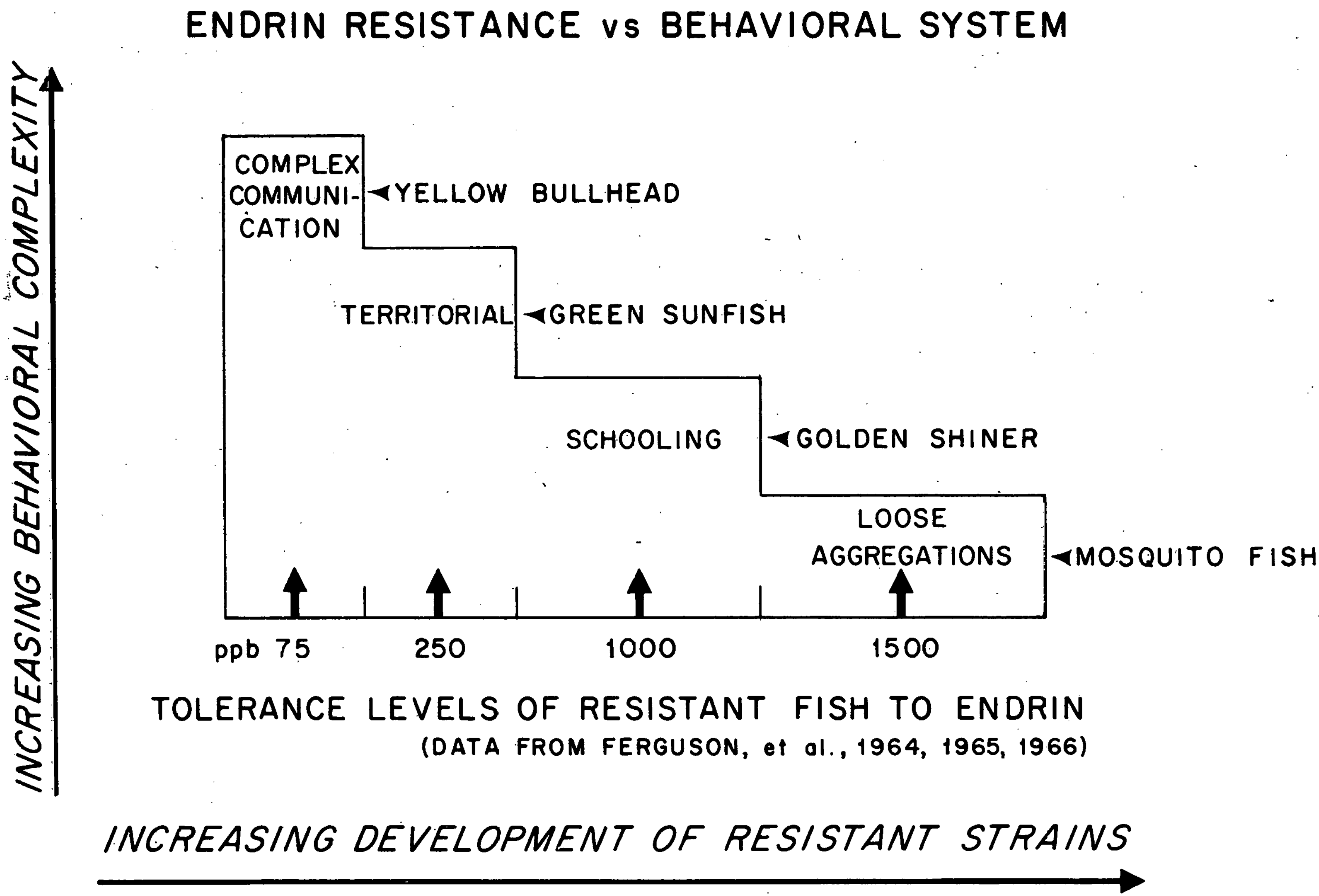

ENDRIN RESISTANCE vs BEHAVIORAL SYSTEM
INCREASING BEHAVIORAL COMPLEXITY
COMPLEX COMMUNI-CATION
◄YELLOW BULLHEAD
TERRITORIAL
◄GREEN SUNFISH
SCHOOLING
◄GOLDEN SHINER
LOOSE AGGREGATIONS
◄MOSQUITO FISH
ppb 75
250
1000
1500
TOLERANCE LEVELS OF RESISTANT FISH TO ENDRIN
(DATA FROM FERGUSON, et al., 1964, 1965, 1966)
INCREASING DEVELOPMENT OF RESISTANT STRAINS

Figure 14.

## BEHAVIORAL STRATEGIES AND ECOSYSTEM DEVELOPMENT

An underlying assumption guiding our thinking is that there must exist links between behavior and ecology, and that the kinds of behavior found within a given ecosystem are in part a reflection of the characteristics of that ecosystem. It may be possible that the strategies of ecological succession and behavioral development have much in common as the evolutionary processes at work in each case are undoubtedly similar.

Eugene P. Odum (1969) in a landmark paper "The Strategy of Ecosystem Development" outlined the basic trends involved in ecological succession within ecosystems from immature stages to highly mature stages. Some of these are worth noting here because in many ways they parallel comparable behavioral strategies, although in the latter case they have yet to be so elegantly and completely defined and understood.

Odum pointed out that information was high in mature stages of an ecosystem and that internal symbioses were well developed. The trend in ecological succession, no matter what the environmental type, seemed to be towards more complex life histories and community stucture within a given ecosystem as succession proceeds; there is also an increasingly greater species diversity and biochemical diversity, as well as a greater degree of stratification and spatial heterogeneity.

What is apparent to us is that ecology over the past twenty years has reached the point where ecological systems can be characterized on the basis of information, diversity, feedback control, symbiosis, nutrient conservation, entropy, etc. and that these qualities tell us something of the maturity, and stability of a given region and its vulnerability to disruption. In brief, ecology has become a predictive science, albeit its most meaningful and accurate predictions ultimately depend upon experiments conducted over many years duration--as the measure is always in successional terms.

But behavior, if it parallels ecology in strategic terms, may enable us to telescope the time scale and look into the future with more immediate tools. It is necessary, of course, to realize that the behavioral component of an ecosystem is only one segment, as animals are ultimately dependent upon plants and other elements of the environment. Nevertheless, the behavior of an animal may be extremely sensitive to change and therefore be, to a large degree, limiting.

If a predictive ethology is to take its place alongside ecology, we need to know to what degree there are behavioral equivalents to those characteristics that define ecosystems. Is it possible that certain types of ecosystems "produce" animal species with certain kinds of behavior? The information does not now exist for us to arrive at any precise conclusion. However, there are several somewhat anecdotal clues. Several years ago we were searching for behaviorally complex animals to study as part of an interest in finding the pinnacle of behavioral evolution in fishes. Our bases for comparison were the scattered literature on life histories and a few comparative studies of the brains of fishes. It was suspected that larger and more complex brains would be an indication of behavioral sophistication. Likely candidates were fishes like the electric fishes of Africa, tropical catfishes and some species inhabiting coral reefs. Our choice of behaviorally sophisticated teleosts were quite inadvertently from regions like the Rift Lakes of Africa, the Amazon Basin or the largest of the coral reef regions, and these environments are those that Sanders and others have characterized as diverse and stable over time.

Another piece of indirect evidence seemed to have some bearing on the relationship between behavior and ecosystems. In 1968, we started to look at the behavior of some southern California inshore fishes, especially the blennies of the genus Hypsoblennius. Several years later, David Engstrom evaluated for us a variety of the Cape Cod fishes for behavioral complexity and none of them approached the bullhead or several of the southern California fishes in the level of their social organization. Was the absence of behavioral complexity caused by the fact that the region was unstable and naturally stressed? Sanders (1969) described the Woods Hole region of Cape Cod (Buzzards Bay) as being unstable and physically controlled, with a low diversity of benthic organisms (less than 20 species of polychaetes and bivalves in some locations).

> In the southern New England area, on the other hand, inshore waters of 20 m and shoaler, as exemplified by Buzzards Bay, have more than 23° C seasonal temperature change. Ice frequently forms on many of the large embayments such as Buzzards Bay for varying periods of time during the winter. Organisms living there must contend with the same minimal temperatures of -1.5° C or less found in arctic and antarctic waters. Summer temperatures rise to 23° C or levels found in tropical seas. (Sanders, 1969).

Stable and diverse shallow marine environments, including regions of comparable latitudes on the Pacific Coast of North America, have, according to Sanders, a benthic species component many times greater than Cape

Cod waters.

It is within these stable regions that we suspect the highest degrees of fish social organization have evolved, but, unfortunately, there is almost no ethological information at the present which could be considered comparative in even the broadest terms. Consequently, it is too soon to characterize the relationships between behavioral development and ecosystem strategies except in speculative terms. Figure 15 is a first such attempt to relate the two kinds of systems. The left hand side of the figure represents the ecological system and the right its behavioral counterpart. The index of ecological complexity, diversity and stability (from Sanders, 1968, 1969) is based upon benthic species diversity measured by the rarefaction method. The index of behavioral complexity is based upon the number of behavioral action patterns and visual or acoustic communication signals.

The bottom of the figure is represented by immature ecosystems and the fishes which predominate within them may be either aggregating or schooling species, whereas higher behaviors within these systems may be confined to seasonal migrants who are present during the most constant or stable periods of the year.

As the aquatic environments increase in stability and diversity, the higher levels of behavioral organization may tend to predominate--those animals which display complex intra and interspecific communication, care of young, territories, etc. Lower levels of behavioral organization will be present as well. Finally, in the most stable and predictable environments, the highest, most complex teleost behaviors might be found--behaviors involving individual recognition, care of the young, cooperative behavior, symbiotic relations,

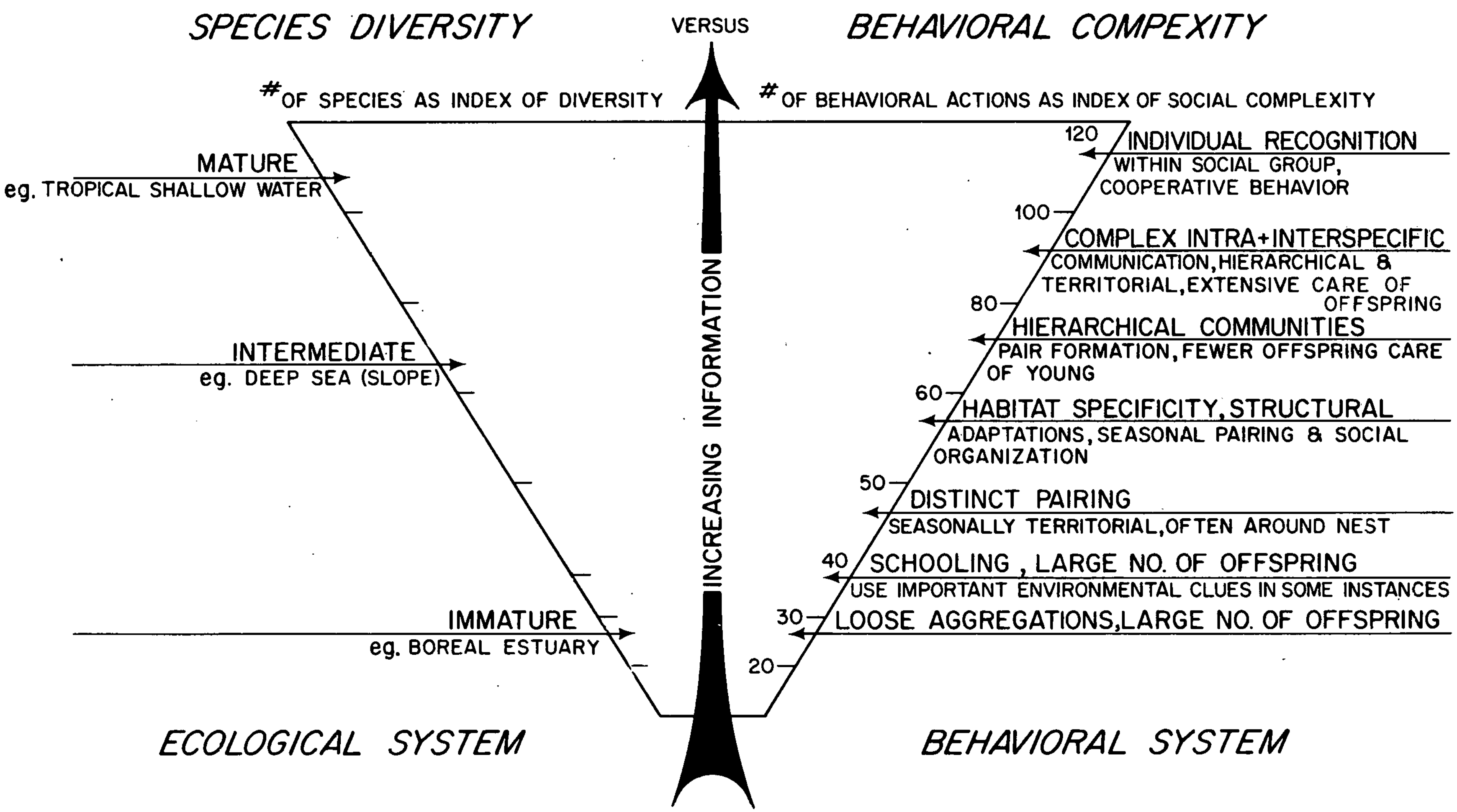

SPECIES DIVERSITY
VERSUS
BEHAVIORAL COMPEXITY
# OF SPECIES AS INDEX OF DIVERSITY
# OF BEHAVIORAL ACTIONS AS INDEX OF SOCIAL COMPLEXITY
MATURE
eg. TROPICAL SHALLOW WATER
INTERMEDIATE
eg. DEEP SEA (SLOPE)
IMMATURE
eg. BOREAL ESTUARY
INCREASING INFORMATION
120
INDIVIDUAL RECOGNITION
WITHIN SOCIAL GROUP, COOPERATIVE BEHAVIOR
100
COMPLEX INTRA+INTERSPECIFIC
COMMUNICATION, HIERARCHICAL & TERRITORIAL, EXTENSIVE CARE OF OFFSPRING
80
HIERARCHICAL COMMUNITIES
PAIR FORMATION, FEWER OFFSPRING CARE OF YOUNG
60
HABITAT SPECIFICITY, STRUCTURAL
ADAPTATIONS, SEASONAL PAIRING & SOCIAL ORGANIZATION
50
DISTINCT PAIRING
SEASONALLY TERRITORIAL, OFTEN AROUND NEST
40
SCHOOLING , LARGE NO. OF OFFSPRING
USE IMPORTANT ENVIRONMENTAL CLUES IN SOME INSTANCES
30
LOOSE AGGREGATIONS, LARGE NO. OF OFFSPRING
20
ECOLOGICAL SYSTEM
BEHAVIORAL SYSTEM

Figure 15.

and intrinsic uses of the local habitat. Their behavior would be dependent upon a level of environmental stability that would enable subtle forms of communication to go on relatively unimpeded by environmental perturbations. These may well be the fishes which cannot withstand stress and which would be susceptible to extinction upon chronic exposure to pollutants.

The relationships outlined in Figure 15, while speculative, may have some basis in fact. We do know that the simplest behaviors predominate for most of the year in disturbed, unstable inshore marine regions off Cape Cod, and it seems likely that the pinnacles of piscean evolution have taken place in highly stable complex environments. We know almost nothing of the behavior of the majority of fishes in environments that are intermediate between the two extremes of stability and diversity. Perhaps from these regions the relationships that we propose here will be most clearly elucidated.

THE FUTURE

We intend to continue the research on the behavior of the selected species from both experimental ecosystems under thermal and oil stress conditions. Also, there are plans to begin immediately behavioral observations of the test species in their natural ecosystems. It should be possible to observe their behavior under normal conditions and during unusual perturbations, should they occur. (During the summer of 1971 there was a fish kill of bullheads, the behaviorally most highly developed fishes in Ecosystem 1--cause unknown.) Such observations might provide fundamental clues to understanding the links between stress and behavior.

In order to explore more fully the couplings between behavior and ecology, it is our intent, if support can be found, to study two marine ecosystems which are comparable in most respects except for the fact that one of them is naturally unstable due to periodic natural stresses. These regions should be in clear tropical waters in order to make direct observations. According to Sanders (personal communication) two suitable areas exist off the Pacific coast of Central America. One of the regions is representative of a stable, diverse, mature environment, while the other, which is comparable in most respects, is occasionally and unpredictably visited by cold upwellings. These upwellings have arrested ecological succession at an immature level. Comparison of the behavioral strategies employed by fishes in the two regions should provide a wealth of information and permit a critical evaluation of the concepts outlined in this report.

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Woods Hole Oceanographic Institution
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AN INTRODUCTION TO ENVIRONMENTAL ETHOLOGY: A PRELIMINARY COMPARISON OF SUBLETHAL THERMAL AND OIL STRESSES ON THE SOCIAL BEHAVIOR OF LOBSTERS, AND FISHES FROM A FRESH-WATER AND A MARINE ECOSYSTEM. By John H. Todd, David Engstrom, Stewart Jacobson and William O. McLarney. Principal Investigator John H. Todd. 104 pages,15 figures and 9 tables. July 1972. AT (11-1) - 3567.

An environmental ethology founded upon the biological relationships linking environmental stresses, animal behavior and organization and the development of ecosystems is proposed. The concept of stress in relation to animal behavior and aquatic ecosystems has been reinterpreted. Extrinsic stresses have been separated into two categories: 1. Historical stresses, for which animals have a prior evolutionary history (e.g. thermal pollution): 2. Artifical stresses, those that have played little or no role in animal evolution (e.g. oil, chlorinated hydrocarbons, radioactive wastes) and are primarily the products of man's technologies. Experiments evaluating the impact of the two classes of stress on the social organization and behavior of fishes and lobster are described.

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2. Thermal Pollution
3. Oil Pollution
4. Sublethal Effects
5. Fishes

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16. Abstracts

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