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Hypsoblennius Ionthas (Teleostei: Blenniidae), On Oyster Reef
Substrate.**

Douglas Gordon Clarke
University of Alabama at Birmingham

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ASPECTS OF RESOURCE UTILIZATION IN THE FRECKLED BLENNY,
HYPSOBLENNIUS IONTHAS (TELEOSTEI: BLENNIIDAE), ON OYSTER
REEF SUBSTRATE

The University of Alabama in Birmingham

PH.D.

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ASPECTS OF RESOURCE UTILIZATION IN THE
FRECKLED BLENNY, *HYPSOBLENNIUS IONTHAS*
(TELEOSTEI: BLENNIIDAE), ON OYSTER REEF SUBSTRATE

by

DOUGLAS GORDON CLARKE

A DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in the
Department of Biology in the Graduate School,
University of Alabama in Birmingham

BIRMINGHAM, ALABAMA
1979

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ABSTRACT OF DISSERTATION
GRADUATE SCHOOL, UNIVERSITY OF ALABAMA IN BIRMINGHAM

Degree Ph. D. Major Subject Biology
Name of Candidate Douglas Gordon Clarke
Title Aspects of Resource Utilization in the Freckled Blenny, *Hypso-*
blennius ionthas (Teleostei: Blenniidae), on Oyster Reef Substrate

In the area of Mobile Bay, Alabama, the freckled blenny, *Hypso-*
blennius ionthas, is the most abundant fish occurring throughout the
year on oyster reefs. Ecological and behavioral studies concerned
with utilization of food resources indicate that *H. ionthas* is an
important consumer in oyster reef communities.

Examination of gut contents in 316 freckled blennies reveals a
diet consisting mainly of, in decreasing order of volume: algae-
detritus, amphipods, barnacles, polychaetes, tanaids, xanthid crabs,
and decapod megalops. There are no significant changes in diet with
respect to season or blenny body size, indicating that intraspecific
competition for food resources is not intense.

Trophic niche breadth in *H. ionthas* varies on a seasonal basis.
Calculated as b/s , the trophic niche is generally wider during the
winter months than during the summer months. This is attributable to
a higher proportionate volume of algae-detritus present in gut con-
tents samples during the summer months, thus masking the contributions
of animal food items.

Low values of trophic niche overlap (C_λ) between *H. ionthas* and
other fishes of the oyster reef assemblage indicate an absence of sig-
nificant interspecific competition for food resources. Direct competi-

tion appears to be minimized as the fish species select different proportionate volumes of each prey item.

Counts of mature ova within 18 ripe female *H. ionthas* indicate low absolute fecundity for this species. Individual blennies may spawn a number of times throughout the protracted breeding season (March-August), as revealed by variations in gonado-somatic index.

Behavior patterns in *H. ionthas* are similar to those reported in other species of the genus. Males maintain permanent territories, whereas females become less territorial during the breeding season. Analysis of the results of 327 agonistic encounters within a laboratory colony reveal the presence of a size-dominance social hierarchy. Large blennies are more aggressive than smaller blennies, and males are more aggressive than females. Size appears to be a greater advantage in agonistic behavior than sex.

Behavioral studies demonstrate the role of territoriality in both food and space resource utilization in *H. ionthas*. Quantitative measurements of territory size for laboratory colonies at three population densities and under conditions of high and low food abundance reveal several patterns of resource utilization. At both low and mid population density, space utilization is largely a function of body size and social dominance. Larger, dominant blennies use significantly greater amounts of habitat surface area than smaller, subordinate blennies at these densities. At high population density the advantage of large body size is reduced. Blennies in laboratory colonies fed *ad libidum* tend to use greater amounts of space per individual than in colonies on a rationed diet. This response is an apparent stress avoidance, energy conservation mechanism. Social dominance is a factor in competition for

food under low food abundance conditions.

Availability of shelter sites and space appears to be of much greater importance than food abundance in the regulation of population size in *H. ionthas* in nature.

Abstract Approved by: Committee Chairman Kenn R. M. Martin
Program Director Gary R. Bozinger
Date 3/15/79 Dean of Graduate School Kenneth J. Roegner

INTRODUCTION

Insight into the mechanisms of population regulation has long been a major goal of ecological thought. Still, of the various hypotheses that have been proposed to account for observed stabilities or fluctuations in natural populations, the majority have suffered from inordinate numbers of "exceptions to the rule". The complexity of population regulation at the single species population level has defied a general explanation (Hairston *et al*, 1960). Factors involved in population regulation have been categorized as: 1) density independent factors, namely climatic and catastrophic events; and 2) density dependent factors, such as the abundance of food and space resources. For several decades debate has persisted between supporters of density independent factors (Andrewartha and Birch, 1954), and those who believe in the predominant influence of density dependent factors (Lack, 1954). Overshadowed by the continued controversy, the realization has only gradually surfaced that the size of an individual population at any time is indeed the manifestation of multiple factors, all operating interdependently and synergistically (Huffacker and Messenger, 1964). Only in this light can the true contribution of single factors to the regulation of natural populations be weighed. In the present study, the author has delineated two such factors, the patterns of food and space utilization, in a population of littoral zone fish. These patterns are interpreted in light of their specific contribution to maintenance of stable population size.

Since the resources available to a population vary from habitat to habitat, the environmental conditions under which a study is performed must be defined. Necessary to the present discussion, a clarification of the term "littoral zone" is given. Nomenclature for the grouping of marine habitats into ecological zones has frequently been based on arbitrary guidelines, resulting in ambiguous definitions. "Littoral zone" is a prime example of this ambiguity. Confusion has been fostered by the use of littoral zone to describe completely different environmental situations. Historically, authors have often considered the littoral zone to be synonymous with the intertidal zone (Moore, 1958; Gibson, 1969). Others (Sverdrup *et al*, 1942) have included all or portions of the continental shelves within the littoral zone. Occasionally, the term has even been used to describe the shallow vegetated margins of freshwater lakes (Larkin, 1956). In the present context, the littoral zone is taken to include both intertidal and shallow subtidal habitats. This usage is deemed appropriate in that the vertical distributions of many organisms inhabiting the intertidal zone, particularly the fishes and non-sessile invertebrates, are not restricted to limits imposed by the high and low tide marks. The intertidal status of the fish population involved in the present study is best described by the secondary resident category in the classification scheme of Thomson and Lehner (1976). Secondary residents are defined as shore fishes which utilize the intertidal zone regularly but are also distributed in the subtidal zone.

In terms of volume the littoral zone comprises an exceedingly small fraction of the total marine environment. Yet of the various marine

habitats, those within the littoral zone have been by far the most widely studied. This disproportionate amount of attention is accounted for, at least in part, by the greater accessibility and relative ease of sampling of these habitats. Also, the fact that human industrial, urban, and recreational activities often impinge directly upon the littoral zone has added emphasis to the requirements for knowledge of this zone.

As defined above, the littoral zone encompasses a host of habitat types. Of these only a specific few have been studied in detail. Ecological investigations of the littoral zone have to date been largely concerned with the algal and invertebrate populations and communities of rocky intertidal habitats. Examples include studies by Kohn (1971), Dayton (1971, 1973, 1975), and Menge and Menge (1974). Consequently, communities associated with the lesser-studied habitats remain poorly understood.

Reefs formed by the eastern oyster, *Crassostrea virginica*, fall within the poorly understood category. Oyster reefs are found predominantly within estuaries along the mid-Atlantic and Gulf of Mexico coastlines of North America. Knowledge of the distribution, formation, and structure of oyster reefs is summarized in Hedgpeth (1954). Although a fairly extensive literature exists regarding the biology of the economically important *C. virginica*, relatively little is known of the flora and fauna associated with oyster reefs (Butler, 1954; Taylor, 1954; Wells, 1961; Rhodes, 1970; Bahr, 1976).

Ichthyofaunas of oyster reefs are composed of few resident species. As in fish assemblages associated with a number of other littoral

habitats, members of the teleostean families Blenniidae, Gobiidae, and Gobiesocidae are typically represented (Gibson, 1969). Fishes of these families have been particularly successful in exploiting hard bottom habitats. With few exceptions the blennies, gobies, and clingfishes are highly thigmotropic, and substrate oriented in that they are not adapted for swimming in the water column. Their morphological and physiological adaptations to life in the littoral zone are summarized by Gibson (1969). While the species compositions of oyster reef ichthyofaunas are well recognized, their roles as grazers and predators within the community have for the most part been ignored.

Among the fishes residing on oyster reefs are blennies of the genus *Hypsoblennius* Gill, commonly called combtooth blennies. Species of this genus occur in both the western north Atlantic and eastern Pacific regions, although the Pacific coast species are not oyster reef dwellers. The ecology of the Pacific *Hypsoblennius* has been studied in detail by Stephens *et al* (1970), and their behavior treated by Losey (1968). The two Atlantic species, *H. hentzi* (Lesueur) and *H. ionthas* (Jordan and Gilbert), have not been investigated except for specialized reports on their taxonomy (Hubbs, 1939), developmental stages (Hildebrand and Cable, 1938), and scattered records of occurrence in faunal surveys. Although the geographical ranges of both Atlantic species overlap (Hubbs, 1939), they are seldom found coexisting within the same habitat. Whether this represents a case of habitat segregation is not clear, as both species definitely occur on oyster substrates. In Mobile Bay, the site of the present study, *H. hentzi* is absent. Since logistics prevented the acquisition of live specimens of *H. hentzi* from other areas, the results reported in this study are confined to *H. ionthas*.

Blennies such as *H. ionthas* are ideally suited for studies of space resource utilization (Phillips, 1971a). Their movements within the vertical plane are limited by virtue of their substrate-oriented behavior, while the high degree of territoriality shown by many blenniid species limits the scope of movement within the horizontal plane. In addition, their hardy nature is advantageous to their use as experimental animals in both field and laboratory situations. Furthermore, the behavior patterns of blenniids are at least as well known as those of any other group of marine fish, with the possible exception of the damselfishes (Pomacentridae). Such a base of knowledge is necessary before empirical data on resource utilization can be applied to the fundamental concepts of population regulation.

Territoriality and its role in both space and food resource utilization has been the subject of much speculation (Brown and Orians, 1970; King, 1973). Studies incorporating quantitative approaches to territoriality have appeared mainly in the literature on avian and reptilian species (Rand, 1967; Brown, 1969). Treatments of territorial behavior in fishes have been largely qualitative and subjective in design. In fish populations, territoriality is a manifestation of aggressiveness, which is an aspect of fish social structure. As pointed out by Brothers (1975), the adaptive significance of fish social structure has not been clarified. The general lack of quantitative information concerning fish social structures has resulted from difficulties inherent in observing either undisturbed natural populations or adequate numbers of fish in the laboratory. The present study has circumvented these limitations, using an approach previously untried with fishes.

The three primary objectives of this study include: 1) characterization of the life history parameters of the freckled blenny, *Hypsoblennius ionthas*; 2) description of its trophic position within the oyster reef community; and 3) determination of its pattern of space and food resource utilization.

MATERIALS AND METHODS

Ecological Studies

Stomach Contents

Monthly field samples for stomach contents were collected by various means from the jetties and seawalls at the eastern edge of Dauphin Island, Alabama. The most efficient technique for the collection of live fish was the use of the "slurp gun", a clear plastic tube utilizing suction created by piston action to capture fish. Employment of slurp guns eliminated the need for bait and thus avoided the problem of biasing the stomach contents. Seasonally, however, poor water visibility and low water temperatures precluded the use of slurp guns by divers. On these occasions Erhlemeyer flasks baited with oyster tissue were used as traps. At regular time intervals the traps were brought to the surface by pulling monofilament lines attached to the necks of the flasks. Captured blennies were then removed. Preliminary stomach contents analysis had revealed that oyster tissue was not a significant natural food item of *H. ionthas*. Therefore, the easily recognized bait could later be separated from the stomach contents and disregarded in the volumetric analyses. On occasion, small aquarium dip nets were used to collect fish in shallow, confined areas.

Samples for stomach contents are best taken just after the peak of daily feeding activity. At this time the majority of fish should contain the greatest amount of identifiable food items. To determine

the feeding periodicity of *H. ionthas*, samples were taken at 0800, 1100, 1400, and 1700 hrs on the same day. Blennies at earlier and later time intervals were not seen outside their shells and were presumed to be inactive. Samples were preserved in the field, and body weight and total length (TL) measured in the lab. Stomachs and intestines were removed and weighed (to nearest 0.01 gram) with their contents. Percent body weights for the guts plus contents were then calculated.

All specimens were immediately preserved in 10% formalin in individual plastic bags. Regurgitated food materials were retained. Immediate preservation was required since digestive rates, accelerated by high ambient temperatures during summer months, quickly rendered unpreserved samples useless for food item identification. Prior to examination, the specimens were transferred to 70% isopropanol and stored.

Body wet weight (to nearest 0.01 gram), total length (TL to nearest mm), and gonad wet weight (to nearest 0.00001 gram) were measured and recorded for each fish. Stomachs and intestines were then removed by dissection and stored in labeled vials. Measurements of intestinal length (to nearest mm) were taken for subsamples.

During examination all contents of the digestive tract for individual fish were isolated in a small petri dish. Food items were separated under a dissecting scope at a magnification of 40X. Algal and detrital material, which were impossible to adequately separate from one another, were removed with eyedroppers to labeled vials for each fish. All other food items were grouped as monthly samples and stored in additional labeled vials.

Whenever possible, each food item was enumerated; otherwise, the relative amounts were noted. For example, the number of amphipods in

a particular stomach could be accurately counted and recorded, but the remains of nereid polychaetes could be estimated only as the presence of acicula, small parts, large parts, entire worm, etc.

Food materials in all vials were centrifuged in graduated tubes at 1250 RPM for 10 minutes to standardize their packing. Volumes were then read (to nearest 0.25 ml) and recorded. From these data the volumes of the algae-detritus fraction from each stomach were obtained directly. Values for the remaining food items were calculated using the volumes for the total monthly sample of each item and notes on their frequency and relative volume in each stomach.

Generally, no single methodology of stomach contents analysis is suitable for every investigation. Accepted methods have been reviewed by Hynes (1950). For the present study, both frequency of occurrence and volumetric methods were used. The frequency of occurrence method indicated the number of stomachs in which a food item occurred, here expressed as a percentage of the total number of stomachs examined. Likewise, results of the volumetric method, indicating volume contributions of each food item in the diet, were expressed as a percentage of the total sample volume. By themselves, frequencies of occurrence would favorably bias the contribution of small but ubiquitous items in the total diet. The volumetric method alone would tend to exaggerate the significance of large but infrequent items and underestimate the importance of soft-bodied, rapidly digested forms. Awareness of these prejudices must be maintained in interpretation of the obtained results.

Since intestinal contents were included in the analyses, food items such as amphipods and xanthid crabs were evidenced by the presence of their usually intact exoskeletons, but internal soft tissues

had generally been completely digested. Therefore, a gravimetric method was not used, as biomass measurements would merely represent the weight of non-nutritive materials. Also, the dietary contribution of items such as barnacles would be overestimated, reflecting the weights of their large exoskeletons.

Trophic Niche Parameters

Breadth and overlap in food resource utilization was determined according to the methods of Bray and Ebeling (1975). Values of trophic niche breadth were calculated for individual fish (b), individual monthly samples (B), and pooled monthly samples (PB) using the formula:

$$\text{Breadth } (b, B, \text{ or } PB) = 1 / \sum_{i=1}^S p_i^2$$

in which p_i is the proportionate volume of food item i in the respective fish or sample, and S is the total number of different food items in the diet (MacArthur, 1972). In the present study S was taken as the total number of different food items which contributed at least 1% to the total volume of pooled samples. Values of breadth thus computed were scaled as b/S , B/S , or PB/S , thereby ranging from $1/S$ when the proportions p_i were maximally uneven, to unity when all items were present in equal proportions (Bray and Ebeling, 1975).

The coefficient of overlap employed here is a measure of dietary overlap between species j and k (Bray and Ebeling, 1975). The formula for computation of trophic niche overlap,

$$\text{Coefficient of Overlap } C = \frac{2 \left(\sum_{i=1}^S p_{ij} p_{ik} \right)}{\sum_{i=1}^S p_{ij}^2 + \sum_{i=1}^S p_{ik}^2}$$

is taken from Horn (1966). The symbols p_{ij} and p_{ik} are the proportionate volumes of food item i in species j and k respectively. S is the total number of different food items used by either or both species.

Fecundity

Relative fecundity varies greatly among fish species and is indicative of the particular reproductive strategy to which a species is adapted. To measure fecundity in *H. ionthas*, eighteen females were collected in April 1978, when females were in peak reproductive condition. In the lab their body weights and TL were measured and their ovaries removed. Under a dissecting microscope at 40X, the ovarian membranes were opened and the ova teased apart with fine forceps. Counts were taken of all ova in the later stages of development (as determined by size) in both ovaries of all fish. Linear regression of log-transformed egg count on body length data was then performed.

Developmental Stages

Reproductive strategies are also characterized by developmental rates and egg and larval morphologies. Aquarium held blennies were observed spawning in gaping oyster shells in April 1976. Shortly after spawning activity ceased, the shells were removed and examined under a dissecting microscope. Patches of eggs in different stages of development were found. Diameters of eggs were measured with an optical micrometer for stages just after fertilization and just prior to hatching. Samples of eggs were scraped from shells taken directly from the field and measured in the same manner.

Newly hatched larvae were siphoned out of the laboratory aquaria and their TL measured with an optical micrometer. Photographs were

taken (using magnifications of 10 and 50X) of the developing ova and larvae. All attempts to rear the larvae beyond 5 days failed.

Behavioral Studies

Ethogram Construction

An ethogram is a qualitative description of the behavior exhibited by a taxon, usually at the genus or species level. The description breaks down behavior patterns into their basic acts, such as displays involved in courtship or agonistic behavior. Prior to the present study, Losey (1968) had produced a generic ethogram based on the Pacific species of *Hypsoblennius*. For comparison, a description of the behavior of *H. ionthas* was undertaken.

Initial observations on the behavior of *H. ionthas* were conducted by snorkeling along the seawall and jetty habitats of the field population. Field notes were also taken during the collection of monthly samples. In the two-year course of the study, a total of approximately 110 hours of field observation time was accumulated. Water clarity at the sites varied considerably between observation periods, ranging from visibilities of virtually zero to over 3 meters, but averaging less than 1 meter. Under low visibility conditions *H. ionthas* showed little reaction to the presence of divers, although the divers necessarily hovered closer to the substrate. When the water was clearer, however, blennies were often attracted to areas on the bottom agitated by the divers' movements.

Further observations were conducted on blennies held in isolation tanks in the laboratory. These tanks consisted of two 39-liter aquaria enclosed and separated within partitions of 2-cm thick fiberboard, with

an inner lining of 1.3-cm thick Styrofoam. A blind allowed observation through narrow viewports located at distances of 25 cm in front of the aquaria. Aquaria were provided with subgravel, air-lift filters and scattered oyster shells resting on the bottom. Blennies were introduced in male-male, male-female, and female-female pairs, and their behavior observed.

Spawning and parental behavior were observed by attaching single valves of *C. virginica* to clear Plexiglas plates. The plates were then positioned in the isolation aquaria in such a manner that activities within the shell cavity could be watched.

Feeding behavior was observed by placing clumps of live oysters with their associated flora and fauna in 133-liter aquaria with small groups of blennies. Notes were also taken opportunistically during the laboratory space and food utilization studies described below.

Social Structure

A male-female colony was observed for 2.5 hours per day for 4 days. During this period notes were taken on the results of 326 aggressive encounters between fish. Sex and size (visual estimate of total length to nearest cm) were recorded for both aggressor, i.e., individual initiating the encounter, and opponent blennies. Results were recorded either as wins or losses with respect to the aggressor, or as draws, in which neither the aggressor nor the opponent exhibited submissive behavior. Submissive behavioral actions are described in the ethogram section. Numbers of wins, losses, and draws were then calculated as percentages of total bouts between aggressor and opponent blennies of various size-sex categories.

Laboratory Experiments on Resource Utilization

Live specimens of *H. ionthas* were captured with slurp guns and transferred to a wet-lab facility containing a circular tank of 3.66 m diameter, 10.6 m² bottom surface area, and 0.68 m water depth. The tank was equipped with a subgravel, air-lift filter and shredded oyster shell substrate. Oyster shells were randomly scattered over the tank bottom, except for a 20 cm wide buffer zone along the sides of the tank. This buffer zone served to keep most fish within the observational areas defined below. A black plastic shroud surrounded the exterior of the tank to prevent extraneous activity from disturbing the experimental fish. Lighting was provided by two double units of 1.83 m fluorescent tubes. White translucent plastic sheeting suspended below the light units from wall to wall effectively diffused the ambient light. All experiments were performed under a 12 hr. light: 12 hr. dark photoperiod.

Salinity of the tank water was maintained at 16 ± 1 parts per thousand (ppt), a value in the mid-range of field salinity measurements. Water temperature was held at $24.4 \pm 1.1^{\circ}\text{C}$ to prevent a possible Q_{10} effect on the activities of the experimental blennies. Nitrite and pH levels were monitored at regular intervals with a Nektonics (TK-1) test kit. The air-lift filtration system maintained the dissolved oxygen level at 8-9 parts per million (ppm).

Laboratory colonies were established with either 75, 150, or 225 blennies, which correspond to population densities of 7.1, 14.3, and 21.4 fish per square meter, hereafter referred to as LPD, MPD, and HPD for low, medium, and high population densities.

From preliminary observation of *H. ionthas* held in unshielded aquaria, it became obvious that these blennies were easily conditioned to associate feeding periods with activity outside the aquaria. Within a relatively short period after their introduction, captive blennies would respond to movements on the part of the observer by swimming to the surface in anticipation of receiving food. To avoid this response in the experimental colonies, the following precautions were taken. First, the tank itself was screened from outside activity. Second, the fish were fed only after the conclusion of observation sessions. Third, a method of feeding was chosen which offered as few collateral cues as possible. In spite of these precautions, two experiments were terminated prematurely when the fish exhibited signs of conditioning. Colonies were fed a diet of chopped shrimp once daily. Separate pieces of shrimp were affixed to a long glass rod. By slowly moving the rod just below the surface of the tank water, the pieces of shrimp could be quickly and evenly dispersed throughout the tank. Experimental protocol determined whether colonies were fed *ad libidum* or rationed an amount of shrimp in proportion to the population density. Rations were set at 0.067 g of shrimp per fish per day. Feeding regimes are hereafter referred to as HFA (high food abundance) and LFA (low food abundance).

A grid of waxed string forming squares with 0.25 meter sides was erected in a horizontal plane one meter above the tank substrate. The grid provided reference points for positioning a movable blind and mapping of the tank bottom. Constructed of plywood, the blind was positioned at selected points 1.16 meters above the tank substrate. The

underside of the blind was painted flat white to offer as little contrast as possible with the background lighting.

Sectional maps of the tank bottom were produced by the following method. Plumb lines were suspended from the intersections of lines to measure the distances between points on the tank bottom. Positions of oyster shells were then plotted on graph paper to a scale of 1.0 inch = 0.1 meter. Based on the sectional maps, the tank bottom was divided into nine 1.0 square meter quadrants. During experimentation, the four corner quadrants were watched for 3 hours, the remaining quadrants for 4 hours. Shorter observation periods were used for the corner quadrants since they contained fewer oyster shells and harbored fewer fish.

A random numbers table (Rohlf and Sokal, 1969) was used to determine the order of observation for the nine quadrants. Sectional maps of the quadrant being observed were held on a small platform in front of the viewing slit of the blind. Movements of individual blennies were recorded on tracing paper positioned over the map. Tracings were made with a different colored pencil lead for each fish. Sex and a visual estimate of the size (total length in cm increments) of each blenny observed were recorded.

Colonies in all experiments were allowed a 3-day period for acclimation to the tank environment and for establishment of territories prior to observation. Dead or seriously afflicted blennies were removed from the tank daily and counted. Over 320 observational hours were expended in the course of these laboratory experiments.

Nine experiments were performed on the laboratory colonies (experimental protocols are listed in Table 1). In experiments 1 and 8, the

Table 1. Experimental protocols of colony composition, population density and diet in the order experiments were completed. Colonies held under high food abundance conditions were fed *ad libidum*. Under low food abundances, colonies were rationed an amount equal to 0.067 gram of shrimp per fish per day.

Experiment Number	Colony Composition	Population Density (fish/sq. m)	Food Abundance
1	male-female	14.3	high
2	male only	14.3	high
3	male only	7.1	high
4	male only	21.4	low
5	male only	7.1	low
6	male only	21.4	high
7	male only	14.3	low
8	male-female	14.3	high
9	male only	14.3	none

colonies consisted of both male and female *H. ionthas* at sex ratios approximating 1:1. Experiment 1 was run during July 1977, at which time spawning had not abated completely in the field population. Courtship, spawning, and parental behavior occurred in the lab colony. These behaviors were not seen during the course of experiment 8, performed in November 1977. The remaining experiments were completed using male-only colonies to eliminate the variability in behavior that would occur with courtship and spawning activities. Males were chosen rather than females because males exhibit a higher degree of territoriality, which thereby facilitated territory mapping.

At the end of each experiment, blennies were selectively captured and removed from the tank. By noting the particular shelter site of an individual blenny and referring to the record of movements on the sectional maps, identities of most blennies could be determined. Those with identities confirmed in this manner were captured with dip nets, sacrificed, and preserved in labeled containers. Remaining members of each colony were then captured and either sacrificed or released in the field. Since approximately 2,500 *H. ionthas* were used in the ecological and behavioral studies, there was originally some fear that the field population would be seriously depleted. Therefore, those blennies in the initial lab experiments whose identities could not be determined were released in the field in the proximity of their original point of capture. To ensure that the probability of recapturing fish used in previous colonies was low, blennies for separate experiments were collected at widely divergent points along the seawalls and jetties. In later experiments, as the problem of population depletion was alleviated, all blennies were sacrificed. Blennies of both

confirmed and unconfirmed identities were weighed (wet weight to nearest 0.01 g) and measured (TL to nearest mm).

Surface areas (in square meters) encompassed by the perimeters of movement shown by individual blennies were measured with a planimeter (Alvin PL 653). Means of three readings for each fish were calculated. The planimeter was calibrated between sets of measurements for separate colonies. Surface areas thus measured were an index of space utilized by respective blennies and were indicative of relative rather than absolute territory size.

Design of the laboratory experiments was based upon the theory that the habitat surface area used by a blenny in its various activities (exploration, foraging, social, etc.) would be related to body size (TL). See Figure 1. Least squares linear regressions of space utilized (m^2) on TL were calculated for each experiment. Slopes of the regression lines obtained were tested by the F distribution for significant difference ($P < 0.05$) from zero. Sets of regression lines were compared for significant differences ($P < 0.05$) between their intercepts and slopes, again by the F distribution. Statistical analyses are listed in Appendix 1.

Blennies less than 4 cm TL showed little territorial tendency, deserting areas of the substrate whenever harassed by larger fish. Due to the seemingly random nature of their movements, only data for blennies equal to or greater than 4 cm TL were included in the linear regressions. In all experiments, data on space utilization is limited to fish showing some degree of territoriality. Movements of totally submissive blennies were both random and passive in nature and consequently were determined to be unsuitable for comparative purposes.

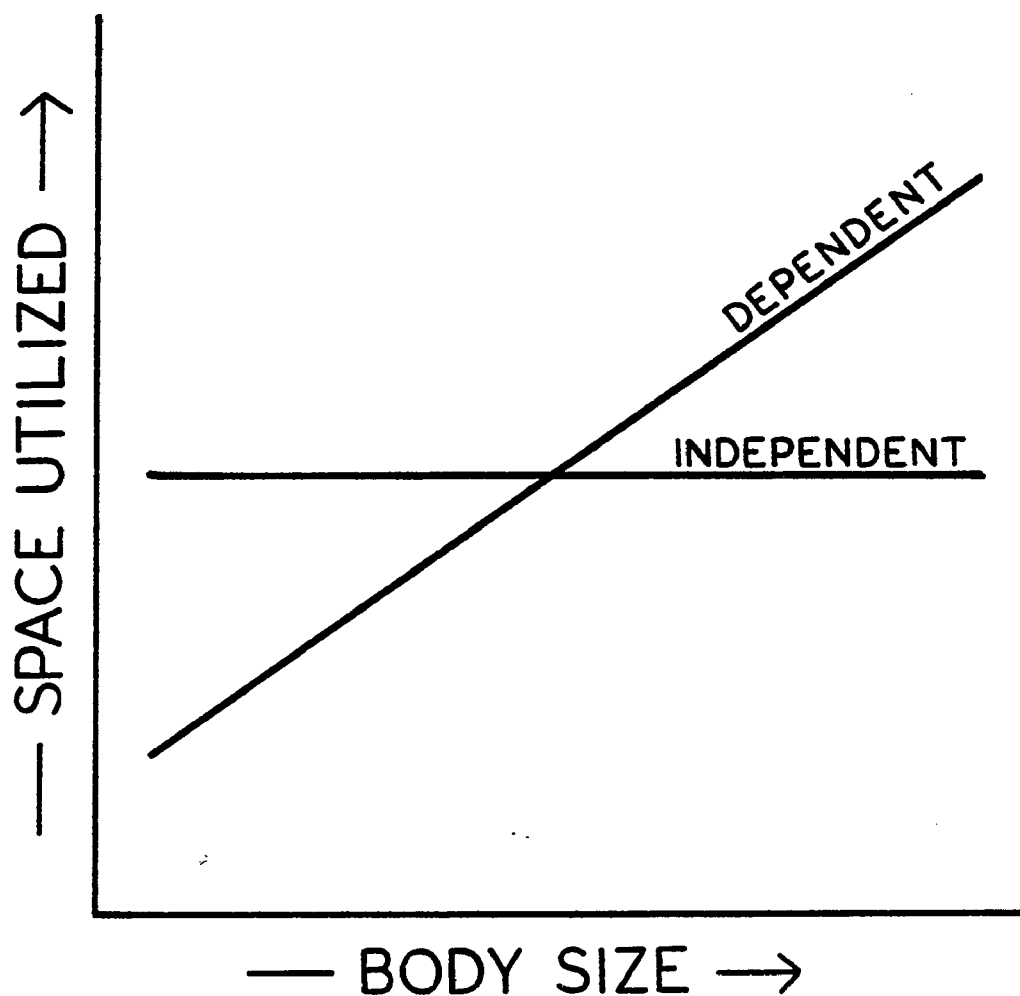


Figure 1. Illustration of the approach used in design of the laboratory experiments. Slopes of linear regressions of space utilized on body size that are not significantly different from zero indicate that the two factors are independent of each other. Significant slopes, whether positive or negative, indicate that space utilized is a function of body size.

Condition Factors

Condition factor (K) has been used by fisheries scientists as an index of "fatness" or density of fish bodies (Weatherley, 1972). In the expression:

$$K = \frac{W \times 100}{L^3}$$

the condition factor K remains constant, regardless of change in fish size, given a constant relationship between body weight W and body length L . Changes in the weight of a fish at a constant L are reflected by variation in K (Weatherley, 1972).

To detect patterns in changes of K for the laboratory colonies, condition factors were calculated for those experiments performed at mid-population density and both high and low food abundances. On the basis of field observations, MPD was taken to be a relatively close approximation of the field population density. Under LFA, there was competition for the available food resource within the colony, whereas under HFA food was assumed to be non-limiting.

Least squares regression lines were computed for K on TL. Each regression line obtained was tested for significant difference from zero slope by the F distribution. Linear regressions were also performed for space utilization data on K . Statistical analyses are listed in Appendix 1. To reveal the "condition" of the field population and to serve as a control, condition factors were also calculated for 164 field collected *H. ionthas*. An additional laboratory colony (experiment 9) was held for 19 days without food to check for the possibility of differential starvation rates among blennies of differ-

ent size classes. If blennies of all sizes starved at the same rate, the regression line would retain a slope of zero.

Physical Environment and Habitat

The morphometry of Mobile Bay, a coastal embayment located on the northeast margin of the Gulf of Mexico (Figure 2), is described by McPhearson (1970). This estuary is 50.0 km long in its north-south axis and 36.7 km wide at its widest east-west axis. Except for a system of dredged channels, the bay is uniformly shallow, with an average depth at mean low water of 2.84 m (McPhearson, 1970).

From January 1976 to March 1978, the weekly means of surface water temperatures at the study site ranged from 31.3°C in August 1976, to 5.9°C in February 1978 (Figure 3). These weekly means were calculated from daily afternoon (1400-1600 hrs) readings. Daily extremes in water temperature were recorded at 31.7°C and 5.0°C.

The tidal regime in Mobile Bay is of the daily type, in which there is usually only one high and one low tide per day (McPhearson, 1970). The interval between consecutive high or low tides averages 24.8 hrs, but is highly irregular (Marmer, 1954). Tidal amplitude is quite small; at the study site a span of 0.67 m separates the mean high and low water marks (McPhearson, 1970).

Salinities were measured with a refractometer at the times of field collections (Appendix 2). Surface salinities were generally lowest during the winter months (December-February) and highest during the summer months (June-August). McPhearson (1970) found a similar trend and correlated average bimonthly surface salinities with river discharge at the head of the Mobile Bay estuary.

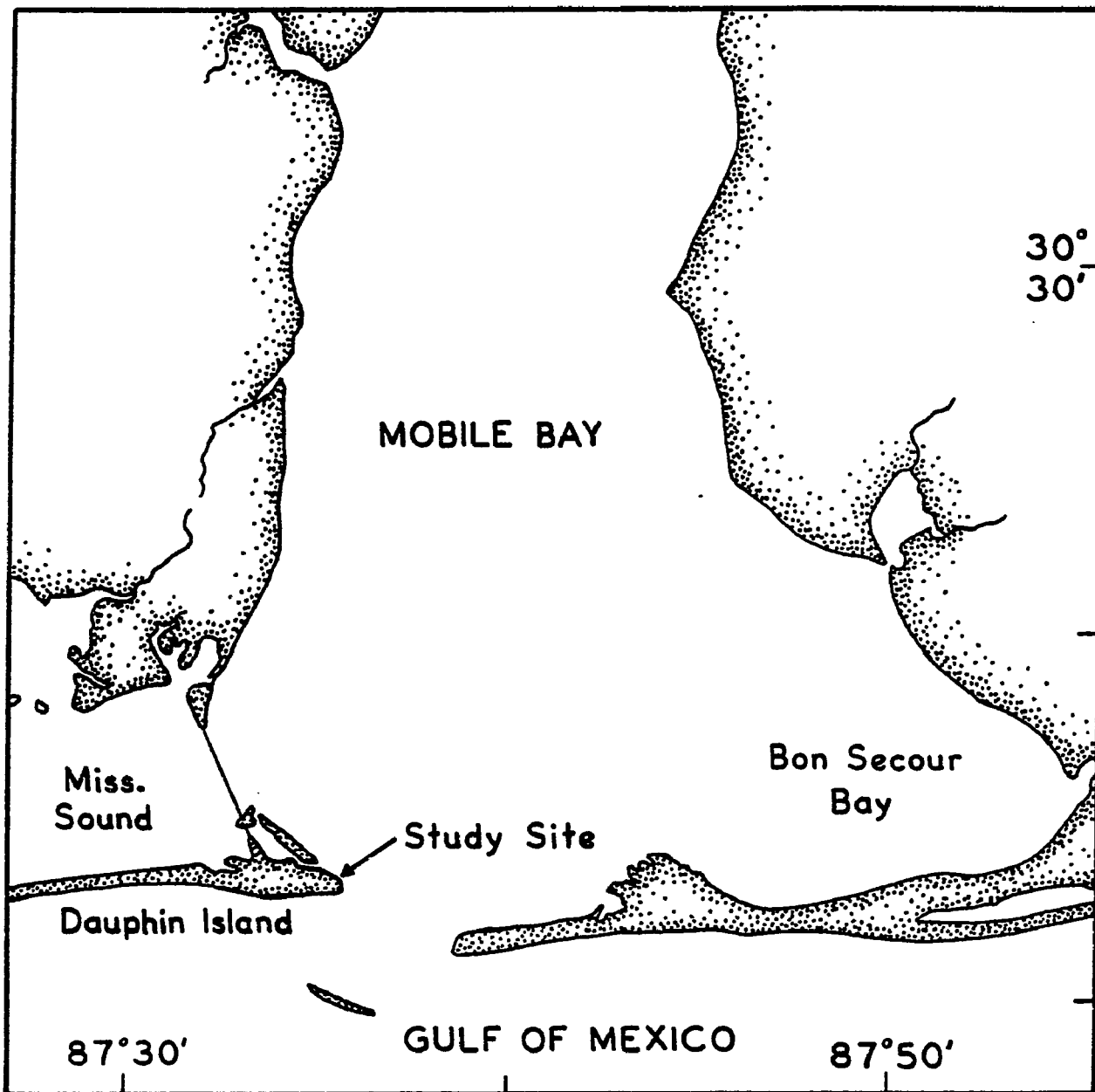
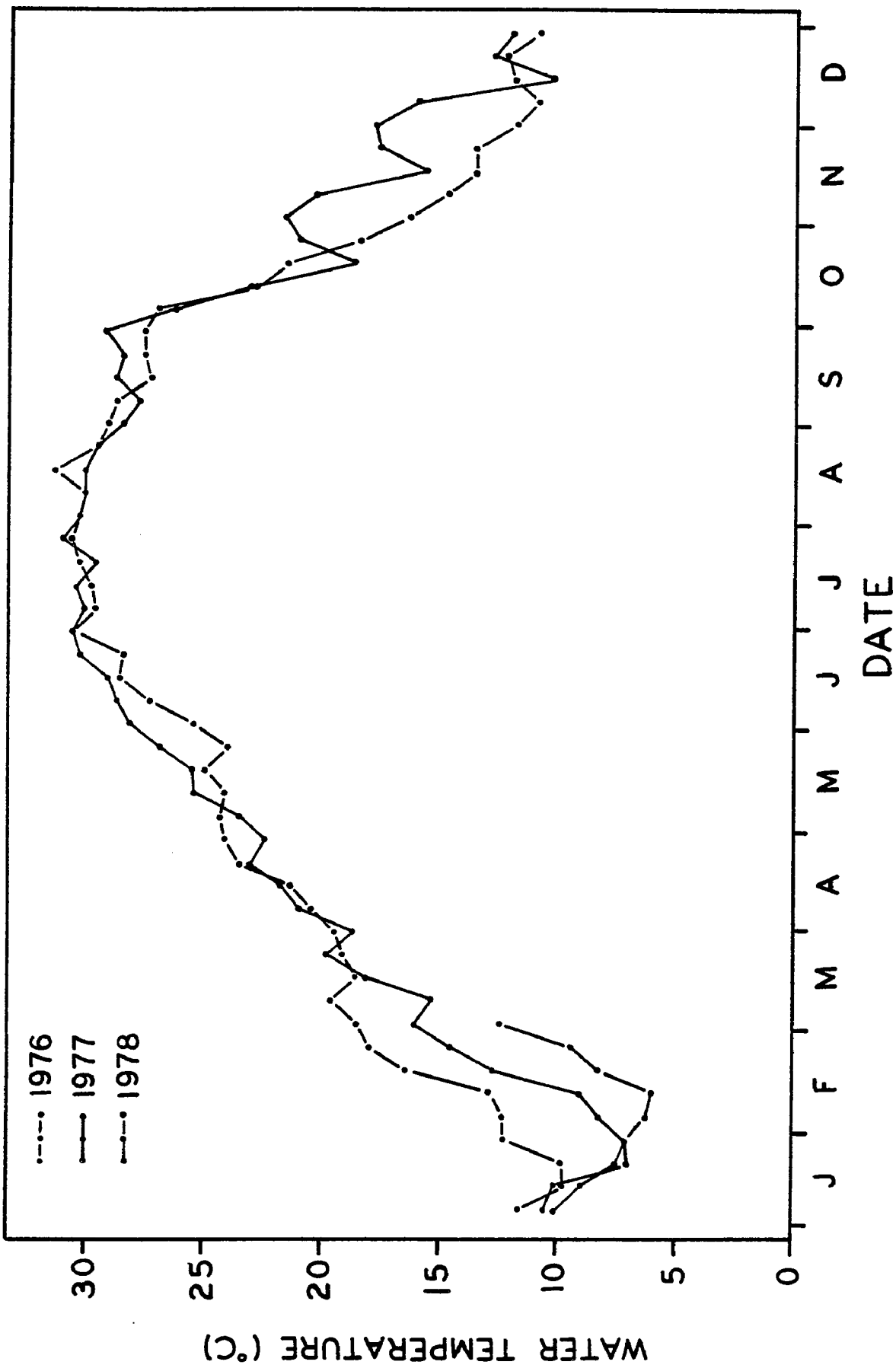


Figure 2. Location of the study site within Mobile Bay.

Figure 3. Weekly means of surface water temperature ($^{\circ}\text{C}$)
at the eastern end of Dauphin Island, Alabama
during the period from January 1976 to March
1978.



Living oyster reefs are located in the mid to lower reaches of the estuary and within adjacent areas of Mississippi Sound. Due to the shallowness of the overlying waters, wind and current generated turbulence may appreciably influence the biology of reef associated species. Activity of resident fishes may be intermittently curtailed during periods of high wave surge and turbulence.

All specimens used in the present study were collected from seawalls and jetties at the eastern edge of Dauphin Island, Alabama. These structures, built of irregularly shaped boulders, extend along the shoreline for about one kilometer. At low tide, water depth ranges from less than 0.5 m on the shoreward sides of the jetties to 1.5 m along the seawalls. The base of the structures is bordered by sandy bottom.

Below the mean low tide level, oysters cover much of the rocky substrate. Scattered clusters of oysters also lie on the sandy bottom. Crevices between the rocks and interstices among oysters offer numerous shelter sites for associated fauna. Algal mats cover most of the open rock facies throughout the year. Although not treated in detail here, a definite algal zonation exists. Dominant algal genera include *Enteromorpha*, *Cladophora*, *Dictyota*, and *Polysiphonia*.

Common invertebrates at the study site include: the mussel *Ischadium recurvum* (= *Brachiodontes*); the barnacle *Balanus eburnea*; the amphipods *Corophium louisianum* and *Amphithoe* cf. *valida*; the polychaetous annelid *Nereis succinea*; the common mud crab *Panopeus herbstii*, flat mud crab *Eurypanopeus depressus*, stone crab *Menippe mercenaria*, and the striped hermit crab *Clibanarius vittatus*; the tanaid *Hargaria rapax*;

the grass shrimp *Palaemonetes pugio*; and the intertidal isopod *Ligia exotica*.

Oyster Reef Fish Associates

Freckled blennies, *H. ionthas*, and skillettfish, *Gobiesox strumosus*, are the only fish species occurring throughout the year at the study site. Hoese and Moore (1977) state that *H. ionthas* seems to prefer hard bottoms of low salinities, although it is occasionally taken in the Gulf of Mexico outside the estuaries. *G. strumosus* has previously been noted as an oyster reef dweller by Wells (1961) and Dahlberg and Conyers (1973). All other species at the study site are seasonal in occurrence.

In early spring the naked goby, *Gobiosoma bosci*, becomes locally abundant as water temperatures rise and salinities remain fairly low. In Georgia, Dahlberg and Conyers (1973) found *G. bosci* over-wintering in burrows in soft bottom areas. Sensitivity to cold in *G. bosci* has been reported by Gunter and Hildebrand (1951), and its preference for low to moderate (less than 22 ppt) salinities documented by Dawson (1966, 1969). *Gobionellus boleosoma*, the darter goby, appears in quite large numbers somewhat later than *Gobiosoma bosci*. Temperature and salinity preference are less well known for *Gobionellus boleosoma*, but Dawson (1969) states that this species is most common in lower estuaries and sounds. Both *Gobiosoma bosci* and *Gobionellus boleosoma* are known to be associated with oyster reefs elsewhere (Hildebrand and Cable, 1938; Breder and Rosen, 1966; Hoese, 1966; Hoese and Hoese, 1967; Dahlberg and Conyers, 1973). Abundances of both species decline sharply at the study site in late spring, although they reoccur sporadically in smaller numbers until early December.

In late June and early July the striped blenny, *Chasmodes bosquianus*, arrives on the oyster substrate in considerable numbers. This particular blenny, a close taxonomic relative of *H. ionthas*, is frequently collected in grass beds or on shell bottoms in the Dauphin Island area. The majority of early arrivals are small juveniles, easily identified by a distinctive, checkered color pattern. Numbers of small *C. bosquianus* soon decrease, but adults are consistently present until October, occurring infrequently thereafter. *C. bosquianus* has previously been reported to inhabit oyster reefs (Hildebrand and Schroeder, 1928; Hildebrand and Cable, 1938; Springer, 1959; Phillips, 1971a; Dahlberg, 1975), but Hoese and Moore (1977) stated that it is especially common on grassflats. Occasional specimens of *Chasmodes saburrae*, the Florida blenny, have been collected at the study site, but apparently are never abundant in this area. Mobile Bay lies within the narrow coastal range of sympatry in *C. bosquianus* and *C. saburrae* reported by Springer (1959) and Hoese and Moore (1977).

In late June 1976 and late July 1977, large numbers of frillfin gobies, *Bathygobius soporator*, moved into the study area. *B. soporator* is a widely dispersed tropical species, with various populations separated nominally into several subspecies (Ginsburg, 1947). Dawson (1969) has referred the local form to *B. soporator catulus*. The presence of frillfin gobies at the study site appears to be correlated with relatively high temperatures and salinities. Its later arrival in 1977 may be attributable to a colder than normal winter that year (Figure 3). *B. soporator* is a coastal species that has seldom been reported within estuaries along the northern Gulf of Mexico (Dawson, 1969), but can be expected to occur on any hard, shallow bottom when the

salinity is sufficiently high. Although the frillfin goby has not previously been reported to occur on oyster reefs, its preference for shell habitat is well established (Breder, 1950, 1954).

Gulf toadfish, *Opsanus beta*, occur at the study site from late spring through early fall. Although this species is highly cryptic, its presence is often advertised by its audible sound production patterns (as with *O. tau*; Gray and Winn, 1961).

Specimens of the crested blenny, *Hypoleurochilus geminatus*, have been collected infrequently at the study site. This species is common on Atlantic coast oyster reefs (Hildebrand and Schroeder, 1928; Wells, 1961; Dahlberg and Conyers, 1973), but in the Gulf appears to be restricted to areas of high salinity. *H. geminatus* is abundant on jetties at Destin and Panama City, Florida, where high salinities have prevented the establishment of permanent oyster reef substrate (Hastings, 1972). Feather blennies, *Hypsoblennius hentzi*, occur on oyster beds within its range (Hildebrand and Schroeder, 1928; Hildebrand and Cable, 1938; Dahlberg and Conyers, 1973), but Hoese and Moore (1977) point out that *H. hentzi* apparently prefers softer, muddy-bottom habitats. Extensive field collection at the study site did not produce *H. hentzi*. One large feather blenny was taken by Swingle and Bland (1973) in the main ship channel east of Dauphin Island.

When present, the above fish species maintain an intimate association with the oyster reef. The majority of their time is spent within the crevices and interstices of the reef. All except *B. saporator* are known to use gaping oyster shells as spawning and nesting sites. Various other species show some attraction to the reef habitat, either in

search of food or cover. Numerous schools and solitary individuals of unidentified juvenile fishes were observed at the study site from early spring to late fall. The majority of transient species occurring as adults were seen in the summer months. At these times the following species were common: gray snapper, *Lutjanus griseus*; Lane snapper, *L. synagris*; mullet, *Mugil cephalus*; Atlantic spadefish, *Chaetodipterus faber*; sheepshead, *Archosargus probatocephalus*; croaker, *Micropogon undulatus*; pinfish, *Lagodon rhomboides*; pigfish, *Orthopristis chrysoptera*; killifish, *Fundulus* sp.; silversides, *Membras* or *Menidia* spp.

During July 1977, drought conditions led to unusually high and stable salinities within Mobile Bay. Throughout this period spotfin butterflyfish, *Chaetodon ocellatus*, and sergeant majors, *Abudefduf saxatilis*, were repeatedly observed along the seawalls at the study site. Their occurrence is probably an exceptional case for this area.

RESULTS

Life History Characteristics

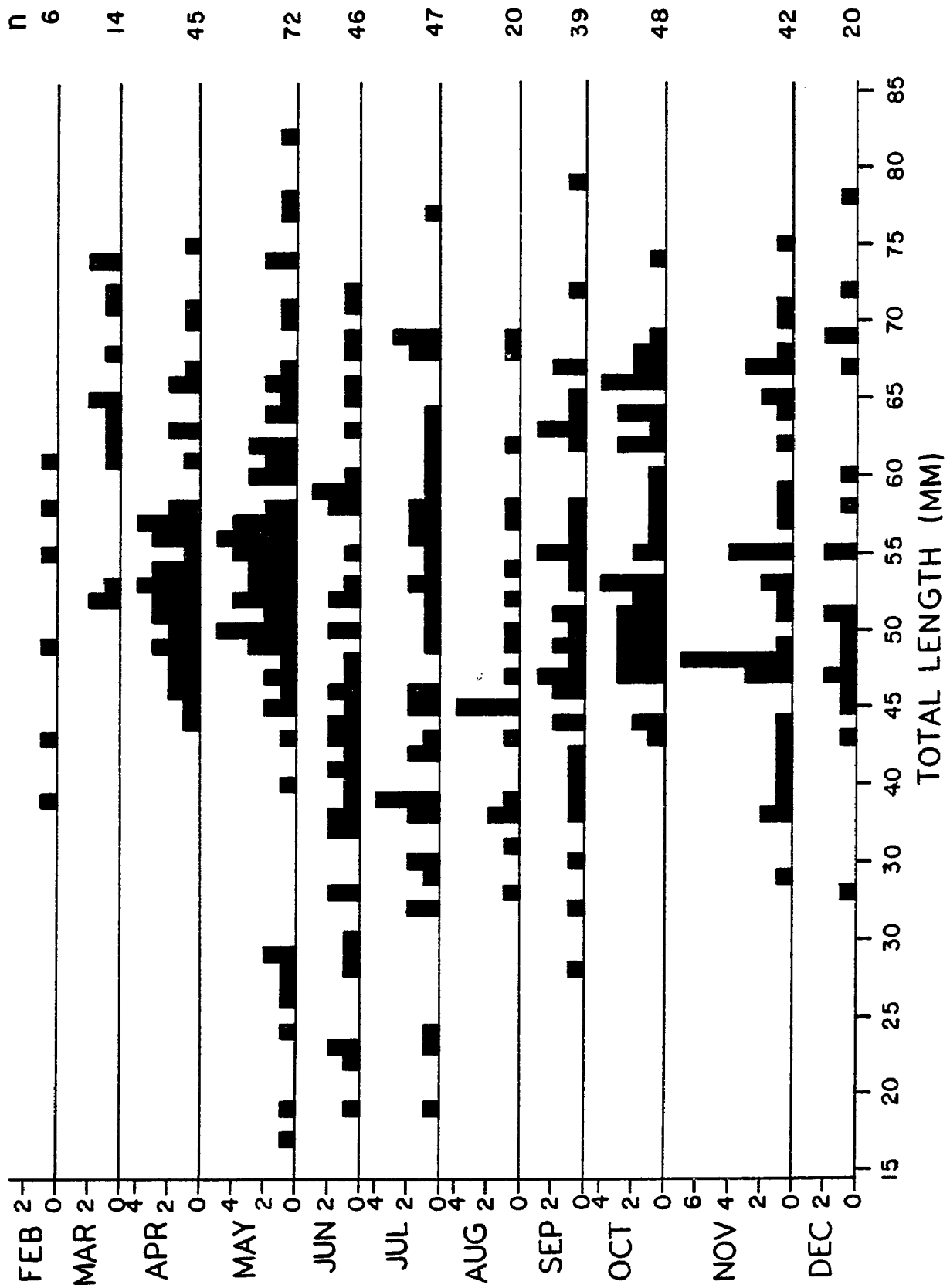
Seasonal Length-Frequency Distributions

Length-frequencies of *H. ionthas* collected in field samples are plotted against month of capture in Figure 4. Sampling emphasis was placed on collection of blennies representing the entire size range present on the sampling date. Therefore, the size-frequency distributions do not necessarily reflect the presence of numerically dominant size classes.

Blennies less than 3 cm TL first appear at the study site in May, 6 to 8 weeks after males begin guarding eggs. Much of this time interval is spent as planktonic larvae. Settlement on the reef presumably occurs shortly after metamorphosis into the juvenile stage. Losey (1968) reported that a similar pattern of larval recruitment exists for the genus *Hypsoblennius* as a whole, but did not present specific data.

Large numbers of newly settled *H. ionthas* between 1.5 and 3.0 cm TL occur on the oyster reef through July. Thereafter their numbers steadily decrease, although occasional blennies of this size are seen as late as December. This numerical reduction in the presence of smaller blennies is the result of growth, mortality, and abated spawning by the parent population.

Figure 4. Length-frequency distributions for field collections of *Hypsoblennius ionthas* on a seasonal basis. Histograms represent frequency and month of capture (ordinate) for each body size category (abscissa). No samples were taken for the month of January.



Gonado-Somatic Index

Gonado-somatic index (GSI) refers to weight of the gonads expressed as percent body weight. Seasonal trends in GSI are plotted in Figure 5. Cycling of both the ovaries and testes shows essentially the same pattern. Gonad weight increases rapidly in March, followed by a gradual decrease in weight through September, at which time the gonadal tissues contribute less than 0.3% of the body weight. Only a slight indication of weight gain is noted for the months of October through December.

During the spawning season the ovaries represent as much as 9.2% of the body weight, whereas testes never surpass 1.1%. High variances in GSI are noted in March and April, indicating that not all individuals reach peak reproductive condition simultaneously. In June the occurrence of high variances in ovarian GSI indicates the presence of both reproductively capable and completely spent females. From the data it is apparent that *H. ionthas* has a fairly protracted spawning season, with spawning activity peaking just after initiation in early spring but continuing until at least August. Individual females may spawn a number of times with one or more males, and shed several hundred eggs per spawning episode.

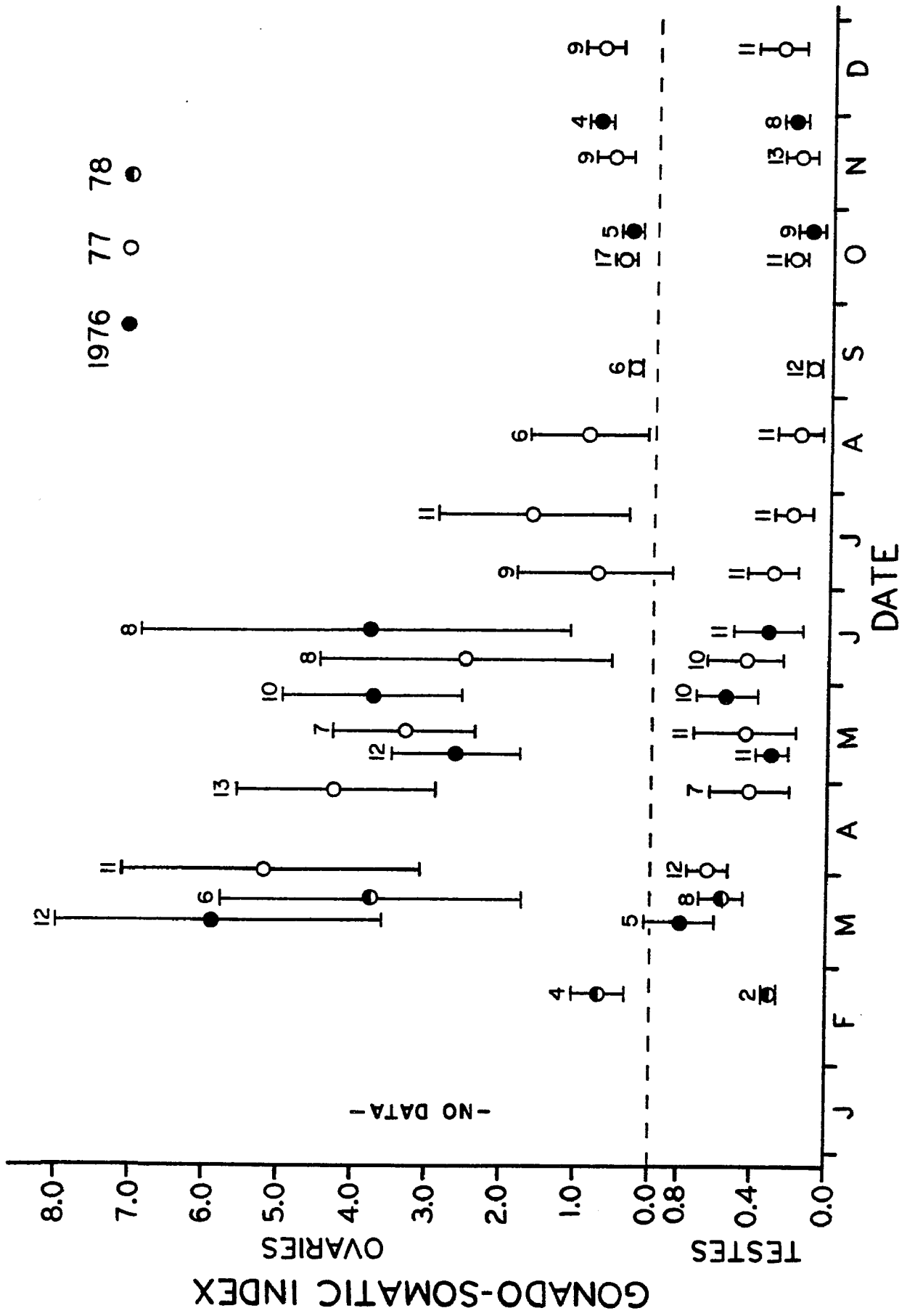
Fecundity

The exponential relationship between fecundity and length can be described by the equation:

$$F = aL^b,$$

in which fecundity F refers to the number of mature eggs in the ovaries of the female, L is body length (cm TL), and a and b are constants

Figure 5. Seasonal variation in gonad weight, expressed as percent body weight, based on collections of *Hypso- blennius ionthas* between March 1976 and March 1978. Vertical bars represent one standard deviation above and below the mean. Sample sizes are given above each symbol.



(Bagenal, 1966). After logarithmic transformation the equation becomes

$$\log F = \log a + b \log L,$$

which allows the relationship to be described by linear regression (Bagenal, 1966). Data for 18 female *H. ionthas* are plotted in Figure 6. The equation for the calculated least-squares regression line is:

$$F = 12.2 \times L^{2.77}.$$

In most fishes the value of the exponent is between 3 and 6 (Brothers, 1975). Lee and Chang (1977) reported an exponent of 2.355 for the blenny *Halmablennius lineatus*. The obtained slope for *Hypsoblennius ionthas* also falls below 3 and is comparable to slopes found in gobiid fishes, as reviewed by Brothers (1975). As in these gobies, *H. ionthas* has a protracted spawning season and is able to spawn a number of times during the breeding season. The relatively low slope, therefore, does not include eggs spent in earlier spawning episodes or immature eggs which develop after the time of collection. Thus, their realized fecundity is somewhat higher than that indicated by the single count method employed.

Development

Developmental stages of eggs and larvae observed in *H. ionthas* closely resemble those described by Hildebrand and Cable (1938) for *H. hentzi*. Newly fertilized eggs are attached to the insides of empty oyster shells by means of adhesive disks and remain attached until hatching. In early stages of development, *H. ionthas* eggs contain a number of colored, spherical bodies resembling those found also in *H. hentzi*. These bodies, which vary in size within the same egg, are either clear, yellow, or reddish-brown in color. They may constitute oil globules and/or pigment concentrations. Hubbs and Stavenhagen

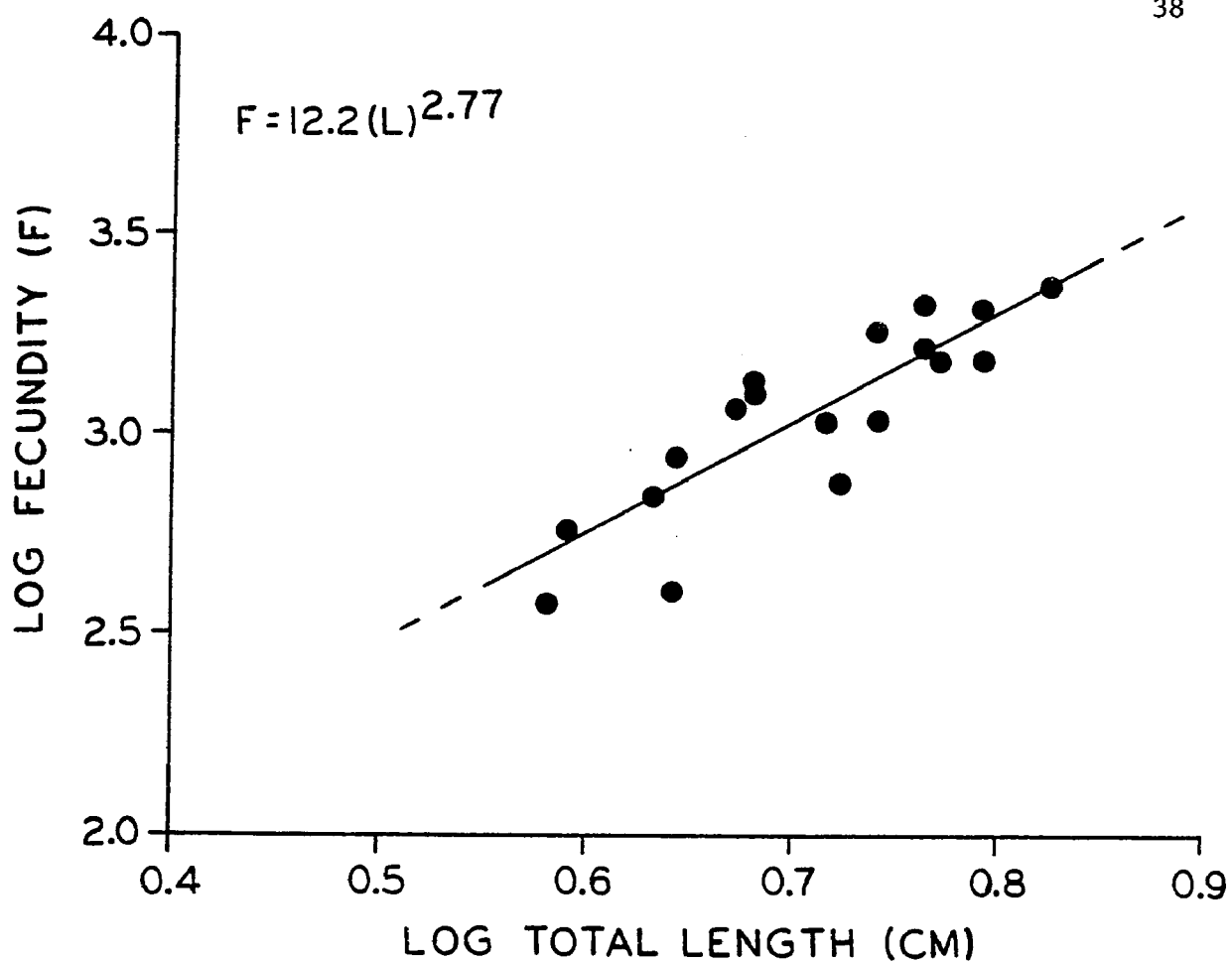


Figure 6. Linear regression of fecundity (number of mature ova in both ovaries) on body size (cm TL) for 18 female *Hypsoblennius ionthas*. The data have been log-transformed in order to fit the equation for a straight line: $\log F = \log a + b \log TL$, in which a and b are constants.

(1958) reported that such pigment concentrations in fish eggs were potential sources of vitamin A and were a factor in egg viability. Eggs less than 2 hours after spawning average 0.80 mm in diameter across their widest axis. As in *H. hentzi*, the blastodisc appears adjacent to the adhesive disk. Just prior to hatching, *H. ionthas* eggs average 0.88 mm in diameter (sample size = 20 eggs).

Newly hatched *H. ionthas* larvae average 2.82 mm in length with little discernible yolk sac (sample size = 20 larvae). Except for the large, dark eyes, the body is highly transparent. Positions of chromatophores and coloration of the larvae at this stage appear identical to *H. hentzi* (Hildebrand and Cable, 1938).

Morphology and Coloration

The moderate lateral compression of *H. ionthas* serves as a morphological adaptation for movement amidst the narrow confines and interstices in the oyster reef. As with *C. bosquianus* (Phillips, 1971a), such a laterally compressed body plan is suitable for entering and exiting the constricted openings of the gaping oyster shells that serve as both nest and shelter sites.

When erected, the median fins considerably increase the lateral profile of *H. ionthas*. This is a conspicuous feature in aggressive and courtship displays. Thirty to forty percent of the males collected at the study site have a large, brilliant blue within white ocellus on the anterior portion of the long, continuous dorsal fin. This ocellus is found in all sizes of males, including many of the newly settled juveniles. Coupled with rapid erection or depression of the dorsal fin, such ocelli may perform a signal function conveying dominance or aggressiveness (Wickler, 1967).

Sexual dimorphism is exhibited by *H. ionthas*. Males attain larger size, up to 8.2 cm in this study, but reportedly to 10.0 cm (Hoese and Moore, 1977). Females did not exceed 6.9 cm TL and rarely were larger than 6.2 cm TL. Orbital cirri, paired fleshy tabs located above and between the eyes, are much longer and more variable in shape in males than in females. During the spawning season, orbital cirri of males become orange-tipped with grayish-white bases. As in other species of blennies (Tomiyama, 1959; Smith, 1973), males develop urogenital papillae and pad-like articulations of anal fin spines and rays. Color patterns, although highly variable, differ distinctly between the sexes. The most common female pattern consists of numerous dark green spots on a greenish-brown background, with paler undersides tending toward yellow. The common name "freckled blenny" more aptly fits the females, as males seldom show this spotted pattern. Males generally show a solid, dark greenish-black body coloration. Although somewhat more pronounced in males, both sexes have a fairly intricate head coloration consisting of dark vertical bars descending in front of and under the eye, accompanied by a dark opercular patch. Since *H. ionthas* customarily lies within oyster shells with only the head exposed, this color pattern may serve to disrupt the outline of the eye in a camouflaging manner, and/or provide some additional signal function. Coloration of the Pacific *Hypsoblennius* is treated in detail by Losey (1968, 1976).

Trophic Studies

Gut Length to Body Length Ratio

Relative intestinal length and comparative gut morphology have been used in the past to indicate the feeding habits of fish species

(Al-Hussaini, 1947; DeGroot, 1971). In general, herbivorous fishes have longer intestines than carnivorous fishes. Using intestinal length to body length ratios, Al-Hussaini (1947) classified herbivores as having ratios generally greater than 3.7:1; omnivores between 1.3 and 4.2:1; and carnivores, less than 2.4:1. Although the reliability of these figures has been recently criticized by Montgomery (1977), they remain suitable for general comparisons.

In *H. ionthas* the stomach is separated from the intestine by a slight constriction. Pyloric caeca are absent, and the intestine forms one loop between stomach and anus. There does not appear to be a differentiated rectum. Lengths of the uncoiled alimentary tract from the esophagus to the anus were measured. Ratios of these lengths to TL are presented in Table 2. The mean ratio for 87 pooled males and females was 0.88:1, in the mid-range of Al-Hussaini's (1947) carnivore category, and well below his minimum omnivore ratio. Stomachs were included in the gut lengths of *H. ionthas*, whereas Al-Hussaini included intestinal length only. Therefore, the obtained ratio for *H. ionthas* is comparable to an even smaller ratio on the Al-Hussaini scale. Mean ratios for male and female *H. ionthas* were approximately equal, 0.863 and 0.902 respectively.

Montgomery (1977) stated that the rate of change in relative gut length with increasing body size may reflect changes in diet with growth. As seen in Table 2, there is a slight trend for allometric growth of the alimentary tract with respect to TL in *H. ionthas*, but the total range in mean ratios between body size categories is small. The range is wider and the trend more consistent in females.

Table 2. Gut length (mm) to body length (mm) ratios for 87 freckled blennies, *Hypsoblennius ionthas*.

Body Length (cm)	MALES			FEMALES		
	Sample Size	Mean Ratio (x:1)	Standard Deviation	Sample Size	Mean Ratio (x:1)	Standard Deviation
3	1	0.757	-	2	0.636	0.134
4	5	0.850	0.057	10	0.845	0.161
5	14	0.898	0.087	23	0.939	0.138
6	22	0.821	0.101	2	1.026	0.129
7	9	0.925	0.110	-	-	-
8	1	0.817	-	-	-	-

Feeding Periodicity

Freckled blennies exhibit a strictly diurnal activity cycle; thus, all feeding occurs during the day. *H. ionthas* retreat to their shelters at the onset of evening twilight and remain there until after sunrise. Their decreased activity under low-light conditions may represent an adaptation for avoidance of the crepuscular feeding activities of many predatory fishes.

Changes in gut weight (including contents) for samples of *H. ionthas* taken at 3-hour intervals are depicted in Figure 7. The first sample was taken 1.4 hours after sunrise. Three of 12 blennies in this sample had completely empty stomachs and intestines. Weights of the empty guts averaged 5.73% of total body weight. For the 9 blennies containing food material, the mean percent body weight comprised by the gut and contents was 6.08. Food material was largely confined to the stomachs and anterior portions of the intestines, indicating that feeding activity had been initiated just prior to capture.

For the sample taken 3 hours later the mean gut contents weight was equal to 7.40% of body weight, which corresponds to a rate gain of food material equal to 0.44% body weight per fish per hour. None of the blennies in this sample was empty. Two of 15 blennies were "full", i.e., they contained food material along the entire length of the alimentary tract. In an additional 4 specimens, food material had reached the posterior portions of the intestines, indicating fairly rapid transfer through the digestive system (approximately 4 hours).

In the 1355 hours sample the mean gut contents weight was equal to 8.91 percent of the body weight, a gain of 1.51% over the preceding 3-hour interval. This corresponds to a rate gain of 0.50% body weight

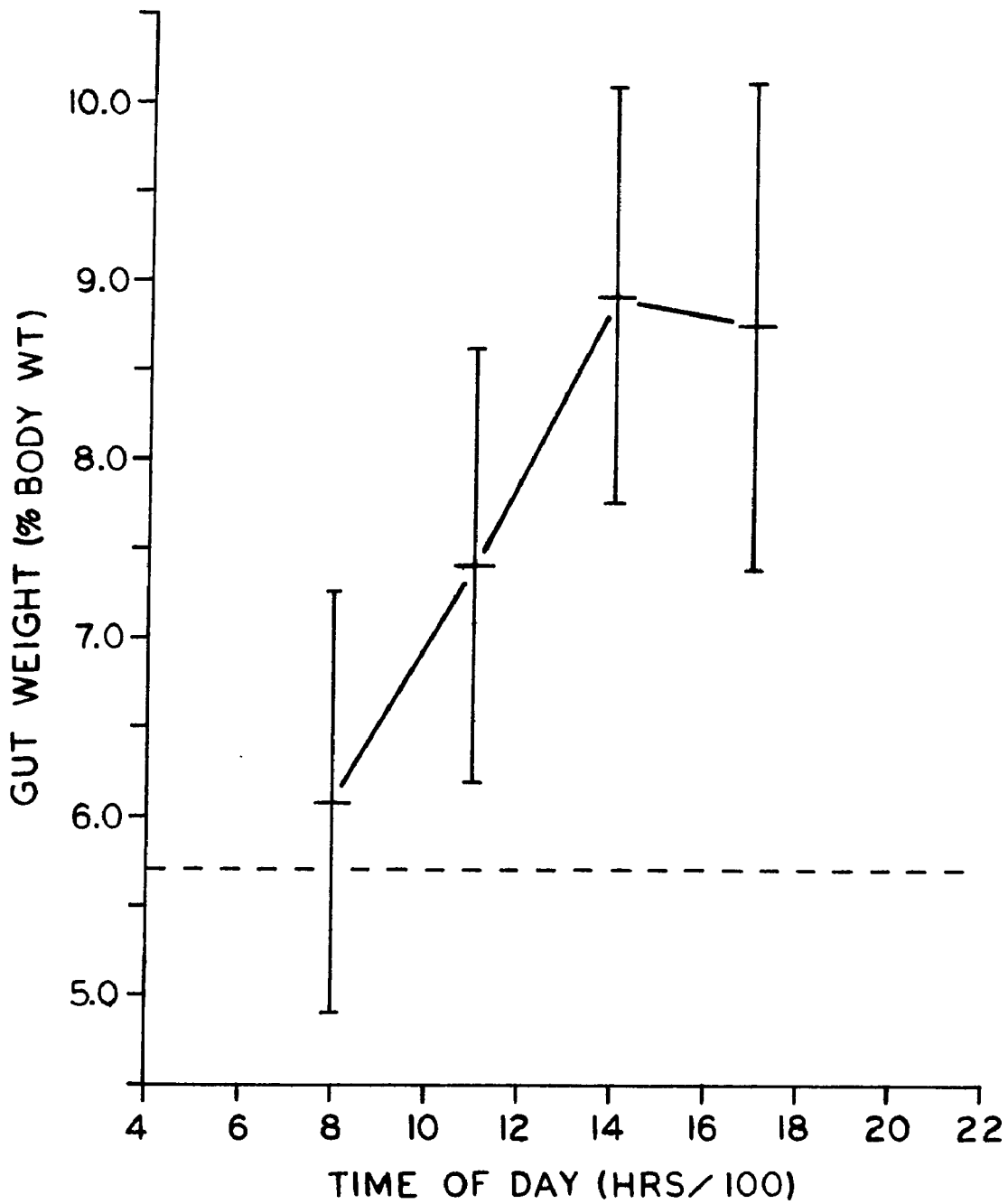


Figure 7. Feeding periodicity of *Hypsoblennius ionthas*. Samples were collected at three hour intervals during the daylight hours. The horizontal dashed line indicates the approximate weight of empty guts. Vertical bars represent one standard deviation around each mean gut weight (includes gut contents).

per fish per hour. Four of 12 blennies in the sample were full, and none was empty.

The final sample was taken 0.05 hours before sunset. Five of 11 blennies were full; none was empty. Although stomachs of all blennies in the sample contained food, the gut and contents weight dropped to 8.74% body weight, a decrease of 0.1% from the preceeding sample.

Results indicate that *H. ionthas* feeds at a fairly constant rate throughout the daylight hours without a discernible peak in feeding activity. Leveling of the curve of weight gain in Figure 6 probably indicated equalization of the rates of food ingestion and elimination, rather than a cessation or reduction of feeding.

Feeding Behavior

Hypsoblennius ionthas apparently primarily uses the visual modality to detect food. Locomotion during foraging activity is predominantly composed of short hops over the substrate. While stationary between hops, the blenny surveys the immediate area. If a potential food item is seen, the blenny visually locks in on its location, often tilting the head to the side. A short, rapid lunge is then made at the prey item. When feeding upon barnacles, the blenny approaches with the characteristic hopping movements until within lunging distance and assumes a stationary stance. Often the rhythmic sweeping of the barnacle cirri will cease at the approach of a blenny. When this happens the blenny may remain motionless for a short period until the barnacle resumes sweeping its cirri. Frequently, fragments of the barnacle test are broken away and ingested. Occasionally, the entire exoskeleton is removed from the substrate.

Tufts of filamentous algae are scraped off the substrate in a seemingly indiscriminate manner. The subterminal location of the jaws and structure of the "combteeth" in *Hypsoblennius* are adaptations for the scraping mode of feeding. The majority of amphipods and tanaids in the guts of *H. ionthas* are intact, which indicates that they are not grasped in the teeth prior to ingestion. On the average, fewer than a dozen amphipods occur in any one fish, but occasional blennies were gorged with several hundred *Corophium*. One large male contained 343 *Corophium* and little algae, which indicated that not all of the amphipods are taken incidentally with algae.

Food Item Percent Frequency of Occurrence

Of 317 *H. ionthas* examined for gut contents analysis, only one contained no food material. Results of frequency of occurrence analysis for the 316 blennies which contained food are summarized in Table 3. Twenty-one different food items were identified, only 7 of which occurred in all blenny size-sex categories. Four of the items (algae-detritus, the amphipod *Corophium louisianum*, the tanaid *Hargaria rapax*, and the barnacle *Balanus eburnea*) were fairly ubiquitous in occurrence, being present in over 50% of the guts for each size-sex category. Three additional items (the polychaetous annelid *Nereis succinea*, copepods, and barnacle larvae) were present in all size-sex categories. The occurrence of *N. succinea* exceeded 50% in all categories except 3 cm males, whereas copepods and cypris larvae never exceeded 50% occurrence in any category.

Xanthid crabs, *Eurypanopeus depressus* and *Panopeus herbstii*, were pooled as one food item, which was present in all categories except 3 cm males, as were the amphipod *Amphithoe* cf. *valida* and decapod megalops. Insect larvae (dipterans and chironomids pooled) and nematodes occurred

Table 3. Percent occurrence of all food items for pooled *Hypso-*
blennius ionthas field samples (N = 316).

TL (cm)	3		4		5		6		7
SEX	M	F	M	F	M	F	M	F	M
<i>Corophium</i>	100	79	87	89	75	83	92	89	89
<i>Hargaria</i>	75	74	76	72	62	81	90	67	89
<i>Nereis</i>	33	53	61	65	61	87	73	89	67
<i>Balanus</i>	58	58	61	83	85	77	75	89	83
Xanthidae	-	16	11	9	13	12	14	33	22
<i>Amphithoe</i>	-	11	13	13	23	14	31	33	17
Insect Larvae	-	-	8	9	12	10	4	11	22
Megalops	-	11	16	6	13	6	14	22	11
Copepods	50	21	29	22	39	10	39	44	11
Nematodes	-	-	3	13	7	4	12	33	6
Bivalves	-	-	-	-	3	-	2	-	-
Cypris Larvae	50	26	37	37	43	37	35	33	39
Fish Eggs	-	-	-	-	2	6	8	-	6
Penaeid Shrimp	-	5	-	-	2	2	2	-	-
Bryozoan	-	-	3	-	-	-	4	-	11
<i>Ligia</i>	-	-	-	-	-	-	2	-	-
Isopods	-	5	3	-	3	-	10	-	-
Gastropods	-	-	3	-	2	-	4	-	-
Fish Scales	-	-	-	2	5	4	-	11	6
Fish Larvae	-	-	-	2	-	-	-	-	-
Algae- Detritus	92	100	100	93	98	98	100	100	100

in all categories except 3 cm males and females. Remaining items occurred infrequently, never exceeding 12% in any blenny size sex category.

Food Item Percent Volume

Volumes of 4 infrequently occurring items (isopods other than *Ligia*, gastropods, fish scales, and fish larvae) were too minute to be accurately measured. Consequently, these 4 items were disregarded in the results of the volumetric analyses (Tables 4 and 5). In terms of volume, algae-detritus was the single dominant food item, comprising no less than 75.1% of the total volume of each blenny size-sex category. A maximum algae-detritus volume of 84.1% was found in 5 cm males. This evidence would support the contention that *H. ionthas* is primarily a herbivore, and yet gut morphology in *H. ionthas* would tend to indicate carnivorous feeding habits. In the author's opinion, the dietary contribution of the algae-detritus fraction is open to speculation. There is a strong possibility that freckled blennies graze upon filamentous algae mainly to obtain amphipods and other algal-associated fauna. Due to the ambiguity concerning the role of algae-detritus in the diet of *H. ionthas*, data were treated as both percent volumes of all food items (Table 4) and percent volumes of animal items only (Table 5). The second treatment was necessary to avoid the masking effect of large algae-detritus fractions on the importance of individual animal food items.

If algae-detritus is included in the volumetric analysis, only two animal items, *Corophium louisianum* and *Balanus eburnea*, contribute 5% or more to the total volume in any blenny size-sex category. Specific contributions among animal items are elucidated when the algae-detritus

Table 4. Percent volumes of food items for pooled *Hypsoblennius ionthas* field samples (N = 316). T indicates the presence of trace amounts of the food item (<0.5%).

TL (cm)	3		4		5		6		7
SEX	M	F	M	F	M	F	M	F	M
<i>Corophium</i>	9	5	8	6	4	5	6	6	4
<i>Hargaria</i>	2	2	3	2	1	3	1	2	1
<i>Nereis</i>	4	2	3	5	2	5	2	1	2
<i>Balanus</i>	4	3	7	7	5	10	4	4	6
Xanthidae	-	4	1	1	1	1	1	3	1
<i>Amphithoe</i>	-	1	T	1	1	1	1	1	T
Insect Larvae	-	-	1	1	1	T	T	T	T
Megalops	-	1	T	T	1	T	T	T	2
Copepods	T	T	T	T	T	T	T	T	T
Nematodes	-	-	T	T	T	T	T	T	T
Bivalves	-	-	-	-	T	-	T	-	-
Cypris Larvae	T	1	1	T	T	T	T	T	T
Fish Eggs	-	-	-	T	T	T	T	-	T
Penaeid Shrimp	-	2	-	-	T	T	T	-	-
Bryozoan	-	-	T	-	-	-	T	-	1
<i>Ligia</i>	-	-	-	-	-	-	T	-	-
Algae- Detritus	81	81	77	77	84	75	83	83	82

Table 5. Percent volumes of animal food items (algae-detritus excluded) for pooled *Hypsoblennius ionthas* field samples (N = 316). T indicates the presence of trace amounts of the food item (<0.5%).

TL (cm)	3		4		5		6		7
	M	F	M	F	M	F	M	F	M
<i>Corophium</i>	46	23	36	27	22	21	36	36	24
<i>Hargaria</i>	12	8	11	10	8	11	9	9	6
<i>Nereis</i>	20	12	13	21	13	18	11	8	12
<i>Balanus</i>	19	17	28	31	33	40	23	22	34
Xanthidae	-	21	2	2	5	5	9	19	6
<i>Amphithoe</i>	-	2	1	3	4	2	6	3	2
Insect									
Larvae	-	-	4	4	4	T	T	T	1
Megalops	-	2	1	1	8	1	2	T	12
Copepods	T	T	1	T	1	T	T	1	T
Nematodes	-	-	T	T	1	T	1	2	T
Bivalves	-	-	-	-	1	-	T	-	-
Cypris									
Larvae	2	3	3	2	T	1	T	T	T
Fish Eggs	-	-	-	1	T	T	T	-	T
Penaeid									
Shrimp	-	10	-	-	2	T	1	-	-
Bryozoan	-	-	T	-	-	-	1	-	3
<i>Ligia</i>	-	-	-	-	-	-	3	-	-

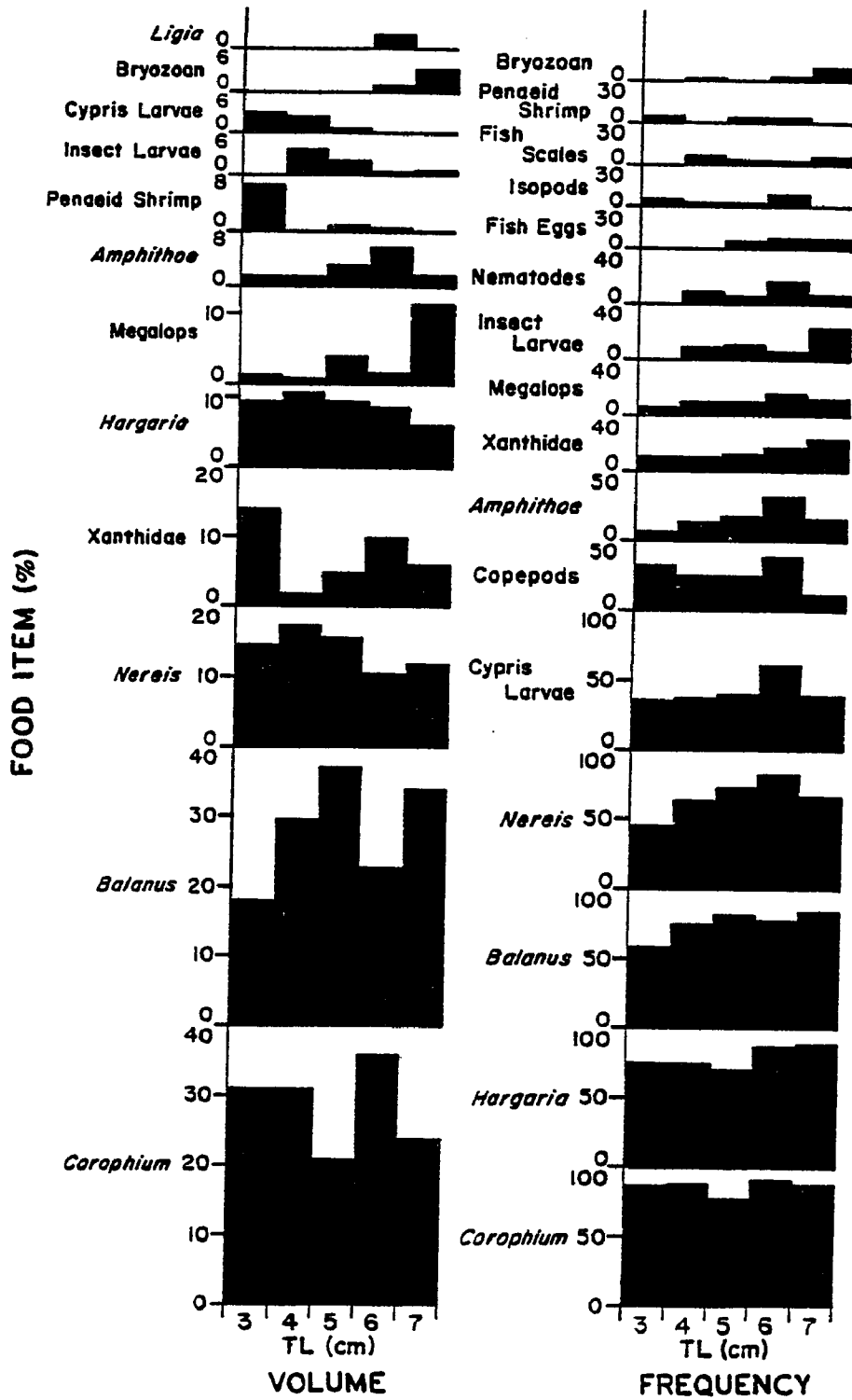
fraction is excluded. Thus treated, *C. louisianum* comprises between 21 and 46% of the animal item volumes for separate categories, and *B. eburnea* comprises between 17 and 40%. In order of decreasing importance are the additional items *Nereis succinea* (2-22%), *Hargaria rapax* (6-12%), xanthid crabs (2-22%), *Amphithoe cf. valida* (0-6%), and decapod megalops (0-7%). Penaeid shrimp occurred in less than half of the categories, but comprised 10.1% of the animal item volume for 3 cm females.

Diet in Relation to Blenny Body Size

Many fishes exhibit changes in diet with growth, such as damselfishes (Emery, 1973) and stichaeids (LeDrew and Green, 1975; Montgomery, 1977). By undergoing dietary changes with growth, intraspecific competition for food may be minimized. In Figure 8, food item percent volume and percent frequency of occurrence are illustrated in relation to body size in *H. ionthas*. Because the algae-detritus fraction has been shown above to be fairly constant in volume and ubiquitous in occurrence for all blenny size-sex categories, only animal food items are considered.

With respect to volume there are few consistent trends in dietary change with increasing body size for the major animal food items. Smaller blennies seem to utilize a smaller percentage of barnacles than larger blennies, but the observed barnacle fraction for 6 cm fish does not conform to the trend. Smaller blennies may be physically limited by the size of their mouth parts to predation on smaller barnacles. This is somewhat contradicted by the ability of 3 cm fish to feed on other items of substantial size, such as xanthid crabs and penaeid shrimp. Small crabs were usually ingested whole, whereas larger crabs were broken into pieces and the carapace and appendages ingested separately. Barnacle cypris larvae were noteworthy only in smaller blenny

Figure 8. Diet in relation to body size for 316 field collected *Hypsoblennius ionthas*. Histograms indicate percent volume and percent frequency of occurrence (ordinates) of each food item found in each blenny size category (abscissas). Algae-detritus is not included in the percentage analyses.



size categories. Decapod megalops, however, were taken in disproportionately high volumes by 7 cm blennies.

Frequency of occurrence data also show few consistent trends with increasing blenny body size for the major food items. Slightly higher frequencies of barnacles, nereids, and xanthid crabs occur in larger blennies, but the total ranges in observed frequencies appear insignificant.

Freckled blennies between 3 and 7 cm TL apparently use the same food resources, with little or no partitioning of available food between the size classes. Feeding is concentrated upon relatively few food items, i.e., algae-detritus, *Corophium louisianum*, *Balanus eburnea*, *Nereis succinea*, *Hargaria rapax*, and xanthid crabs. Additional items are taken opportunistically and perhaps incidentally.

A subsample of 8 *H. ionthas* between 1.7 and 2.9 cm TL was taken in May 1977. The volumes of food items in blennies of this size range were so small that quantitative volumetric analysis was impossible. A number of food items were identified. Small amounts of the green alga *Enteromorpha* sp., mixed with trace amounts of detritus, were present, along with *Corophium louisianum*, *Hargaria rapax*, *Nereis succinea*, and *Balanus eburnea* cirri. Apparently as soon as or shortly after they settle on the reef, very small *H. ionthas* are able to feed on the same food items as the adult population. The results do not preclude the possibility that a dietary shift occurs between blennies less than and greater than 3 cm TL, as a shift could involve changes in proportions of food items utilized. In all probability, blennies less than 3 cm TL are not able to ingest larger items such as xanthid crabs. They may preferentially take nereids and smaller crustaceans.

Diet in Relation to Season

Results of volumetric and frequency of occurrence analyses on a monthly basis are presented in Figure 9. In the winter months (December-February), the contribution of algae-detritus to the diet of *H. ionthas* is reduced. Also during this period there is an overall decline in feeding activity observed in the field population, especially after ambient water temperatures drop below approximately 13°C. In the month of January, no foraging activity was detected during field observations. As a result samples could not be obtained. Although all blennies collected in December and February contained food material, the relative amount of food within the guts was small. Few blennies were full to the point of gut distension, as is common in samples for summer months. Nereids provided the highest percent volume contribution in February, whereas *Amphithoe* represented the highest volume percentage in December. *Balanus* became an important item in April, by which time water temperatures had risen above 13°C and foraging was actively resumed. In May nereids were again the dominant animal food item. From Figure 9, the importance of nereid polychaetes in the diet of *H. ionthas* is fairly obvious, even though their presence is underestimated by the methods of analysis used.

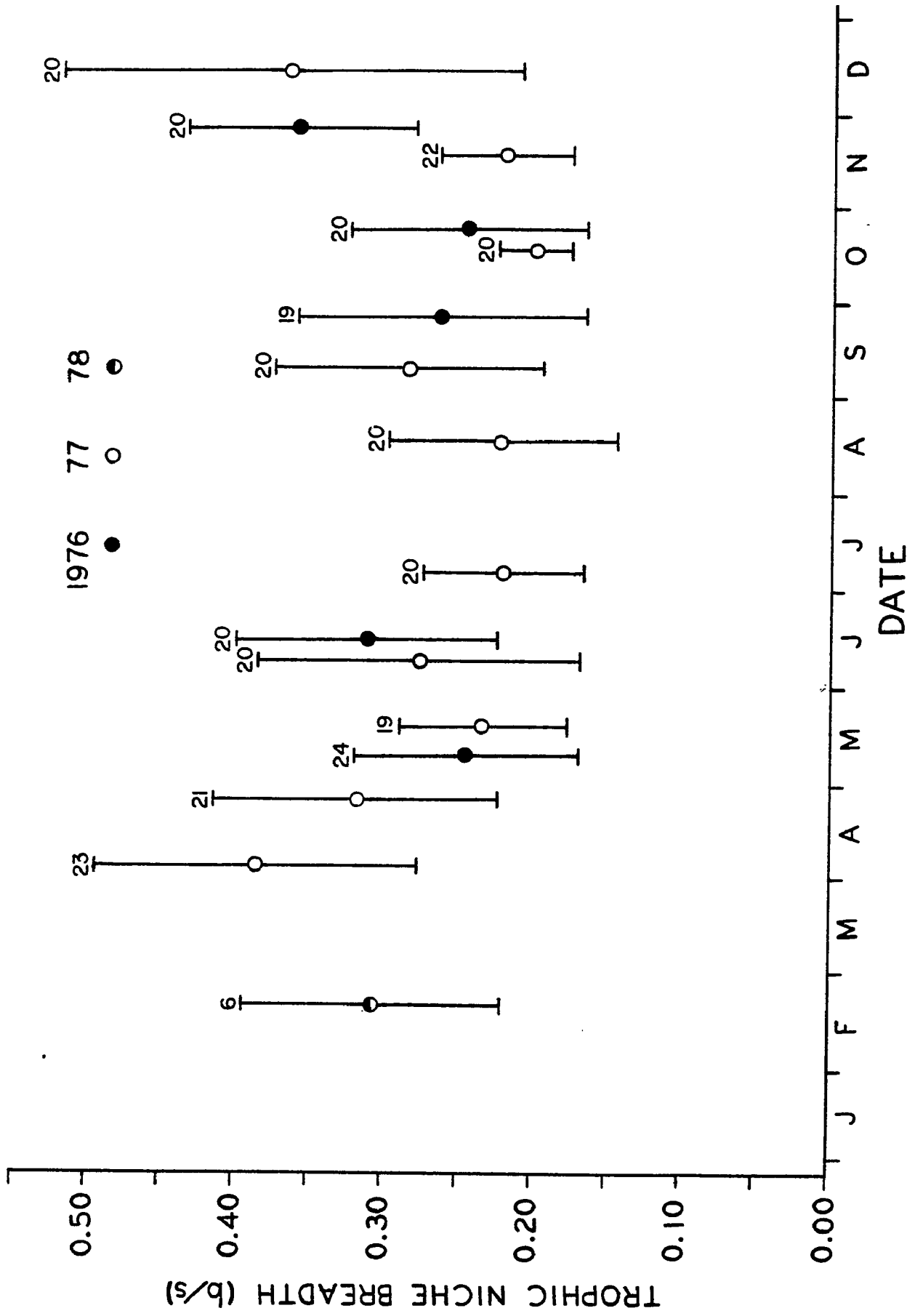
Percent frequencies of occurrence on a monthly basis indicate that the major food items (algae-detritus, *Corophium*, *Nereis*, and *Balanus*) are available throughout the year. Seasonally occurring items such as insect larvae and decapod megalops are taken whenever they become locally abundant.

Trophic Niche Breadth

Changes in trophic niche breadth of individual blennies (*b/s*) on a monthly basis are illustrated in Figure 10. This parameter is obviously

Figure 9. Diet in relation to season for 316 field collected *Hypsoblennius ionthas*. Histograms indicate percent volume and percent frequency of occurrence (ordinates) of each food item for monthly samples (abscissas). Percentages for animal food items do not include algae-detritus data.

Figure 10. Seasonal variation in trophic niche breadth (b/s) for samples of *Hypsoblennius ionthas* collected between March 1976 and March 1978. Vertical bars represent one standard deviation above and below the mean. Sample size is indicated above each symbol.



not static in *H. ionthas*, as monthly means vary from 0.201 (October, 1977) to 0.386 (April, 1977). Although both values are relatively low on the possible 1/s to 1.0 b/s scale, indicating an overall "narrow" trophic niche for *H. ionthas*, the higher niche breadth mean is nearly double the lower.

Wider trophic niche values occurred during the colder months, from late fall through mid spring. The b/s means were generally lower, or narrower, during the warmer months. Narrowness of the summer trophic niche reflects the high proportion of algae-detritus in the diet at that time. Contributions of all other food items are thereby minimized. Increased reliance on algae-detritus by *H. ionthas* may be caused by several factors. Due to accelerated algal growth during the longer photoperiods of summer, the abundance and availability of algae are most likely enhanced. Increased algal density may in turn provide greater cover for amphipods, tanaids, and other prey items. Consequently, blennies would have to ingest greater quantities of algae to remove the associated fauna. Both intra- and interspecific competition for the animal food items may be stiffest during the summer months as a result of recruitment of juvenile *H. ionthas* and intrusions of other species. Although many species of fish cease to feed during the spawning season, this does not appear to be the case in *H. ionthas*. Even females with abdominal cavities greatly swollen by ripened ovaries were found to have guts distended with food material.

Restrictions imposed upon feeding activity due to the presence of predators could indirectly affect niche breadth in *H. ionthas*. Two of the lowest mean b/s values occurred in October and early November 1977

samples, when large numbers of gray snapper, *Lutjanus griseus*, were present at the study site. Blennies seldom strayed from cover whenever snappers were in the vicinity; hence, their foraging activity was noticeably curtailed. Just after the November 1977 sample a cold front lowered water temperatures at the study site and snappers immediately left the area. The freckled blennies were then observed to resume normal levels of activity. Suppressed activity due to predator avoidance limited feeding forays to the immediate shelter areas, which apparently became overworked. Decreased prey diversity and/or abundance could then lead to narrower b/s values.

Calculated trophic niche breadth values of the pooled samples (B/S) are compared with mean b/s values for the same samples in Table 6. Values of B/S reflect the generalized pattern of food resource utilization of the *H. ionthas* population as a whole. In samples where B/S is greater than mean b/s , individual blennies fed on few food items and the items differed between fish. For example, if 3 blennies contained only one of three items each, their individual niche breadths (b/s) would be extremely narrow. If the three were pooled, however, and the volumes of the items were fairly equal, their pooled trophic niche breadth (B/S) would be very wide. Values of B/S exceeded mean b/s in 4 of 16 monthly samples. In 2 samples B/S exactly equaled mean b/s . In the remaining 10 samples, B/S was less than mean b/s , the result of wide disparities in the percent volumes of algae-detritus within the samples.

The total pooled trophic niche breadth (GB/S), which is based on all 316 *H. ionthas* examined, was equal to 0.255. This value may be somewhat biased by the low number of cold months samples, which generally had higher or wider breadths. In any case, the trophic niche

Table 6. Comparison of trophic niche breadth values for monthly means of individual niche breadth (b/s) and monthly pooled sample niche breadth (B/S). Samples of *Hypsoblennius ionthas* were collected between May 1976 and February 1978.

DATE	B/S	b/s
MAY 76	0.223	0.243
JUN 76	0.297	0.311
SEP 76	0.263	0.263
OCT 76	0.223	0.246
NOV 76	0.414	0.359
APR 77	0.373	0.386
APR 77	0.333	0.318
MAY 77	0.231	0.234
JUN 77	0.237	0.277
JUL 77	0.215	0.220
AUG 77	0.205	0.222
SEP 77	0.259	0.284
OCT 77	0.201	0.201
NOV 77	0.214	0.220
DEC 77	0.479	0.367
FEB 78	0.374	0.308

breadth of *H. ionthas* is typically narrow, with some degree of variation on a seasonal basis.

Trophic Niche Overlap

Results of volumetric gut contents analyses for fishes coinhabiting oyster reef substrate with *H. ionthas* are presented in Table 7. Fifteen different food items were found in 74 frillfin gobies, *Bathygobius soporator*. Items not in common with *H. ionthas* were small fish, hermit crab parts, and grass shrimp *Palaemonetes* sp. In contrast with *H. ionthas*, frillfin gobies contained a smaller proportionate volume of algae-detritus (34.8% vs. 80.4%). Algae present were predominantly *Enteromorpha* sp. and *Dictyota* sp., as opposed to *Enteromorpha* and *Polysiphonia* in *H. ionthas*. Although not directly measured, the detrital portion of the food item was markedly smaller than in *H. ionthas*.

Although feeding upon essentially the same food items as *H. ionthas*, *B. soporator* differed in the percentage composition of its diet. Xanthid crabs were a major dietary constituent of frillfin gobies, equal to 25% of the total food volume. Small fish comprised the next largest single item (7.1%), but occurred in only 3 larger specimens. The prey fish species were 2 *Gobiosoma bosci* and a single juvenile *B. soporator*. Calculated *GB/S* for *B. soporator* was equal to 0.490, a value almost double that of *H. ionthas*. The wider trophic niche for *B. soporator* was apparently due to the diminished algae-detritus portion of its diet, accompanied by greater evenness among the contributions of animal items.

Of 24 naked gobies, *Gobiosoma bosci*, only 9 contained algae-detritus (15.9% of the total volume). *Corophium louisianum* (21.2%) and *Nereis succinea* (22.0%) were the major food items. All of the 11 food items found in *G. bosci*, also occurred in *H. ionthas*. A *GB/S* of 0.779 was

Table 7. Percent volumes of food items for three fish species which co-occur with *Hypsobleennius ionthas* on oyster substrate.

SPECIES	<i>Bathygobius soporator</i>	<i>Gobiosoma bosci</i>	<i>Gobiesox strumosus</i>
# EXAMINED	74	24	10
FOOD ITEM (%)			
<i>Corophium</i>	3.8	21.2	2.0
<i>Hargaria</i>	0.6	9.3	-
<i>Nereis</i>	3.7	22.0	4.5
<i>Balanus</i>	5.5	7.3	18.2
Xanthidae	25.0	-	13.8
<i>Amphithoe</i>	-	7.8	3.6
Insect Larvae	-	14.5	-
Megalops	5.8	2.6	-
Copepods	0.1	-	-
Bivalves	0.1	-	-
Hermit Crab	0.8	-	-
<i>Ligia</i>	3.8	-	-
Small Fish	7.1	-	-
<i>Palaeomonetes</i>	2.3	-	-
Penaeid Shrimp	6.6	-	54.5
Isopods	0.1	-	-
Algae-Detritus	34.8	15.9	-
Unidentified	-	-	1.8

calculated for *G. bosci* indicating fairly even utilization of its dietary components.

None of 10 skilletfish, *Gobiesox strumosus*, contained algae-detritus. One fish had eaten a large penaeid shrimp, which accounted for over half of the pooled sample volume. Xanthid crabs and the amphipod *Amphithoe* were the next largest contributors. A GB/S of 0.404 was calculated for *G. strumosus*, but the small sample size limits the reliability of this figure for comparisons.

All specimens in a sample of 28 striped blennies, *Chasmodes bosquianus*, contained a large percentage of an unidentifiable material. Small amounts of *Balanus eburnea*, cypris larvae, *Corophium louisianum*, and fish eggs were identified. The unknown fraction is speculated to be tissue from small bivalves, possibly oyster spat. Stomach contents of *C. bosquianus* from other areas have not been reported, although Phillips (1971a) stated that striped blennies feed on small annelids and crustaceans among epifaunal tunicates, barnacles, algae, and bryozoans.

Coefficients of trophic niche overlap (C) were calculated for species pairs among *Hypsoblennius ionthas*, *Bathygobius soporator*, *Gobiosoma bosci*, and *Gobiesox strumosus*. Highest overlap occurred between *H. ionthas* and *B. soporator* ($C = 0.675$). The following species pairs are given in order of declining trophic overlap: *B. soporator* and *G. bosci* (0.426), *B. soporator* and *G. strumosus* (0.387), *H. ionthas* and *G. bosci* (0.376), *G. bosci* and *G. strumosus* (0.204), and *H. ionthas* and *G. strumosus* (0.015).

Behavioral Studies

Ethogram

A comparison of behavioral actions observed in *Hypsoblennius ionthas* and those reported in the generic ethogram constructed by Losey (1968) for Pacific *Hypsoblennius* is given in Table 8. Of 34 acts described by Losey, 11 occurred unaltered in *H. ionthas*. Five acts of the generic ethogram were not seen in *H. ionthas*. The remaining 18 behavioral actions occurred in *H. ionthas* with some degree of modification, either in form or function. For example, the posture assumed by *H. ionthas* during Head-Up was not as pronounced as that of the Pacific species. In addition, Quiver and Circle Cave are performed by the Pacific species only during courtship and mating behavior, whereas in *H. ionthas* both acts are also performed agonistically.

Social Structure

Results of 327 agonistic encounters observed in a male-female non-spawning colony are graphically presented in Figure 11. Histograms indicate the fate of each encounter with respect to size and sex of both aggressor and opponent.

Several trends can be seen in the data. First, males tend to be more aggressive than females. Although the sex ratio of blennies within the colony was approximately 1:1, females initiated only 85 out of 327 bouts (26%). Second, large males are more aggressive than small males or females of any size. Six and 7 cm TL males comprised just 27 percent of the colony population, but initiated 49 percent of the agonistic encounters. Males under 6 cm TL comprised 22 percent of the colony, but initiated only 25 percent of the agonistic encounters.

Table 8. Comparison between behavioral actions observed in *Hypsoblennius ionthas* and those reported in the ethogram constructed by Losey (1968) for the Pacific species of the genus *Hypsoblennius*.

Behavioral Act	Description (Summary of Losey, 1968)	Status in <i>H. ionthas</i>
1. Swim	Moderate anguilliform swimming.	Occurs unaltered.
2. Hop	Movement in short jumps.	Occurs unaltered.
3. Forewalk, Backwalk	Use of the pelvic and/or pectoral fins to propel the fish forward or backward.	Occurs unaltered.
4. Yawn	Mouth opened wide as the dorsal fin is raised. (Comfort)	Occurs unaltered.
5. Gulp	Gular area distended while the mouth is closed. (Comfort)	This act was not seen in <i>H. ionthas</i> , although it probably does occur.
6. Cough	Water forcefully expelled from the branchial chamber through the mouth. (Comfort)	Occurs unaltered.
7. Curl	The body is curved laterally until the head reaches the caudal peduncle, which may then be scraped with the teeth. (Comfort)	Occurs unaltered.
8. Chafe	While leaning to one side, the fish scrapes its flank against the substrate with a rapid forward movement. (Comfort)	Occurs unaltered.

Table 8. Continued.

Behavioral Act	Description (Summary of Losey, 1968)	Status in <i>H. ionthas</i>
9. Feed	When near a food item, the head is tilted slightly to the side. The food is then taken rapidly into the mouth. (Ingestive)	A short lunge is made at the food item ending in a Tail-Up position. The body then slowly settles to the substrate.
10. Flee	The fish quickly retreats from an opponent, usually with the dorsal fin depressed. (Submissive)	Occurs unaltered
11. Side Roll	The fish leans to one side, at times with its flank parallel to the substrate. The dorsal surface always faces the opponent. The fish remains motionless with its dorsal fin raised but deflected toward the substrate. (Submissive)	The dorsal fin is not always raised and deflection toward the substrate was not detected.
12. Swimming Side Roll	The fish swims in the Side Roll posture in a circle around the opponent. (Submissive)	Occurs, but a complete circle around the opponent is seldom completed.
13. Nod	The head is slowly raised and lowered with the mouth closed and dorsal fin depressed. (Aggressive)	This act is not seen.
14. Head-Up	By arching the body, the head is held in a raised position. The mouth is closed and dorsal fin raised. (Aggressive, Courtship)	Occurs in a less intense form. The pelvic fins remain in contact with the substrate. This act was not seen in courtship behavior, but may occur.

Table 8. Continued.

Behavioral Act	Description (Summary of Losey, 1968)	Status in <i>H. ionthas</i>
15. Tail-Up	The head remains on the substrate while the tail is raised and the anal fin erected. (Aggressive)	An act resembling this was involved in Feed, but was otherwise not seen.
16. Head Jerk	The head is twitched rapidly toward the opponent, often with the mouth maximally open. (Courtship, Mating)	This act is not seen.
17. Bite	Some part of the opponent is held in the mouth for up to several seconds. (Aggressive)	Occurs unaltered.
18. Chase	The fish swims rapidly after the opponent. (Aggressive)	Occurs unaltered.
19. Tail Beat	Water is propelled toward the opponent using the trunk and caudal fin. (Aggressive)	This act was not seen, but may occur.
20. Run	The fish swims toward the opponent in a Head-Up posture, then retreats in a Backwalk. (Aggressive)	Occurs, but the high Head-Up posture is not as pronounced.
21. Carousel	Two fish take up a parallel head to head or head to tail position. In the Head-Up posture both fish turn toward each other and Tail Beat or Bite. (Aggressive)	A head to tail position was assumed most frequently. Both fish would then swim in several tight circles while maintaining their parallel formation.

Table 8. Continued.

Behavioral Act	Description (Summary of Losey, 1968)	Status in <i>H. ionthas</i>
22. Mouth Lock	The fish interlock jaws for as long as several seconds, usually accompanied by twisting movements. (Aggressive)	Occurs for durations as long as 12 seconds.
23. Caudal Fan	Slow Swimming movements of the trunk and caudal fin which propel water backward. (Aggressive, Courtship, Mating, Parental)	This act was seen during parental behavior. It was not observed during aggressive, courtship, and mating behaviors, but may occur.
24. Rub	Slow Swimming movements in which the anal pads are pressed against the walls of the refuge. (Courtship, Mating, Parental, Maintenance)	Occurs unaltered.
25. Stationary Swim	Rapid low amplitude Swimming motions opposed by reverse movements of a pectoral fin. Performed while leaning toward the substrate. (Courtship, Parental, Eliminatory, Maintenance)	Occurs unaltered, but was not seen during courtship behavior.
26. Shake	Carangiform flexures of the trunk varying from low frequency, high amplitude to high frequency, low amplitude motions. (Courtship, Mating, Ingestive)	Occurs unaltered, but only in ingestive behavior.
27. Quiver	Extremely high frequency, low amplitude movements of the body. (Courtship, Mating)	Occurs unaltered. Quiver is also performed as an aggressive display when the performer sees an approaching opponent from within its refuge.

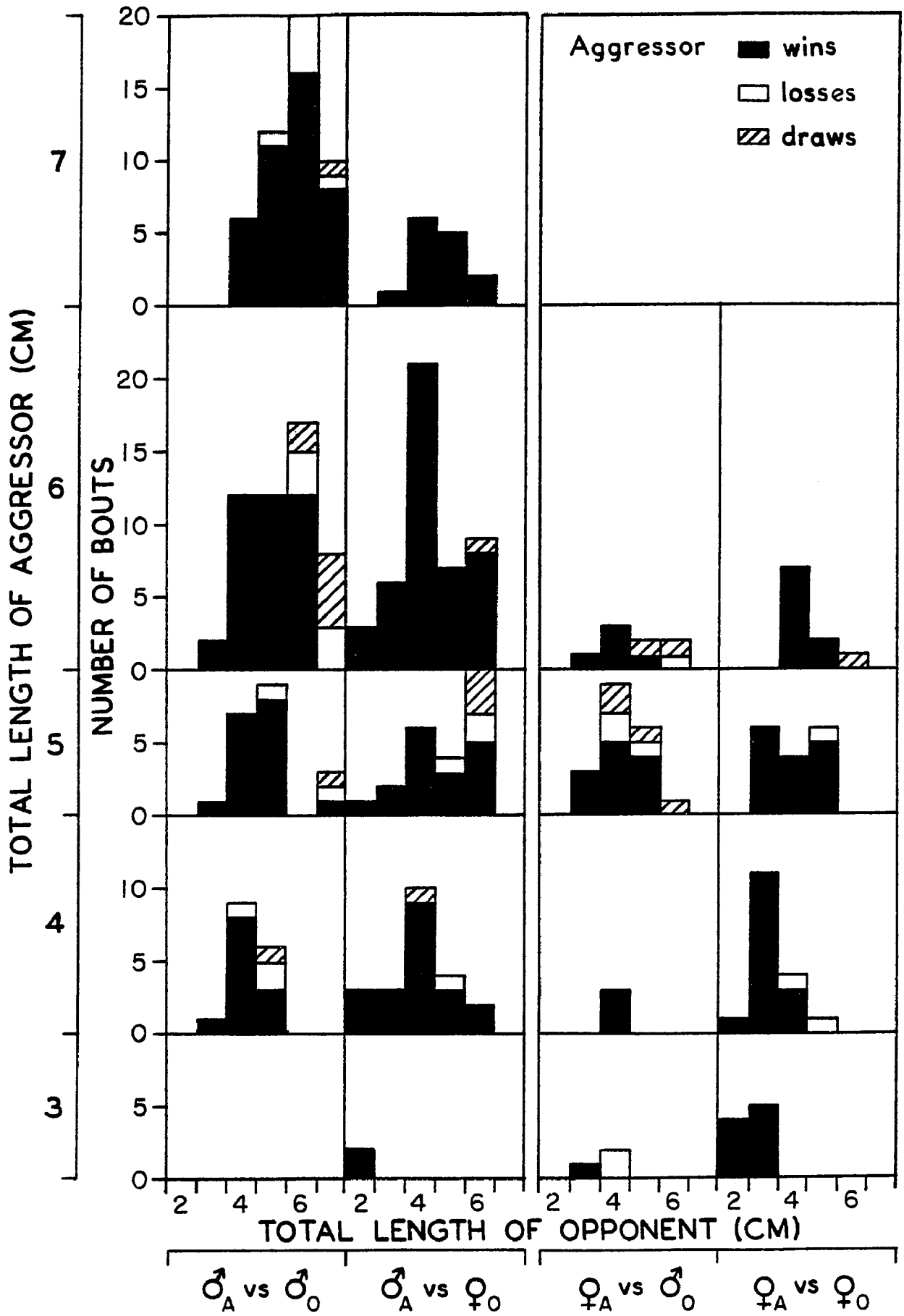
Table 8. Continued.

Behavioral Act	Description (Summary of Losey, 1968)	Status in <i>H. ionthas</i>
28. Pectoral Fan	Beating of one or both pectoral fins. (Aggressive, Courtship, Mating, Parental)	Occurs unaltered during parental behavior.
29. Chew	Scraping of the substrate with the teeth. (Maintenance, Parental)	Occurs unaltered, including in ingestive behavior.
30. Spit	The fish picks up debris in its mouth then expels the debris with a Cough. (Courtship, Maintenance)	Occurs unaltered, but not seen during courtship behavior.
31. Circle Spit	Male picks up debris in its mouth, then Swims upward in a circular path. At the peak of the circle the male usually Spits out the debris. Apparently not involved in maintenance. (Courtship)	This act was performed in a maintenance function. It was not seen during courtship behavior.
32. Circle Chase	Male Swims in an elongate circular path over and beyond a female, ending back at his refuge. (Courtship)	The male, having reached the position of the female, usually Swims several tight circles around her before returning to his shelter.
33. Circle Cave	Male Swims in a Head-Up posture in tight circles around his refuge. (Courtship, Mating)	Occurs unaltered. Males also perform this act in an aggressive manner when they notice an intruder inside a refuge in their territory. Circle Cave is then performed with the refuge entrance at the center of the circle.

Table 8. Continued.

Behavioral Act	Description (Summary of Losey, 1968)	Status of <i>H. ionthas</i>
34. Cuddling	Female presses against the outside of the male's refuge with her head at the entrance. (Courtship)	This act was not seen, but may occur.

Figure 11. Results of 327 agonistic encounters in a male-female laboratory colony of freckled blennies, *Hypsoblennius ionthas*. Histograms indicate the number of bouts won, lost, and drawn by aggressors of each size category (ordinate) versus opponents of each size category (abscissas). Sex of aggressor (A) and opponent (O) blennies are indicated on lower abscissas.



Tables 9 and 10 summarize the relative success of aggressors of each sex with respect to the size and sex of their opponents. Several additional trends can be seen. Except when the opponent was a larger male, the aggressor usually won. This may be due to the fact that most aggressors initiated the agonistic encounter in defense of their territories. The opponents were often intruders without established territories or blennies making forays outside of their normal territorial boundaries. In these cases the holder of the territory in which the bout took place had an advantage even against opponents of equal size; pooled male and female aggressors won 80 percent of their bouts with equal-sized opponents (Table 10).

The data support the conclusion that a size-dominant social hierarchy exists in *H. ionthas*. Aggressors won 95 percent of their bouts with smaller opponents and 80 percent of their bouts with equal-sized opponents, but only 38 percent of their bouts with larger opponents. Male domination over females exhibits a less definite trend. Against equal-sized opponents of the opposite sex, male aggressors won 87 percent of their bouts, whereas females won 67 percent of their bouts.

Effects of Population Density on Resource Utilization

Results of individual laboratory experiments are presented in Figures 12 through 17. For convenience in comparison, their order of presentation is based upon experimental protocol rather than their numerical designation in Table 1. Population densities of 7.1, 14.3, and 21.4 fish per square meter are hereafter referred to as low population density (LPD), mid population density (MPD), and high population density (HPD). Likewise, food resource abundances will be referred to as high (HFA) or low (LFA).

Table 9. Summary of the results of 327 agonistic encounters within a male-female laboratory colony of *Hypsoblennius ionthas* at a population density of 14.3 fish/sq. m and at high food abundance. W indicates bouts won by the aggressor, L indicates bouts lost by the aggressor, and D indicates draws in which neither the aggressor nor the opponent exhibited submissive behavior.

Male Aggressor vs Smaller Male Opponent		Male Aggressor vs Equal-sized Male Opponent		Male Aggressor vs Larger Male Opponent		Male Aggressor vs Smaller Female Opponent		Male Aggressor vs Equal-sized Female Opponent		Male Aggressor vs Larger Female Opponent	
W	L	W	L	W	L	W	L	W	L	W	L
70	5	36	5	4	6	4	0	66	0	20	0
93.3	6.7	80.0	11.1	23.5	35.3	41.2	100	0	87.0	0	13.0
Female Aggressor vs Smaller Male		Female Aggressor vs Equal-sized Male		Female Aggressor vs Larger Male		Female Aggressor vs Smaller Female		Female Aggressor vs Equal-sized Female		Female Aggressor vs Larger Female	
W	L	W	L	W	L	W	L	W	L	W	L
13	2	8	2	0	2	1	35	0	13	2	1
72.2	11.1	66.7	16.7	0	66.7	33.3	100	0	81.3	12.5	6.3
BOUTS		BOUTS		BOUTS		BOUTS		BOUTS		BOUTS	
%		%		%		%		%		%	
0		0		0		0		0		0	
3		2		1		0		1		0	
10		16.7		33.3		100		12.5		18.8	
30		50		83.3		350		156.25		225	

Table 10. Summary of the results of 327 agonistic encounters within a male-female laboratory colony of *Hypsoblennius ionthas* at a population density of 14.3 fish/sq. m and at high food abundance.

W indicates bouts won by the aggressor, L indicates bouts lost by the aggressor, and D indicates draws in which neither the aggressor nor the opponent exhibited submissive behavior.

	Male Aggressor vs Opponent			Male Aggressor vs Opponent			Female Aggressor vs Opponent		
	W	L	D	W	L	D	W	L	D
BOUTS	110	16	11	96	3	6	21	6	6
%	80.3	11.7	8.0	91.4	3.1	6.3	63.6	18.2	18.2
	All Aggressors vs Smaller Opponents			All Aggressors vs Equal-sized Opponents			All Aggressors vs Larger Opponents		
BOUTS	184	7	3	77	9	10	14	12	11
%	94.9	3.6	1.6	80.2	9.4	10.4	37.8	32.4	29.7
	Male Aggressor vs Opponents			Female Aggressor vs Opponents					
BOUTS	206	19	17	69	9	7			
%	85.1	7.9	7.0	81.2	10.6	8.2			

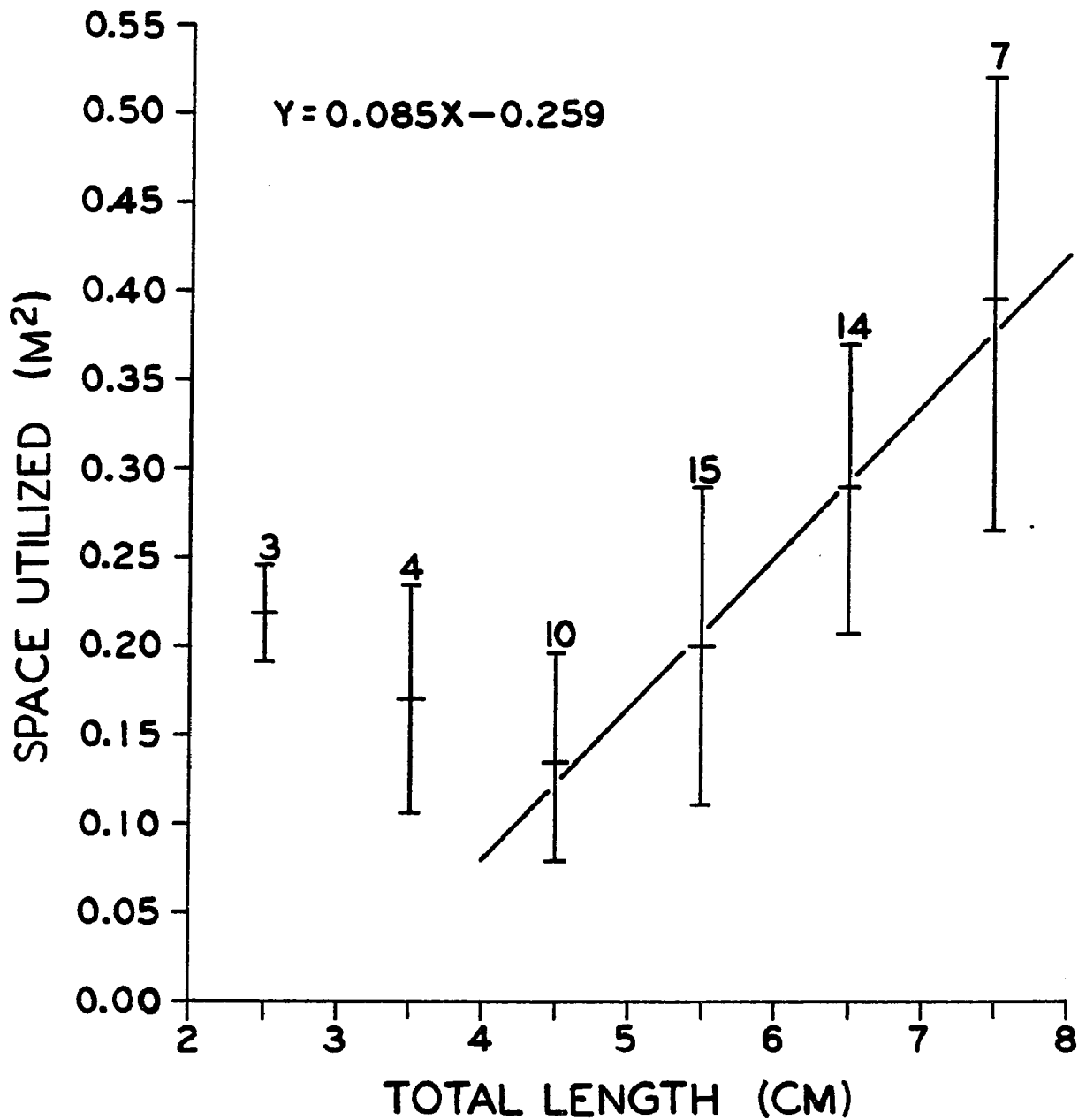


Figure 12. Linear regression of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 7.1 fish per square meter and fed *ad libidum*. Blennies less than 4 cm TL are not included in the regression. Vertical bars indicate one standard deviation around the mean for each size category. Sample size is given above each symbol.

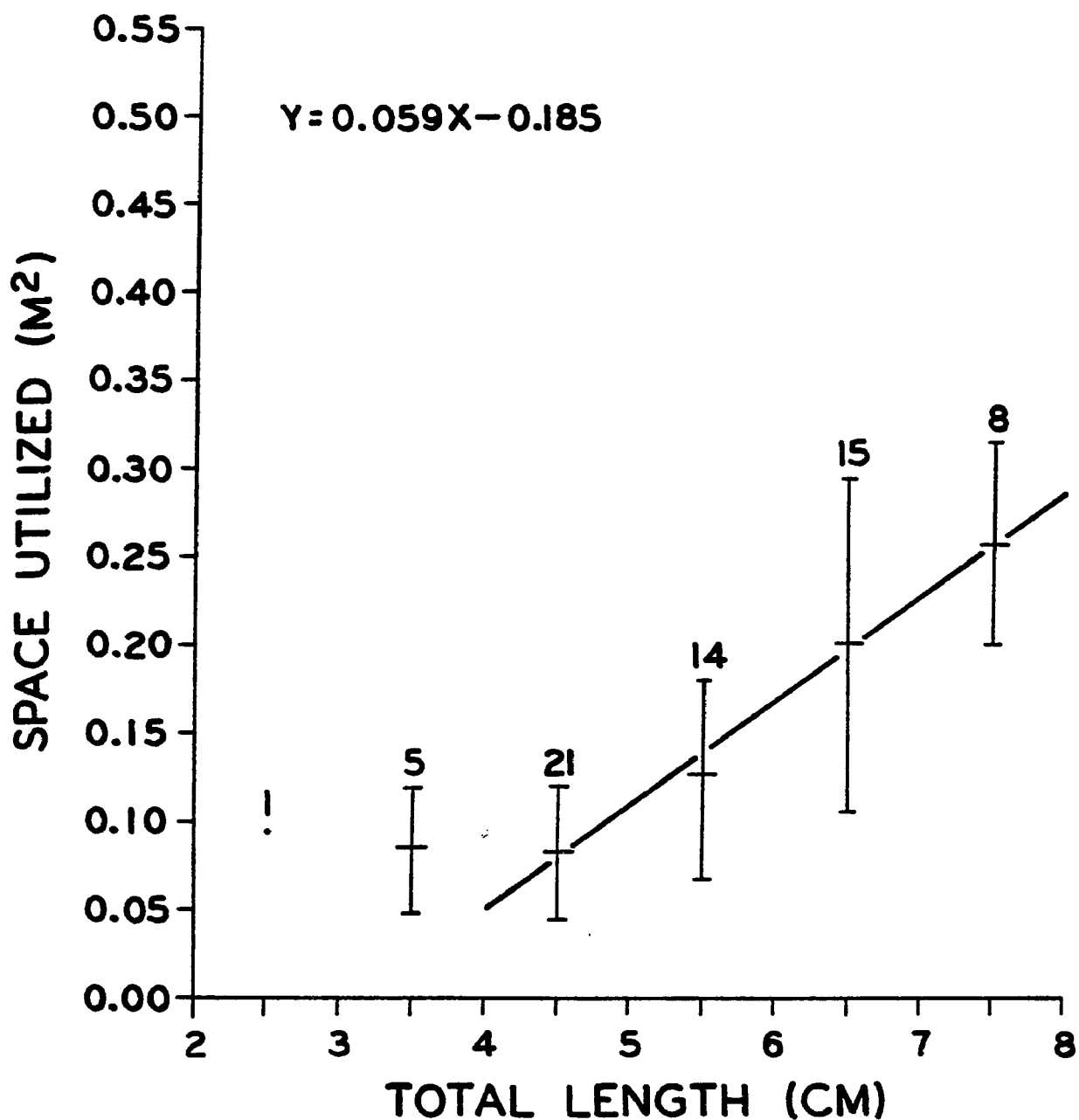


Figure 13. Linear regression of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 14.3 fish per square meter and fed *ad libidum*. Blennies less than 4 cm TL are not included in the regression. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

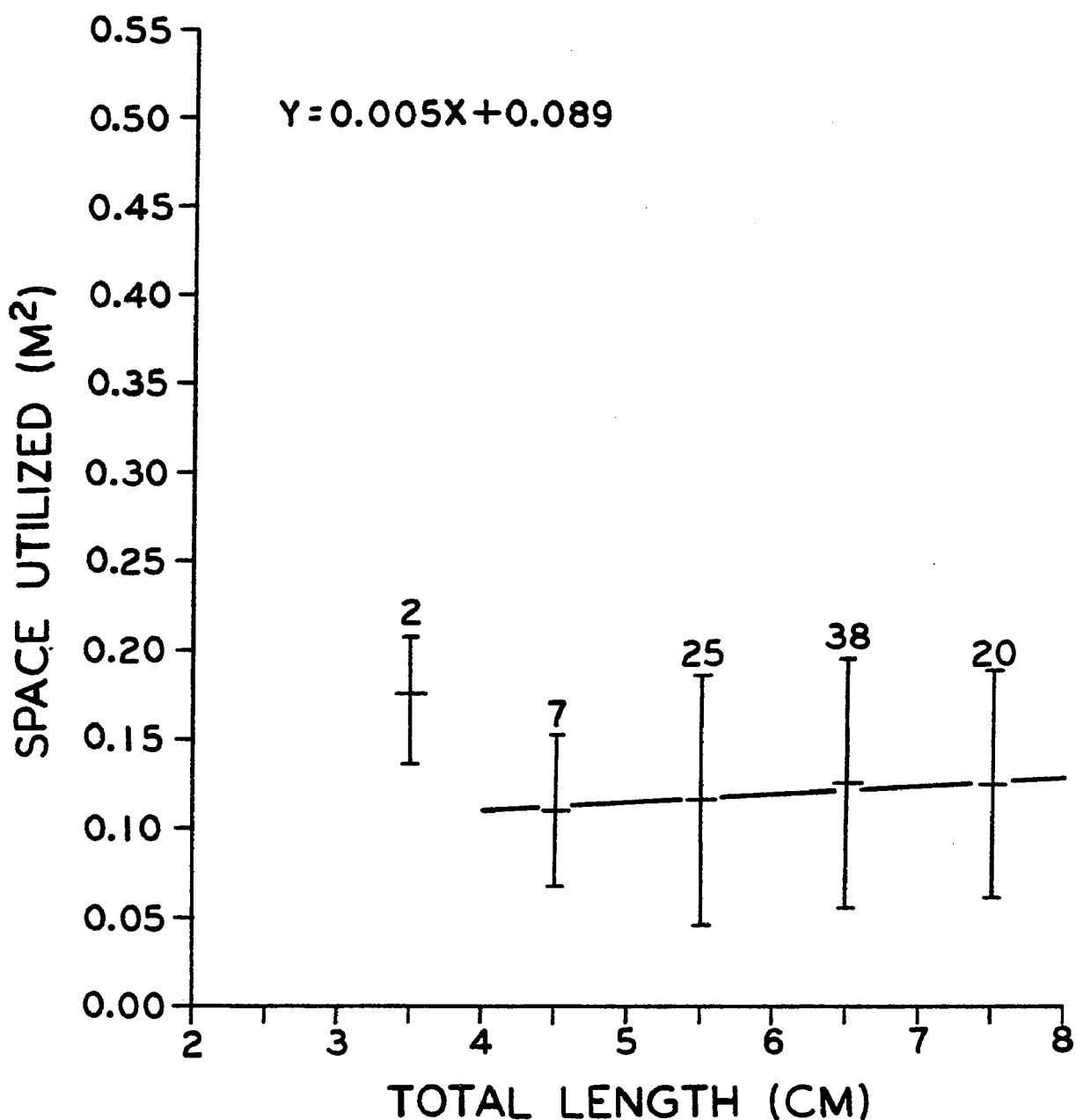


Figure 14. Linear regression of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 21.4 fish per square meter and fed *ad libidum*. Blennies less than 4 cm TL are not included in the regression. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

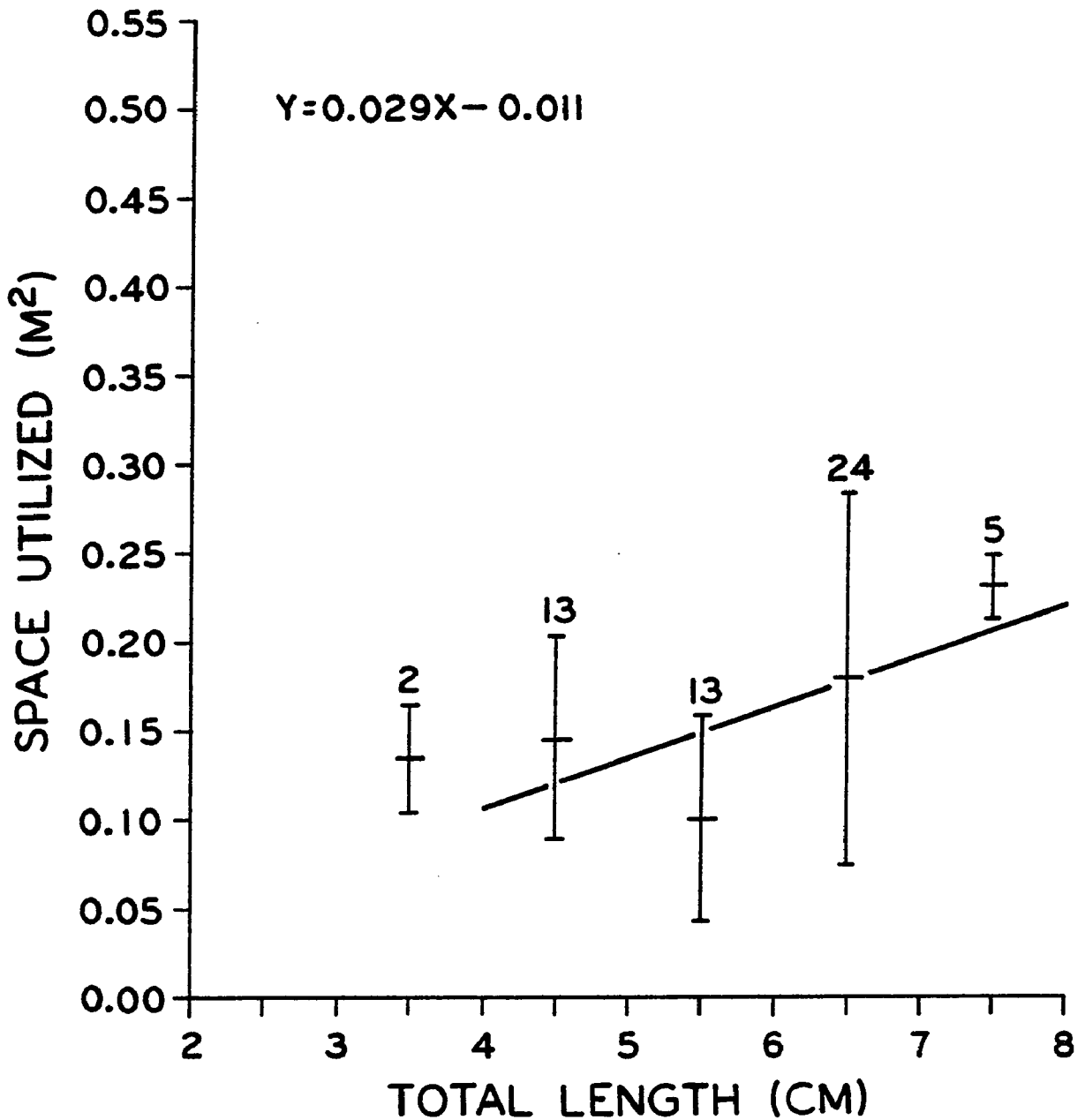


Figure 15. Linear regression of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 7.1 fish per square meter and fed a small ration of shrimp. Blennies less than 4 cm TL are not included in the regression. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

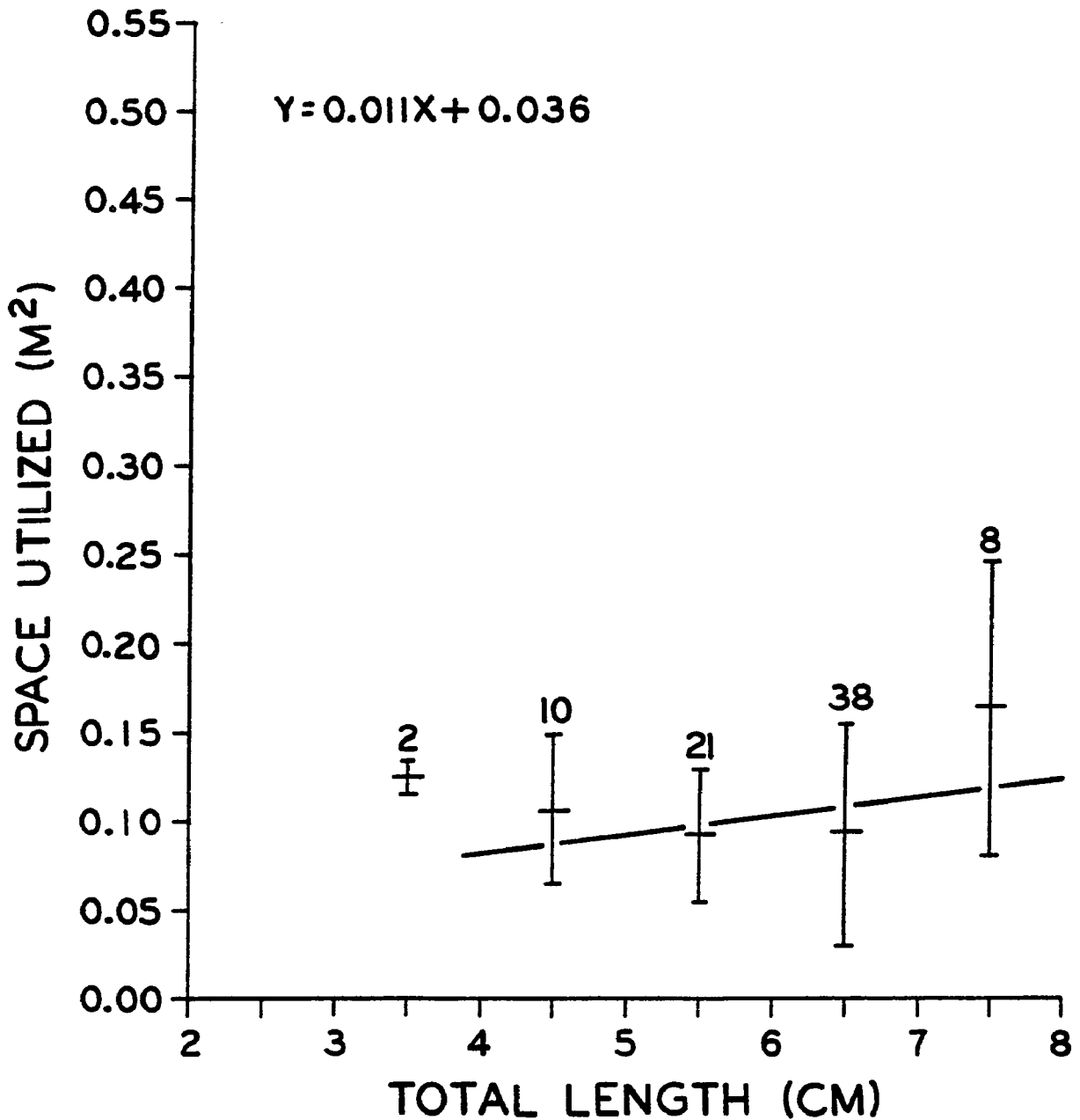


Figure 16. Linear regression of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 14.3 fish per square meter and fed a small ration of shrimp. Blennies less than 4 cm TL are not included in the regression. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

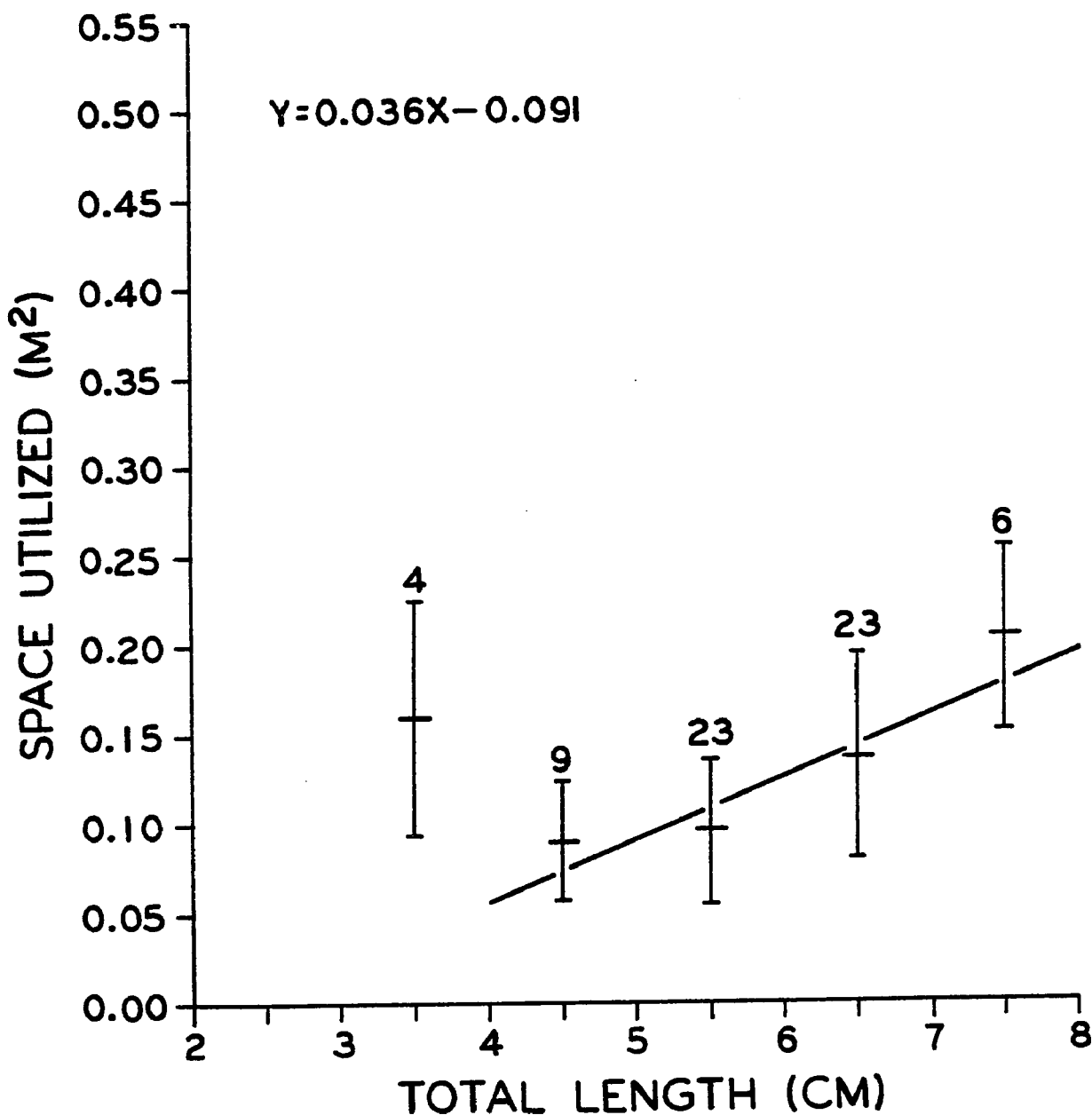


Figure 17. Linear regression of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 21.4 fish per square meter and fed a small ration of shrimp. Blennies less than 4 cm TL are not included in the regression. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

Considered first are the series of experiments in which food resource abundance was held constant, but population density was changed. Comparison of the regression lines for experiments at HFA and at three population densities (experiments 2, 3, and 6) are given in Figure 18. At HFA and LPD, a definite relationship exists between space utilized and body size, as evidenced by a highly positive slope of the regression line (slope = 0.085, $P < 0.001$). The relationship holds also for the HFA-MPD experiment, but at a reduced slope (0.059, $P < 0.001$). At HFA-HPD, however, the relationship between space utilized and body size breaks down. The slope of the regression line (0.005) no longer differs significantly from zero ($P > 0.5$). Slopes and intercepts of all three regressions were found to be significantly different from each other (Appendix 1).

As population density decreases, blennies in successively larger size categories use increasing amounts of habitat surface area (Figure 18). Standard deviations around the mean values of space utilized overlap greatly between experiments for 4 cm blennies, indicating little effect of population density on their space utilization. On the other hand, hardly any overlap occurs between standard deviations for 7 cm blennies. The effect of population density change is, therefore, most evident in the larger size categories.

In the LPD, MPD, HPD series of experiments at HFA, numbers of blennies in each size category are roughly proportional between experiments with the exception of 4 cm fish at HPD. This exception is not due to a smaller proportion of 4 cm fish in the colony, but rather reflects a reduced ability of 4 cm fish to defend and hold territories at HPD.

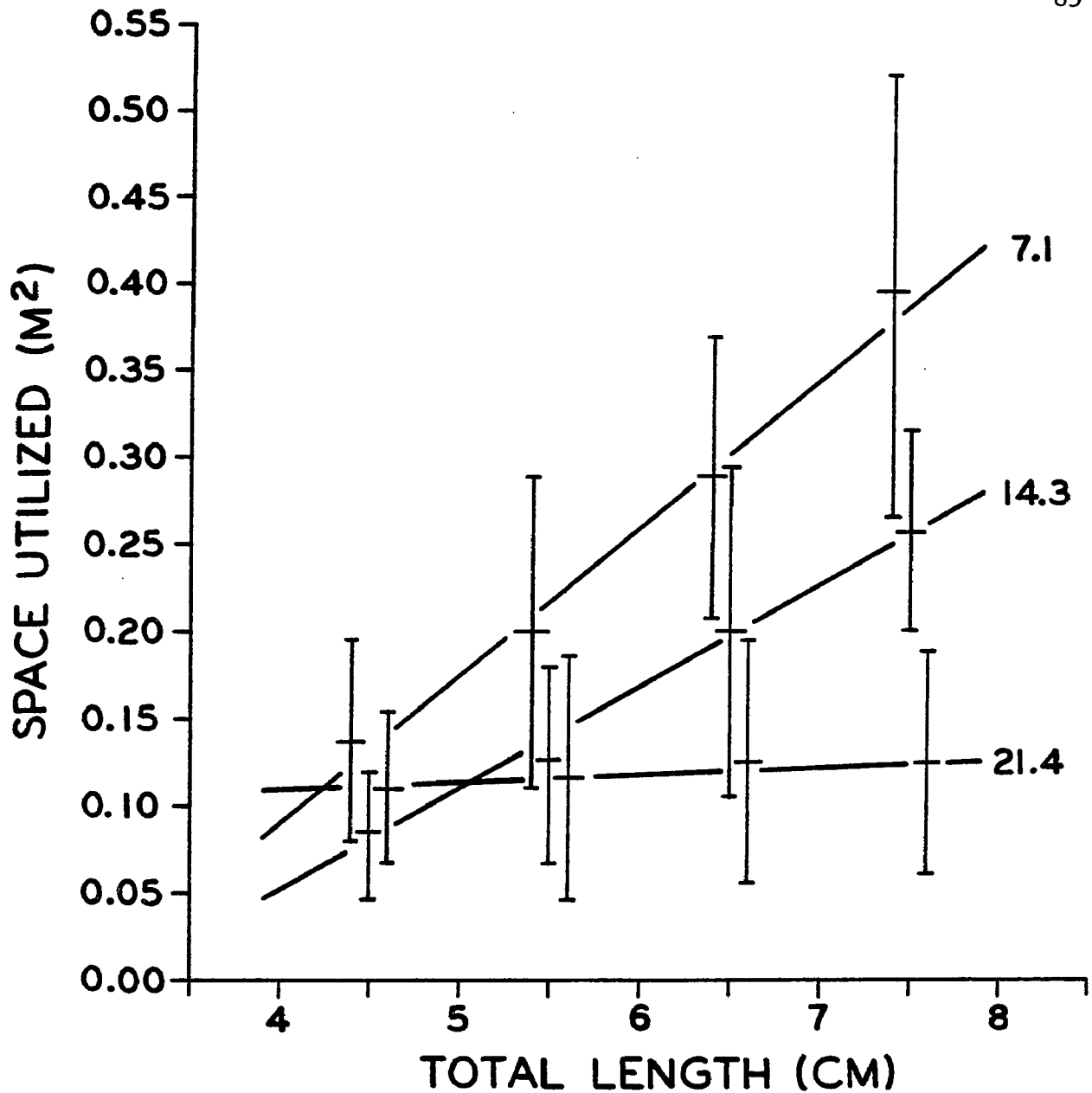


Figure 18. Comparison of linear regressions of space utilized on body size for laboratory colonies of *Hypsoblennius ionthas* males at population densities of 7.1, 14.3, and 21.4 fish per square meter. All colonies were fed *ad libidum*. Vertical bars represent one standard deviation around the mean for each size category.

Under these conditions, movements of the majority of smaller *H. ionthas* became random.

Figure 19 compares the regression lines for the LPD, MPD, HPD experimental series run under LFA conditions (experiments 4, 5, and 7). All three regression lines are significantly different from each other (Appendix 1). An overall reduction in amounts of space utilized is seen. The relationship between space utilized and body size persists in the LPD (slope = 0.029, $P < 0.025$) and HPD (slope = 0.036, $P < 0.001$) experiments, but is lost in the MPD (slope = 0.011, $P < 0.184$) experiment. As in the HFA-LPD experiment, blennies in the LFA-LPD colony averaged greater amounts of space utilized for each size category than did the MPD and HPD colonies. Regression lines for the LFA-MPD and HPD experiments, however, are transposed from their expected positions. This anomaly in the increasing density - decreasing space utilized trend may be due to a disproportionately high number of large fish present in the LFA-MPD colony. The regression lines for the LFA-MPD and HPD experiments are significantly different from each other ($P < 0.01$), although mean values of surface area used are measurably different only for the two higher size categories. The differences are small in terms of space utilized per fish (less than 0.05 square meter).

As population density increased, there was a slight trend for a reduction in the percentage of territorial fishes within a colony. Among the HFA colonies, 61% of the blennies at LPD, 39% at MPD, and 45% at HPD maintained territories. Percentages for the LFA colonies were 73% at LPD, 66% at MPD, and 35% at HPD. Total amounts of surface area utilized (summed for all territorial blennies in a colony) did not show a consistent trend with respect to changes in population density.

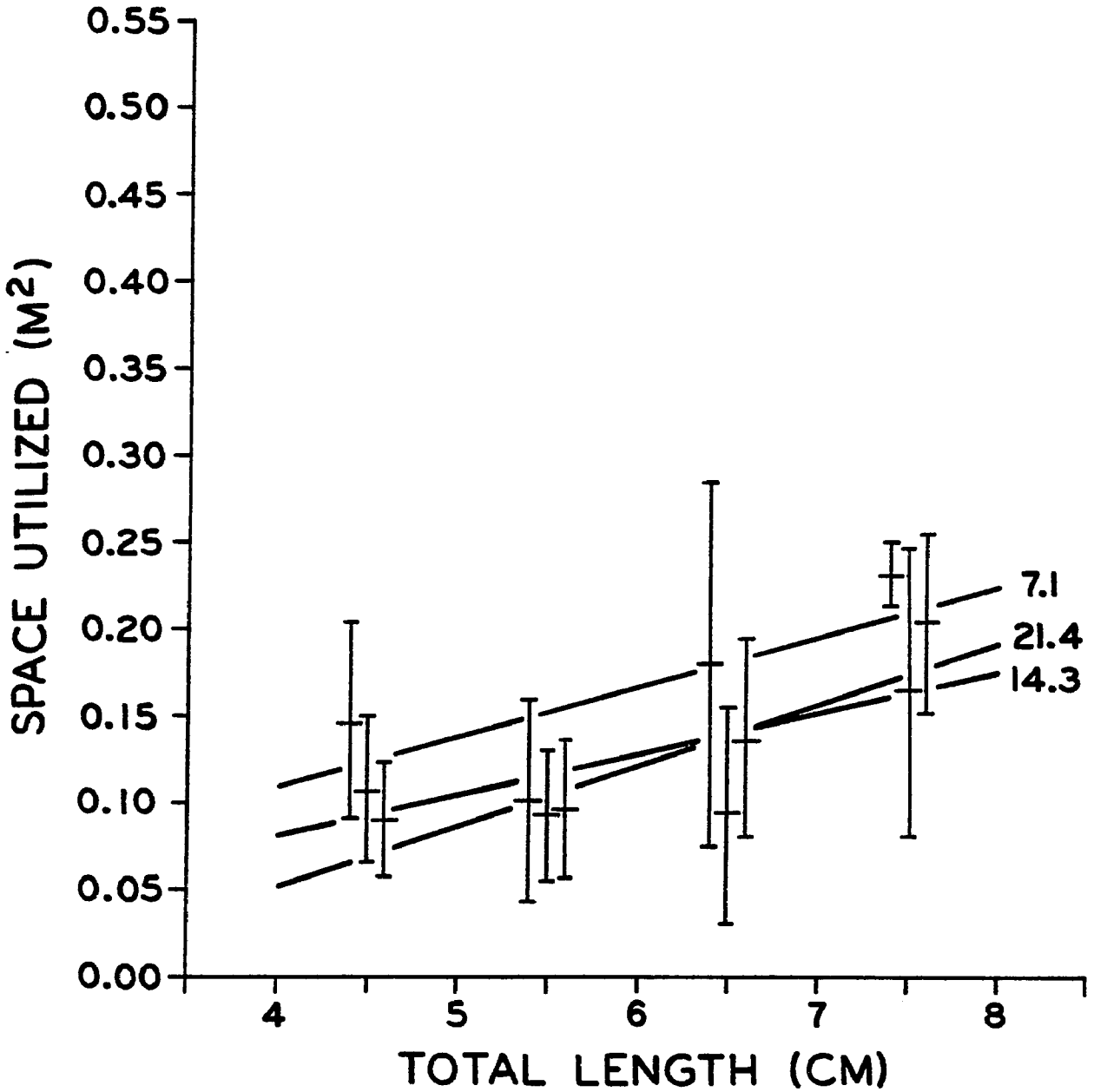


Figure 19. Comparison of linear regressions of space utilized on body size for laboratory colonies of *Hypsoblennius ionthas* males at population densities of 7.1, 14.3, and 21.4 fish per square meter. All colonies were fed a small ration of shrimp. Vertical bars represent one standard deviation around the mean for each size category.

Effects of Food Abundance on Resource Utilization

The regression lines in Figures 20 - 22 compare the results of experiments performed at the same population density but under different food abundances. In Figure 20, the regression lines of LPD-HFA and LFA experiments are compared. The two lines are significantly different from each other ($P < 0.001$). Amounts of space utilized are nearly identical for 4 cm blennies in both experiments. With increasing size, however, an increasing disparity in space utilized is seen, with the blennies fed *ad libidum* using more space per fish.

The increasing food abundance-increasing space utilized pattern is continued in the comparison of regression lines for the MPD-HFA and LFA experiments (Figure 21). Again, the regression lines are significantly different from each other ($P < 0.001$). There may be some depression of the MPD-LFA intercept and slope due to the high number of large fish, but certainly not enough to account for the wide disparity shown.

In the comparison of HPD-HFA and LFA regression lines (Figure 22), positions of the lines as predicted by the increasing food abundance-increasing space utilized trend are reversed. The regression lines are significantly different from each other ($P < 0.05$). In this case, depression of the HPD-HFA regression line may indeed be the result of a disproportionately high number of large blennies. Roughly 60% of the HPD-HFA colony consisted of fish greater than 6 cm TL. In contrast, approximately 40% of the HPD-LFA colony fish were greater than 6 cm TL.

Effects of Sexual Behavior on Resource Utilization

Space utilization by male and female blennies in colonies at MPD-HFA during non-spawning and spawning seasons are compared in Figures 23 and 24 respectively. In both experiments, regression lines of space

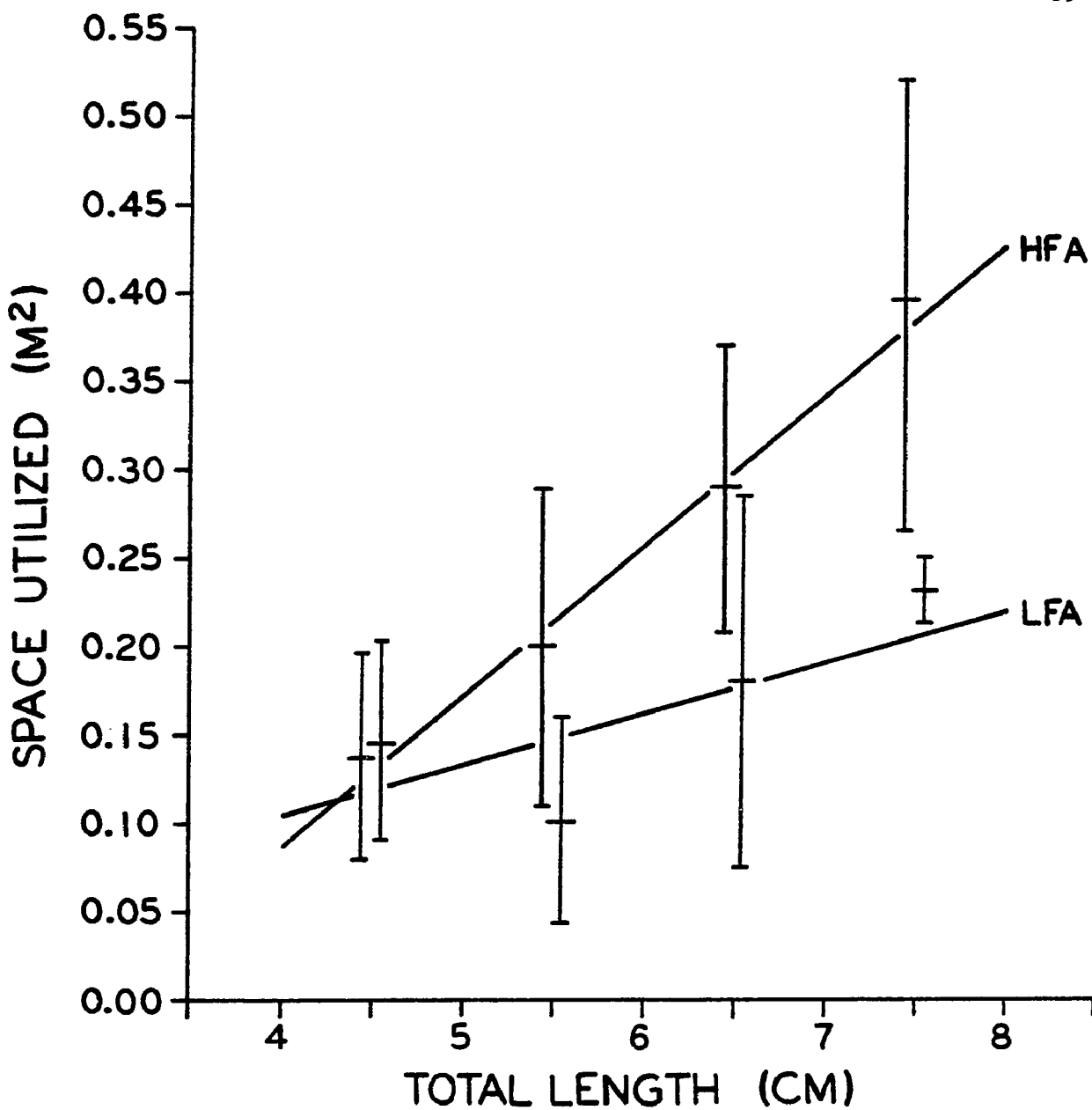


Figure 20 Comparison of linear regressions of space utilized on body size for laboratory colonies of *Hypsobleennius ionthas* males at a population density of 7.1 fish per square meter and under conditions of high (HFA) and low (LFA) food abundance. Vertical bars represent one standard deviation around the mean for each size category.

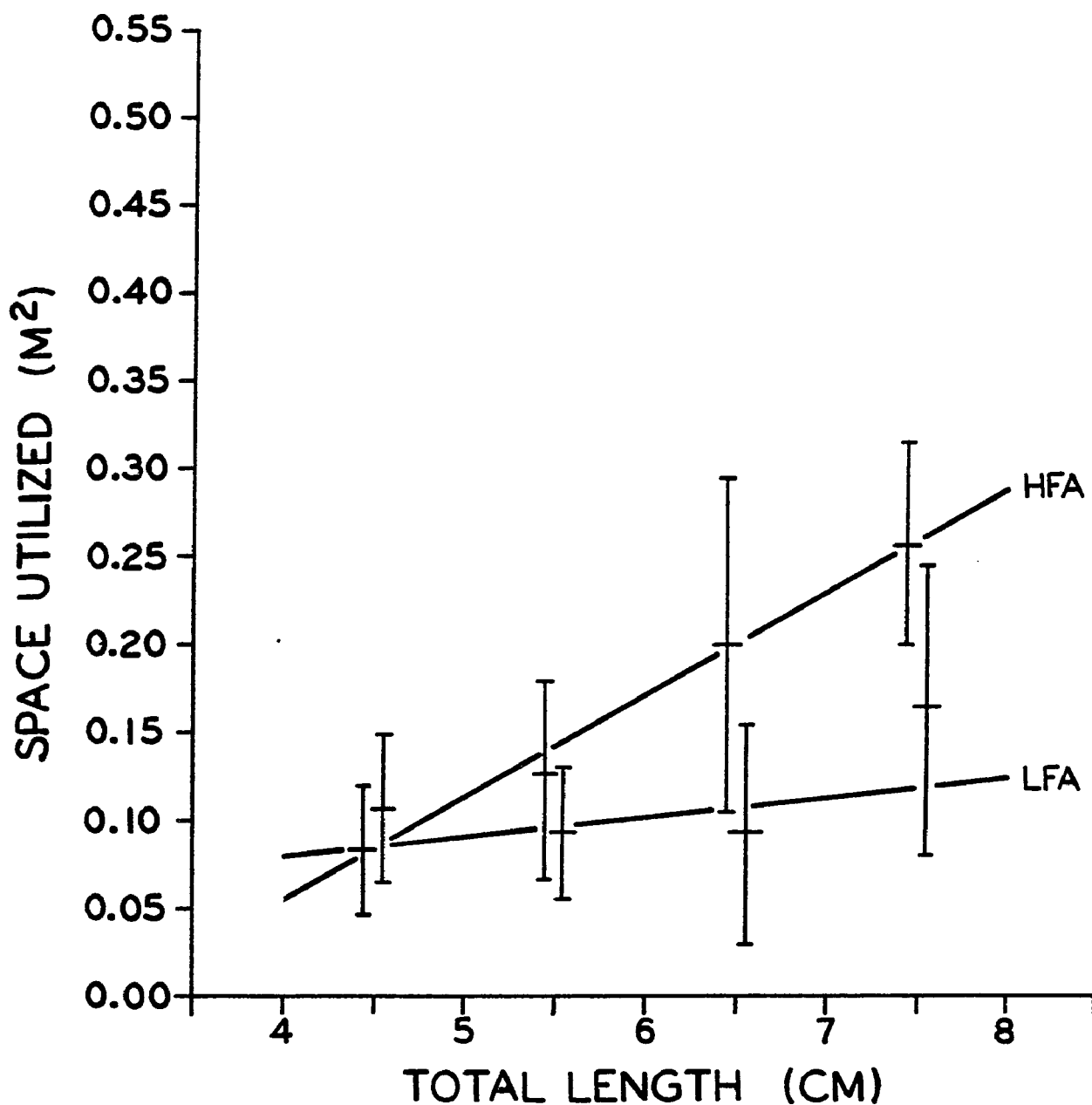


Figure 21. Comparison of linear regressions of space utilized on body size for laboratory colonies of *Hypsoblennius ionthas* males at a population density of 14.3 fish per square meter and under conditions of high (HFA) and low (LFA) food abundance. Vertical bars represent one standard deviation around the mean for each size category.

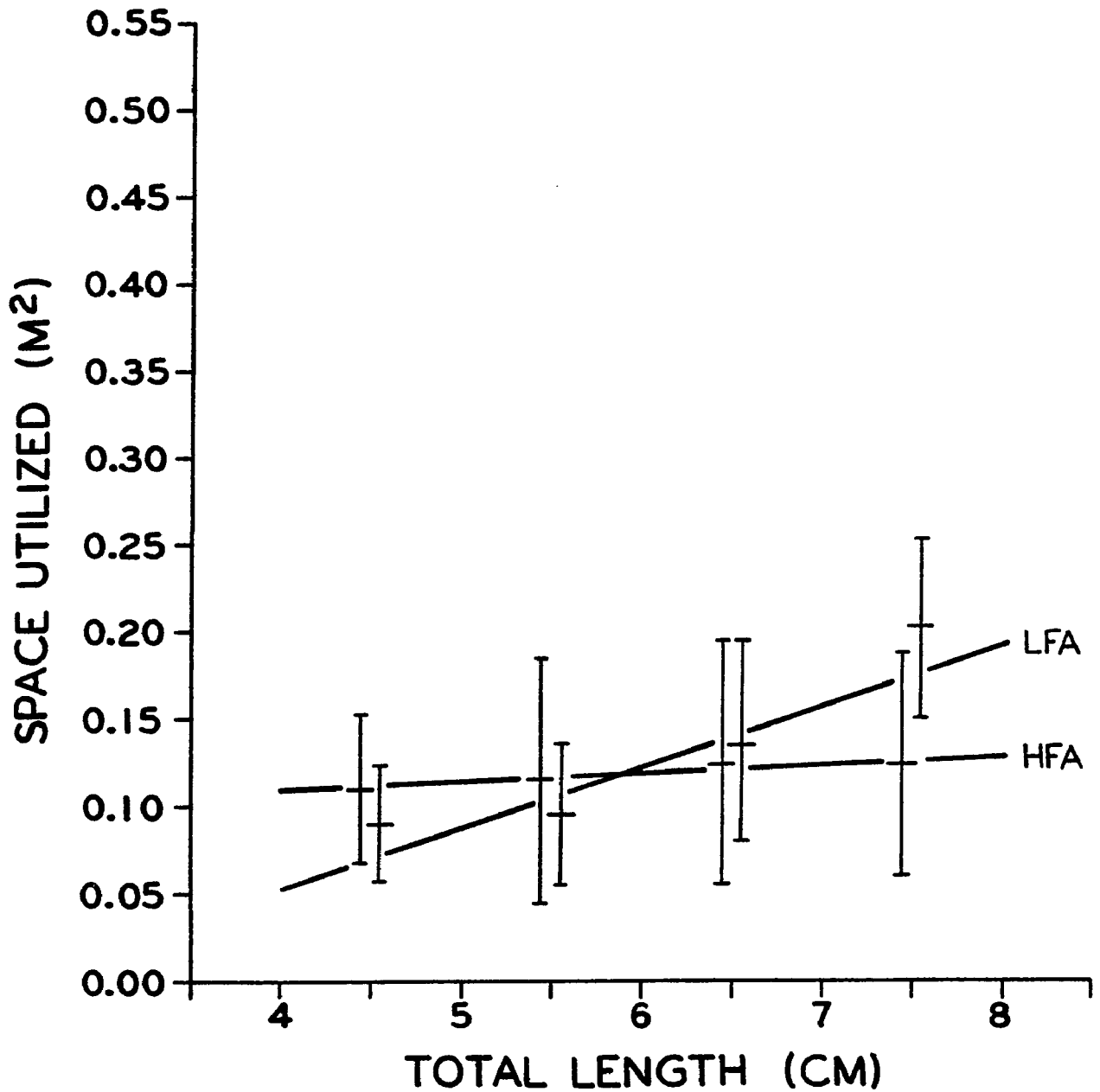


Figure 22. Comparison of linear regressions of space utilized on body size for laboratory colonies of *Hypsoblennius ionthas* at a population density of 21.4 fish per square meter and under conditions of high (HFA) and low (LFA) food abundance. Vertical bars represent one standard deviation around the mean for each size category.

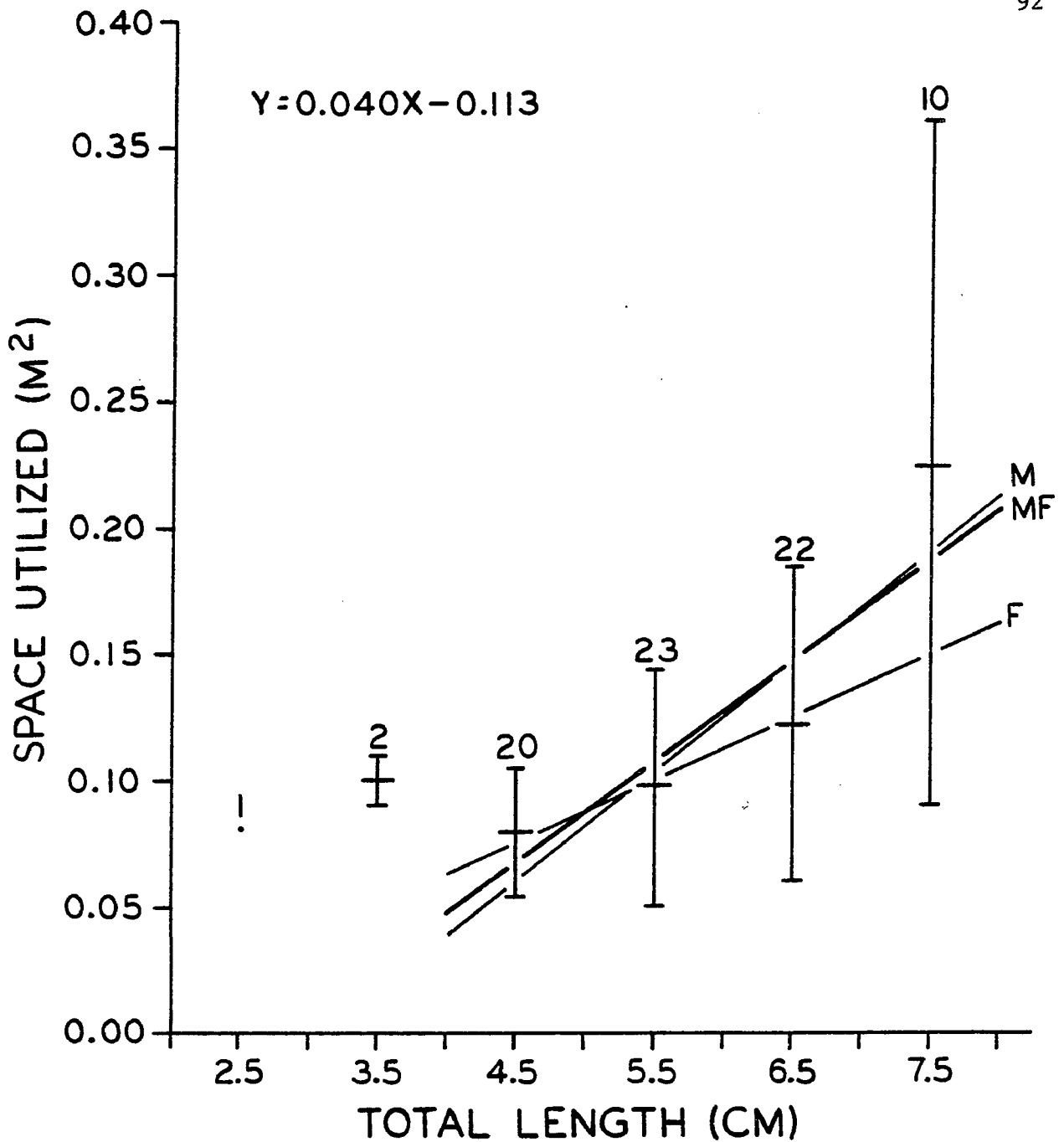


Figure 23. Linear regressions of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* in the absence of spawning activity. The colony, at a population density of 14.3 fish/sq. m, was fed *ad libidum*. Vertical bars represent one standard deviation around the mean for each size category. Separate regressions are shown for males (M), females (F), and pooled males and females (MF).

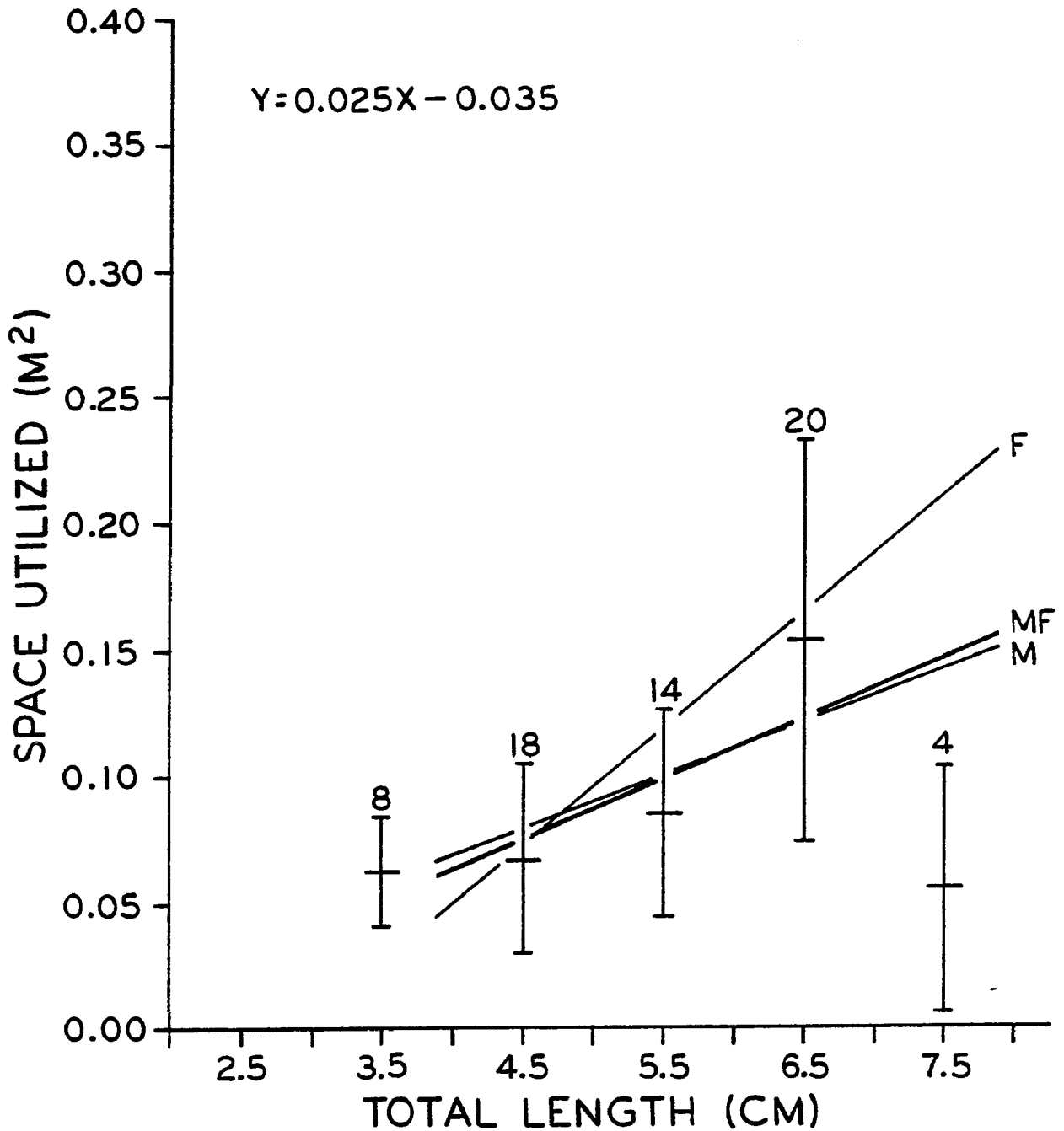


Figure 24. Linear regressions of space utilized on body size for a laboratory colony of *Hypsoblennius ionthas* during spawning activity. The colony, at a population density of 14.3 fish/sq. m, was fed *ad libidum*. Vertical bars represent one standard deviation around the mean for each size category. Separate regressions are shown for males (M), females (F), and pooled males and females (MF).

utilized on body size for males, females, and pooled males and females have positive slopes. As in the preceding experiments, larger blennies, both male and female, used more habitat surface area than smaller blennies.

In the non-spawning colony, larger males used considerably more space than females of any size (there were no 7 cm females). In the spawning colony, positions of the regression lines for each sex are inverted, with larger females utilizing appreciably more habitat surface area than males of any size category. The greatest change between experiments occurs in the 7 cm blennies. In the spawning colony, all 7 cm males and many 6 cm males were guarding eggs. Parental behavior severely limited their space utilization, since each male remained in or near the shell containing his clutch of developing eggs.

Effects of Social Dominance on Resource Utilization

In an earlier section on social structure, social dominance in *H. ionthas* was shown to be size-dependent, i.e., larger blennies were dominant over smaller blennies. It has also been established that larger blennies utilize more habitat surface area than smaller blennies, except under abnormally high population density and low food abundance conditions. To test whether the larger, dominant blennies were able to outcompete submissive blennies for food resources, condition factors (K) of fish held under different food abundances were regressed on body size.

In Figure 25, K is regressed on TL for field collected male blennies. The slope of the least squares regression line is not significant (slope = 0.002, $P > 0.75$). Although there is a great deal of scatter in the data, evidenced by large standard deviations around mean K values for each size category, it would appear that small blennies in the field

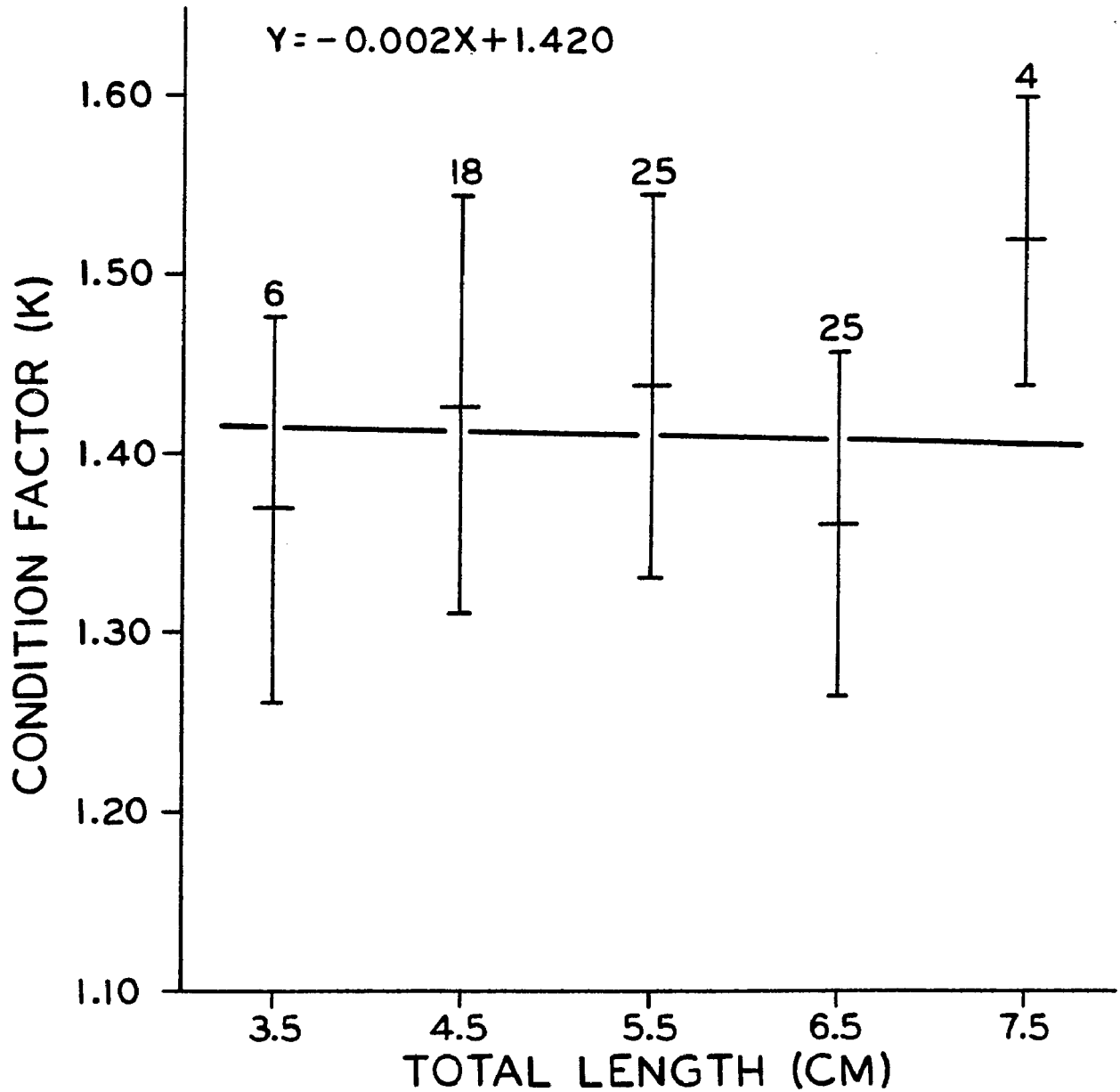


Figure 25. Linear regression of condition factor on body size for male *Hypsoblennius ionthas* field samples (N = 78). Condition factors were calculated immediately after capture. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

population are able to maintain their "fatness" at a level equal to larger, more dominant fish.

Condition factors were calculated for all blennies in the MPD-LFA experiment and regressed on TL (Figure 26). Under the conditions of artificially lowered food abundance, competition for the available food resource was severe. A positive, significant slope was found for the regression line obtained (slope = 0.045, $P < 0.001$). The results indicate that large, dominant blennies were better able to compete for the available food supply and thus maintain their "fatness" than were smaller, subordinate blennies. Again, there is a great deal of scatter in the data, perhaps indicating that there are degrees of dominant and submissive tendencies within and between size categories.

A regression of space utilized on K for the same MPD-LFA colony (Figure 27) shows a similar positive significant slope (0.274, $P < 0.005$). Dominant blennies which were better able to maintain their "fatness" also utilized greater amounts of habitat surface area.

In the MPD-HFA colony, blennies were fed *ad libidum*; therefore, competition for food was negligible. Condition factors were calculated for those blennies whose territories were measured (the remaining fish had been released). The regression of K on TL (Figure 28) has a negative, significant slope (-0.025 , $P < 0.025$), which indicates that during HFA conditions, low social status does not deter smaller blennies from maintaining "fatness". The negative slope obtained may reflect higher energy demands in territorial defense by larger blennies. Also, these data may be biased by the fact that K values were obtained primarily for the territory holders and that the majority of released blennies were probably subordinates.

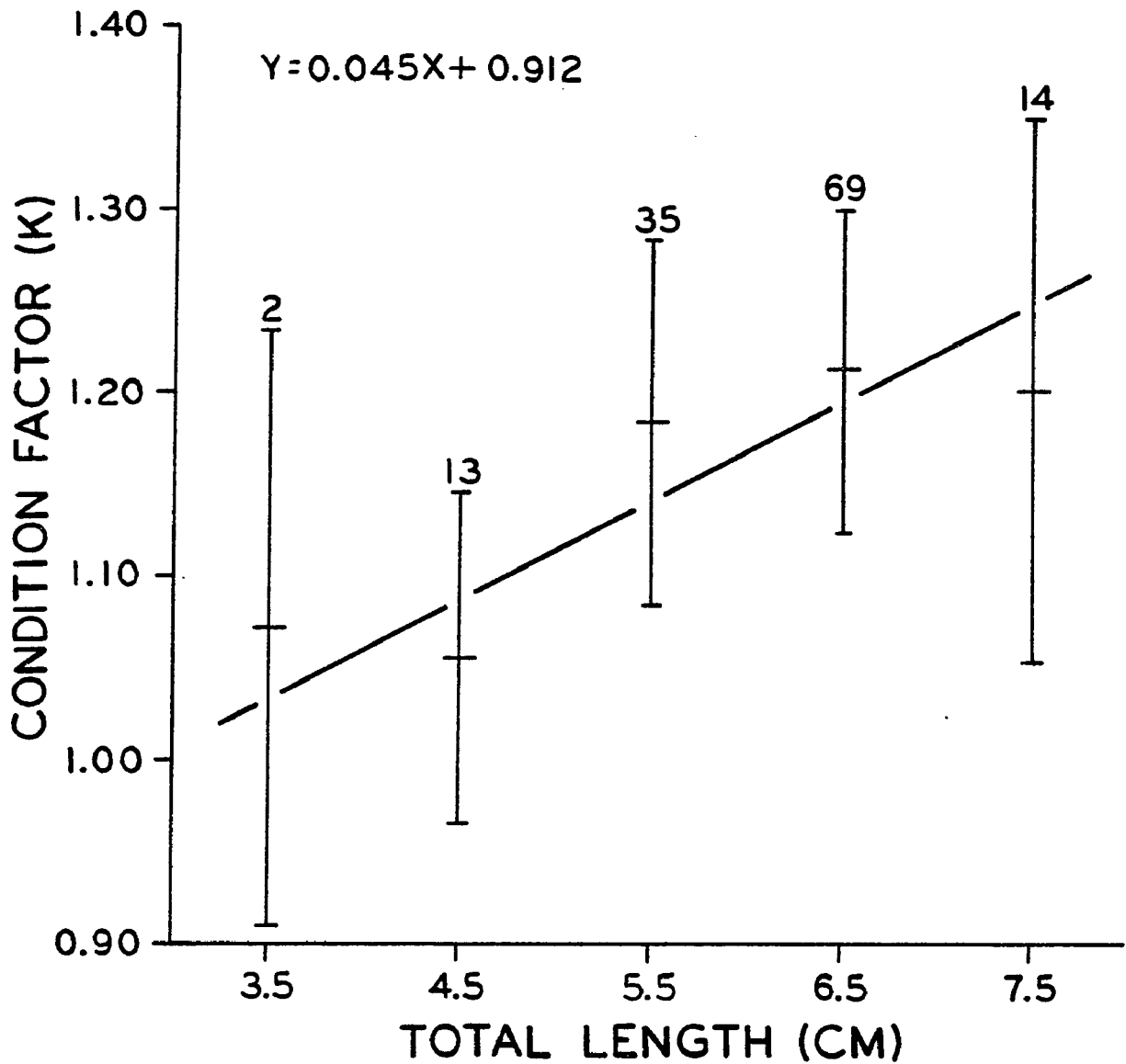


Figure 26. Linear regression of condition factor on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 14.3 fish per square meter and under low food abundance conditions. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

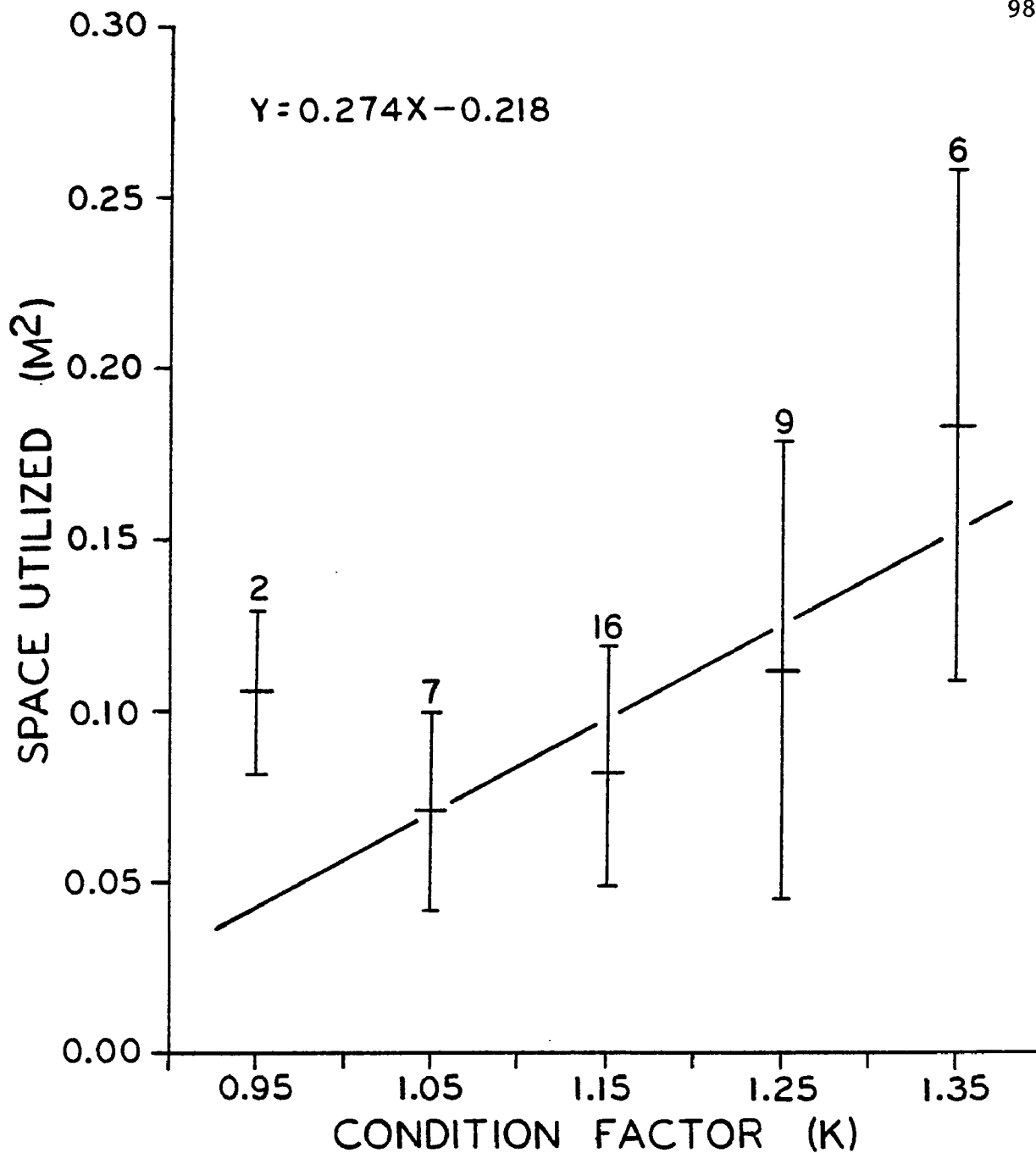


Figure 27. Linear regression of space utilized on condition factor for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 14.3 fish per square meter and under low food abundance conditions. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

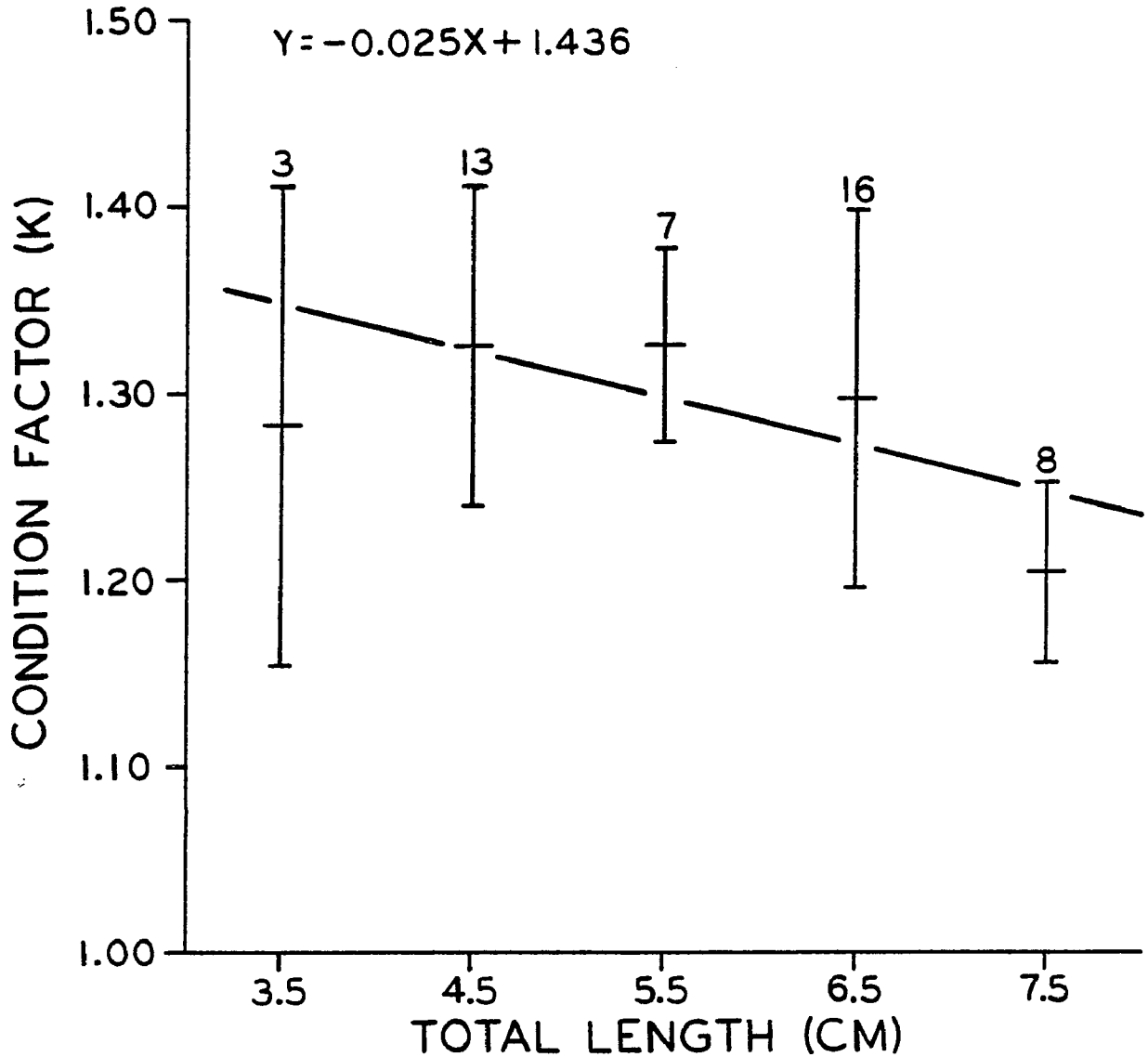


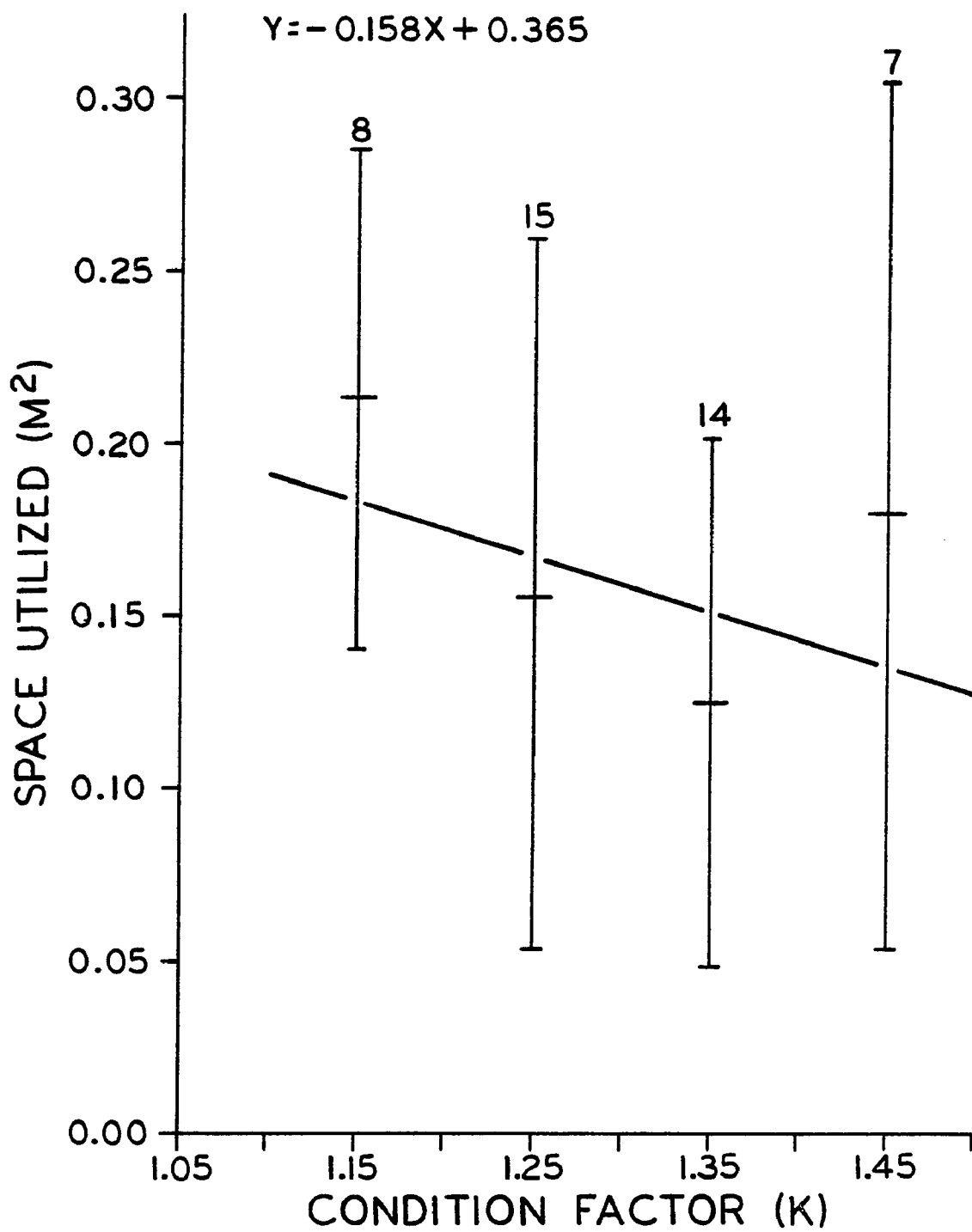
Figure 28. Linear regression of condition factor on body size for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 14.3 fish per square meter and under high food abundance conditions. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

Regression of space utilized on K for the MPD-HFA colony (Figure 29) produced a negative slope which was not significant (slope = -0.158 , $P > 0.5$), with very large standard deviations around the mean values of space utilized. The smaller blennies, although they had maintained slightly higher K values than larger fish while at HFA, still utilized generally smaller habitat surface areas.

As a check against the possibility that smaller blennies simply starved faster than larger blennies during the LFA experiment, a laboratory colony was held without addition of food for 19 days. Condition factors for these blennies regressed on TL (Figure 30) yielded a positive, significant slope (0.023 , $P < 0.001$). This would indicate that smaller blennies, possibly due to higher metabolic rates, did starve somewhat faster than larger blennies. The results are complicated, however, by the fact that cannibalism did occur within the colony. Although dead blennies were removed from the tank daily, 17 blennies remained unaccounted for when the experiment was terminated. The positive slope observed for the regression line could be explained if larger, dominant blennies were able to avoid starvation by means of cannibalism.

Comparison of the four K on TL regressions is illustrated in Figure 31. The experiments shown were performed at MPD, with the exception of the field population sample, which was assumed through observation to correspond fairly well with experimental MPD. Even at HFA, the blennies show some reduction in mean K values for each size category. This may have been caused by stress associated with adjustment to the tank environment. As expected, mean K values are further reduced in the LFA experiment and are lowest in the starved colony.

Figure 29. Linear regression of space utilized on condition factor for a laboratory colony of *Hypsoblennius ionthas* males at a population density of 14.3 fish per square meter and under high food abundance conditions. Vertical bars represent one standard deviation around the mean for each condition factor level. Sample size is given above each symbol.



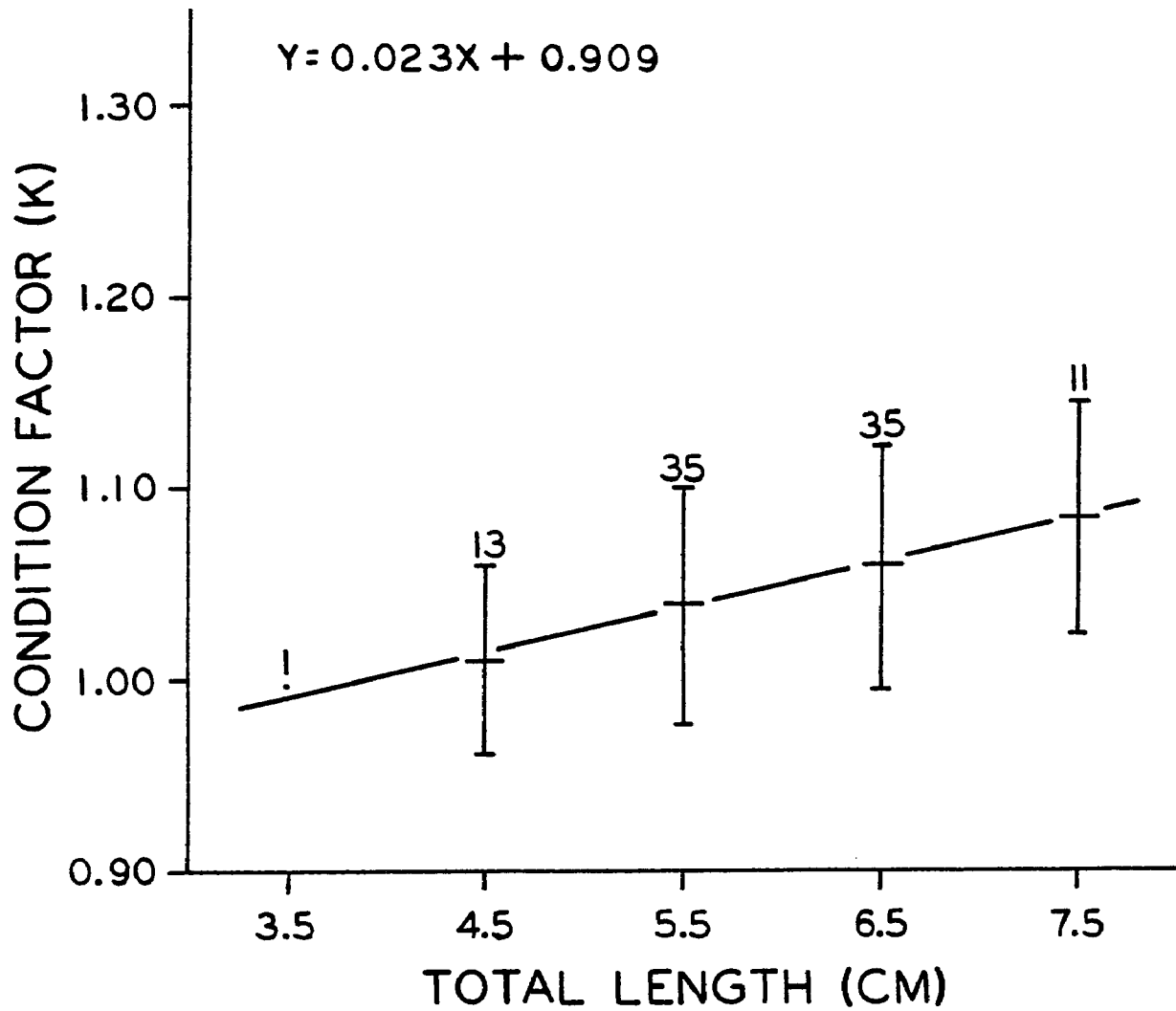
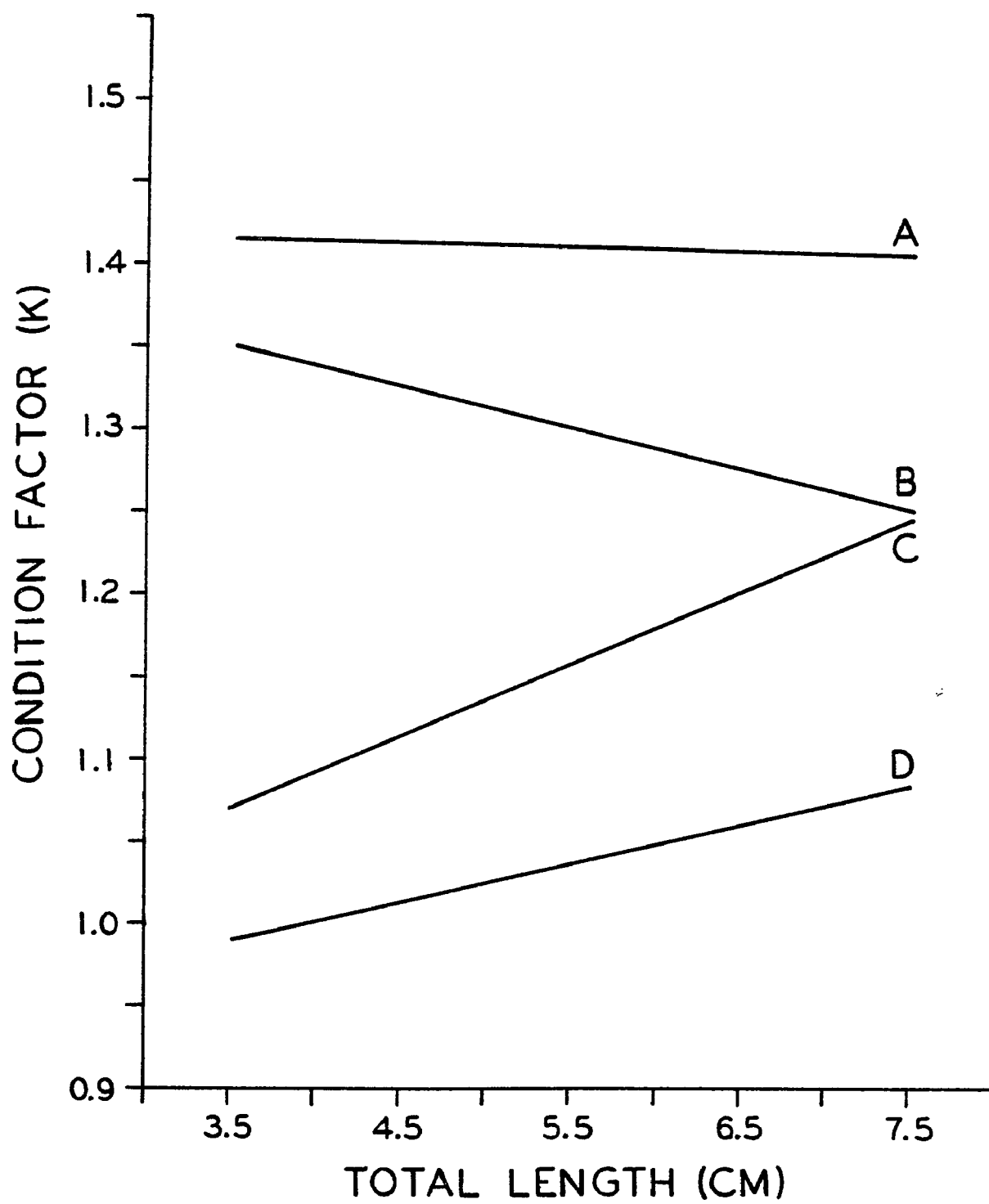


Figure 30. Linear regression of condition factor on body size for a laboratory colony of *Hypsoblennius ionthas* at a population density of 14.3 fish per square meter and held without the addition of food. Vertical bars represent one standard deviation around the mean for each size category. Sample size is given above each symbol.

Figure 31. Comparison of regression lines of condition factor on body size for *Hypsoblennius ionthas* males. Regression lines are illustrated for field samples (A), lab colony under high food abundance (B), lab colony under low food abundance (C), and lab colony held without addition of food (D). Laboratory colonies had a population density of 14.3 fish per square meter.



DISCUSSION

Life History Strategies

The adaptive significance of a specific life history strategy can be speculated upon with respect to concepts of r- and K-selection (MacArthur and Wilson, 1967). The term r refers to the intrinsic rate of population increase during the growth phase of an individual population, and is mathematically defined as the maximum reproduction potential of the population. K, on the other hand, refers to the carrying capacity of the environment, approximately equal to the upper density limit of the population capable of being stably supported by that environment.

Species exhibiting r-selected strategies are typically colonizers, i.e., those species appearing in unstable environments or early successional stages. In these environments resources are often sporadic or ephemeral in availability. Under these conditions, selection favors species with high reproductive potentials (high r) that are capable of rapidly utilizing available resources and producing large numbers of offspring to ensure survival of sufficient progeny until new resources become available. In contrast, species exhibiting K-selected strategies typically occur in more advanced successional stages, where conditions are more stable and the availability of resources more consistent. K-selected species are more efficient in their resource utilization, using the minimum amounts required to produce successful offspring.

Oyster reefs may be classified as a physically controlled environment, subject to wide, rapid fluctuations and extremes in temperature, salinity, turbidity, turbulence, and other physical parameters. Due to the physically controlled nature of the oyster reef, populations inhabiting this environment would tend to be r-selected.

If the life history strategies of *H. ionthas* are reviewed, we would, therefore, expect to find such predominantly r-strategies as early reproductive maturity, short life span, small body size (Pianka, 1970), rapid development (MacArthur and Wilson, 1967), low parental care (Hirston *et al.*, 1960), and large clutch size (Cody, 1966). Freckled blennies do indeed reach sexual maturity at an early growth stage. Females as small as 3.4 cm TL were collected with ovaries containing mature ova. Although attempts at age determination for *H. ionthas* were unsuccessful, it is expected, on the basis of growth rates noted for aquaria-held specimens, that a 3.5 cm TL freckled blenny is well under one year in age. Stephens *et al.* (1970) found variable growth rates and longevities among *H. gilberti*, *H. gentilis*, and *H. jenkinsi* on the Pacific coast, but blennies under 4 cm TL were generally one year or less in age. In fact, *H. gilberti* reached 7.5 cm TL in its first year, two years before its congeners. Longevities in these Pacific blennies ranged from 8 to 10 years for *H. gilberti*, to generally less than 4 years for *H. jenkinsi*. *H. ionthas* probably have a relatively short life span of 3 to 4 years. Blennies as a group are small in comparison with many other fishes, although some blennies such as *Blennius pholis* reach 16 cm TL or more (Qasim, 1957). Large body size beyond certain limits would be a distinct disadvantage for fishes associated with oyster reef habitats, as

maneuverability within the narrow confines of the reef would be limited and the number of suitable shelter sites small.

With respect to parental care and clutch size, *H. ionthas* diverges somewhat from the expected r-selected strategies. Spawned eggs are guarded by the males, which also aerate the eggs by caudal and pectoral fanning and remove dead or diseased eggs from the nest. Clutch size in *H. ionthas* is small. Shells of guarding males usually contain patches of eggs spawned at different times, as evidenced by their different stages of development. Females, although carrying up to several thousand mature ova, shed less than 500 eggs per spawning episode. Even though females are able to spawn a number of times during the breeding season, absolute fecundity of *H. ionthas* is relatively low. Counts of mature ova in large female *H. ionthas* approached 2,500, and counts for the Pacific species by Stephens *et al.* (1970) did not exceed 1,700.

Size characteristics of oyster shell refuges impose a physical limit on optimal maximum blenny size. In turn, maximum body size sets a limit upon absolute fecundity. Apparently, selective advantages associated with the r-strategy of large clutch size are outweighed by the selective disadvantage of being too large to effectively utilize available shelter. The degree of parental care shown by *H. ionthas* may be a compensatory mechanism for lower than optimal fecundity, in which survival of the offspring until hatching is maximized. Intimate association with the preferred oyster substrate may, therefore, be responsible for divergence from expected r-strategies.

Food Resource Utilization Patterns

Freckled blennies are opportunistic feeders, taking whatever items are most available. This is evidenced by the short term importance of seasonal items such as decapod megalops. Also, although *Amphithoe* occurs in stomachs throughout the year, its volumetric contribution peaks in the winter months, probably coinciding with dieoffs of adult *Amphithoe*. It would be misleading to say that *H. ionthas* is a specialist rather than a generalist regarding diet. Narrow trophic niche values calculated for *H. ionthas* may partly be attributed to low diversity of potential food items at the study site and not entirely due to specialization on algae-detritus.

Hypsoblennius ionthas is undoubtedly an important agent of energy flow through the study site oyster reef community. A significant amount of algae is cropped throughout the spring, summer, and fall months, although how much of this is assimilated by the blenny population is uncertain. Much of this algal material may be unused by the blennies and added to the detrital food chain. Freckled blennies are noteworthy predators of several invertebrate members of the oyster reef community, namely *Corophium louisianum*, *Hargaria rapax*, *Balanus eburnea*, *Nereis succinea*, and the xanthid crabs *Panopeus herbstii* and *Eurypanopeus depressus*.

A portion of the energy assimilated by the *H. ionthas* population is passed on to predators (discussed below). Much of the assimilated energy may be accumulated and tied up in maintenance of a high blenny standing crop. Mortality from causes other than predation would channel additional energy both into the detrital component of the oyster reef community and to scavengers such as crabs.

There appear to be no major trends in food resource utilization by *H. ionthas* with respect to body size or season. The same food items are eaten by blennies of all size and sex categories in roughly equal proportions, indicating that intraspecific competition for these food items is not intense.

Perhaps most importantly, results of the trophic studies demonstrate that the width of the trophic niche is not static, but dynamic on a seasonal basis. Therefore, studies which describe trophic niche parameters based on short term sampling schedules may represent only part of a larger pattern.

Space Resource Utilization Patterns

Territoriality

Territoriality is the most prominent manifestation of space utilization in *H. ionthas*. The role of territoriality in space utilization by fishes has been treated by previous workers with salmonids (e.g. Larkin, 1956; Newman, 1956; Chapman, 1966), centrarchids (e.g. Greenberg, 1947), pomacentrids (e.g. Clarke, 1970; Thresher, 1977), and blenniids (e.g. Phillips, 1971a, 1971b, 1974, 1977; Nursall, 1977). Thresher (1977) has proposed a scheme in which territoriality is a function of two motivational states, attack readiness and spatial commitment. Attack readiness, a measure of aggressiveness against intruders, is correlated with defendability of the protected resource. Efficiency of resource defense is determined by the amount of energy expended in defensive activities (i.e., aggression). Beyond a certain energy expenditure, defense of a resource becomes impractical. According to Thresher, spatial commitment is correlated with resource abundance. Required resources available in high concentrations demand

utilization of less space than widely dispersed, scarce resources. In this scheme, species with high spatial commitment and low attack readiness are typically holders of non-exclusive home ranges. In contrast, species with low spatial commitment and high attack readiness characteristically possess small but vigorously defended territories, often with well-developed dominance hierarchies. Thus, aggression, territoriality, and resource quality affect the ecology of species in an interrelated manner.

Although Thresher (1977) based his territoriality scheme on observations of pomacentrids, its application to other taxa is of value. Among Pacific *Hypsoblennius*, more aggressive species showed higher habitat specificity than less aggressive species, which occupied a variety of habitat types (Losey, 1968). Species exhibiting high aggressiveness (attack readiness) were found in habitats where intraspecific competition for shelter sites was intense. Freckled blennies clearly fit into the low spatial commitment, high attack readiness category. This implies that *H. ionthas* expends energy in defense of a highly concentrated, "easily" defendable resource, which unquestionably is space itself or shelter sites.

While the territory boundaries of an individual blenny may be relatively stable, at least for short periods, space within the territory is not uniformly utilized. Topography has an important effect upon the location of preferred areas. Phillips (1977) reported that *Chasmodes bosquianus* follows paths or "runs" between landmarks in its territory. Nursall (1977) observed similar behavior in redlip blennies, *Ophioblennius atlanticus*. As much as 80% of a redlip blenny's time is spent within 5% of its territory surface area. *Hypsoblennius ionthas* exhibits

similar patterns of movement. In contrast to some pomacentrids (Myrberg, 1972a, 1972b), freckled blennies observed in the field spend little time in actively patrolling their territorial boundaries. The majority of time is spent in head-exposed postures within the oyster shell refuges. Movements during extra-shelter activity occur repetitively along paths between oyster shells. Exposed areas are generally avoided. Likewise, most movement by blennies in laboratory colonies occurs between selected oyster shells. Territories are seldom regular in shape, boundaries being determined largely by the randomized layout of oyster shells in the vicinity of each shelter.

Population Regulation

Resources such as food, space, shelter sites, nest sites, and even the availability of mates exert some degree of influence on population size. Discerning the relative importance of each resource in population regulation is unavoidably difficult in view of their complex interrelationships. With respect to *H. ionthas* several points can be made. Individual blennies, at least over a short term, are sedentary. Therefore, all of their resources must be derived within the same limited area of the oyster reef habitat. As evidenced by the trophic studies, food material is available in abundance; hence, large territories are not required. Field and laboratory observations both indicate that all available habitat space is used. Very few gaping oyster shells are unoccupied, and those that do remain unoccupied are usually immediately adjacent to occupied shells. In the LPD laboratory colonies, blennies occasionally defended two and rarely three shelter sites. Instances of individuals holding multiple residences were much less frequent in the

MPD and HPD colonies. Since shelter sites of males also serve as nest sites, these are inseparable resources for *H. ionthas*. Breakdown of territorial tendencies on the part of ripe females ensures that availability of mates is not a limiting resource for freckled blennies. In the spawning laboratory colony, males were seen to spawn with as many as 4 different females in the course of several hours.

In a series of papers, Sale (1974, 1975, 1978) and Sale and Dybdahl (1975) have developed an hypothesis to account for the coexistence of guilds of pomacentrids having similar ecological requirements on coral reef habitats. The hypothesis, in brief, states that stochastic processes, namely generation of unused living space by predation and other causes of mortality, and larval settlement, form the basis for regulation of the guild populations. Observed features of the biology of *H. ionthas* suggest that similar mechanisms operate and are applicable on a single population basis. At any time nearly all suitable habitat space is utilized. As free space becomes available due to the death or migration of former residents, the space is soon occupied by expansion of neighboring territories, recruitment of blennies from other areas, or by settlement and establishment of juveniles.

Once an individual blenny has established a territory which contains sufficient sustaining resources, it would be advantageous for that individual to remain in the same location. In species exhibiting size-dominance hierarchies, as does *H. ionthas*, the longer a blenny maintains its territory, the less likely would be eviction by another blenny. With time the blenny's size advantage over newly settled blennies would steadily increase, while its size disadvantage with respect to older blennies would gradually decrease.

Predation and disease are sometimes considered to be significant factors in limiting fish population size (Chapman, 1966). There are apparently few natural predators on *H. ionthas*. One notable predator on freckled blennies is the gulf toadfish, *Opsanus beta*, which was observed to prey on *H. ionthas* on several occasions in the field. Gulf toadfish are cryptic predators which lie in hiding places until prey approach rather than stalking their prey. When present, snappers, *Lutjanus griseus* and *L. synagris*, probably capture blennies that stray from cover. As previously stated, blennies significantly reduce their activity whenever snappers are in the area. In contrast, blennies were observed to forage in the immediate vicinity of toadfish, which apparently were unnoticed. No other predatory fish were seen at the study site. During periods of low tide, however, snowy egrets (*Egretta thula*) often feed on *H. ionthas* in shallow areas along the seawalls. Total mortality to these few predators does not appear sufficient in itself to limit the local abundance of freckled blennies.

Disease may also act as an agent of mortality. McCosker (1969) and Stephens *et al.* (1970) reported high frequencies of lymphocystis (viral) infection in Pacific *Hypsoblennius* populations. The incidence of infection was correlated with heightened agonistic behavior between blennies during spring and summer months. Similar viral or other types of infection were not seen in *H. ionthas*.

Resource Utilization Patterns in the Laboratory Colonies

Results of the laboratory experiments revealed two major trends in space utilization. First, with increasing population density, surface areas used by individual blennies are reduced. At LPD, although larger

fish use much greater surface areas, the probability of encountering neighboring blennies is low. At MPD and HPD, time and energy spent in territorial defense are successively greater, and defenders seldom wander from the immediate area surrounding their shelters. Second, space utilization is greatly reduced under LFA conditions. This trend was highly unexpected. In territorial birds (Brown, 1964), iguanid lizards (Simon, 1975), and anurans (Wilbur, 1977), territories have been demonstrated to increase in size in response to decreased food availability. *Hypsoblennius ionthas* apparently uses a different strategy, speculated here to be a generalized response to stress in the form of an energy conservation mechanism. Reduced activity in the field during periods of wave turbulence, low ambient temperature, and predator presence may reflect manifestations of the same response. Hence, stress is minimized by remaining within the protection of shelter until favorable conditions return.

Existence of a size-dominance hierarchy, as demonstrated in the laboratory colonies, has definite implications on patterns of resource utilization (MacPhee, 1961). Chapman (1966) suggested that hierarchies develop where there is a direct intraspecific competition for food, whereas territories develop where spatial isolation prevents direct competition. Presumably, dominant blennies are more successful in acquiring and defending high quality territories. Most juvenile blennies, subordinate to and harassed by larger, established blennies, appear to be forced out of primary habitat into "fringe" areas. At the field sites in spring, juveniles first appear dispersed throughout the oyster substrate. As time passes, these small blennies become concentrated on

substrate just below the water surface, probably representing those juveniles unable to locate uncontested living space. Soon, they disappear from the oyster reef.

Establishment of territories within the laboratory colonies followed a particular pattern. Larger blennies (>6 cm TL) effectively divided all of the tank bottom area among themselves. At HPD the finite number of suitable shelter sites in the tank limited dispersion of larger blennies. Where two larger blennies were forced to reside in close proximity to one another, one of the pair always became dominant, usually after intense agonistic behavior. The subordinate member of the pair then either remained under cover or moved to a different area of the tank bottom. Several days after blennies were introduced to the tank, subordinates began to be forced out of the observational areas into the buffer zone along the base of the tank walls. Numbers of "excluded" subordinates gradually increased thereafter. Blennies in the 4 to 5 cm TL range set up territories, usually using smaller oyster shells or cover provided by overhanging projections of shell, within the territorial boundaries of one or more larger blennies. Thus, in *H. ionthas*, territories of approximately equal-sized fish are contiguous, whereas considerable overlap occurs between territories of blennies of unequal body size.

Losey (1968) recognized various degrees of territory sharing (two blennies of approximately equal size and dominance occupying refuges within the same territorial boundaries) and pseudo-territoriality (a subordinate blenny occupying a refuge within the territory of a large male) in Pacific *Hypsoblennius*. "Pseudo-territories" resemble "interstitial territories" described by Nursall (1977) for redlip blennies,

Ophioblennius atlanticus. This type of spacing system may be widespread among blenniids and offers an interesting comparison with that of pomacentrids, which typically defend contiguous, nonoverlapping boundaries against conspecifics (Clarke, 1971; Itzkowitz, 1977). As pointed out by Losey (1968), both territory sharing and pseudo-territoriality ensure efficient utilization of the available space resource. Nursall (1977) believed that interstitial territories were precursors of later full-fledged territories, expanded as surrounding area became vacant or dominance relations changed. Territory sharing does not occur in *H. ionthas*, at least in the laboratory colonies, whereas pseudo-territories or interstitial territories are common. Dominance hierarchies may be essential in this type of spacing system. Subordinate blennies are allowed to infringe upon territories of dominant blennies, but are subject to periodic harassment. In effect, the dominants retain control over resource utilization by the subordinates. Spacing systems which permit overlap obviously allow maintenance of a higher population density than contiguous spacing systems. Overlap in space utilization would be less likely to occur in habitats where food abundance is limiting.

Although the feeding regime for the laboratory colonies was highly artificial, the experimental results indicated that at LPD larger blennies were capable of outcompeting smaller blennies for space, but had no advantage in competition for food. At MPD and HPD, however, the situation is reversed as larger blennies lost their competitive advantage for space, but gained an advantage in competition for food. Magnuson (1962) observed that medaka, *Oryzias latipes*, developed size-

dominant hierarchies only when food was in short supply. Dominant medaka within the established hierarchies had higher growth rates than subordinates. At higher population densities, however, the growth advantage of large medaka was reduced.

At HPD, the spacing system in the laboratory colonies was overloaded. Competitive advantage for space conferred by large body size was reduced under pressure of increased numbers of neighboring blennies. Intercepts of the regression lines for the HPD experiments approached 0.1 square meter, which may represent a minimum amount of space required by individual blennies even when food is abundant.

Interspecific Competition

Similar ecological requirements of fishes composing the oyster reef assemblage may predispose *H. ionthas* to interspecific competition for food and space. Generally low diversity of potential food items at the study site may be responsible for the similarities in occurrence of food items in the diets of freckled blennies, frillfin gobies, naked gobies, and skilletfish. Calculated values of trophic niche overlap among these species, however, were typically low. Differences in proportionate contributions of food items between species apparently minimizes competition for food within the assemblage. Highest overlap occurred between freckled blennies and frillfin gobies, the former a permanent oyster reef resident, the latter a seasonal migrant. Lowest overlap occurred between the only year-round residents, freckled blennies and skilletfish. Striped blennies, the oyster reef associate of closest taxonomic relationship to *H. ionthas*, specialized on an unidentified food item not seen in any of the other oyster reef associates.

It would appear that competition for food is not intense among oyster reef fishes. However, since all of the associated species have been collected in reproductively ripe condition at the study site, and all are known to use shells as breeding sites, competition for shelters may indeed be important. In both laboratory and field situations, *H. ionthas* has been observed to interact agonistically with *B. soporator* and *C. bosquianus*. Interspecific agonistic encounters most frequently involved larger fish of nearly equal body size. Even when *G. bosci* were present in considerable numbers, *H. ionthas* appeared to be indifferent to their presence. On the basis of comparative body size and weight, *G. bosci* are smaller and pose little threat of spatial displacement to the much more aggressive *H. ionthas*. On the other hand, both *B. soporator* and *C. bosquianus* attain equal or larger body size than *H. ionthas*. Interspecific aggression in fishes has been found to be correlated with such factors as threat to food supply (Low, 1971), threat to eggs (Ebersole, 1977), similarity in use of space (Moran and Sale, 1977), and taxonomic affinity (Myrberg and Thresher, 1974). Evidence is strongest that interspecific aggression noted in *H. ionthas* is in response to potential space and shelter competitors. The majority of *C. bosquianus* at the study site inhabited the fringe area of oyster substrate along the base of the seawalls. Whether this represents an example of depth preference, microhabitat preference, or inability to compete with *H. ionthas* higher in the littoral zone is not clear.

Skilletfish, *Gobiesox strumosus* often occupy gaping oyster shells within the territorial boundaries of larger *H. ionthas*. In fact, male skilletfish and freckled blennies were observed guarding eggs in immediately adjacent shelters on a number of occasions, yet agonistic

behavior between these species was never witnessed. Some behavioral or ecological compensatory mechanism may allow space sharing by these species. Extreme dorso-ventral body compression in *G. strumosus* may enable it to utilize oyster shells with a narrower gape than those used by *H. ionthas*, thereby minimizing direct competition for shelter sites. A similar situation has been reported by Stephens, et al. (1970) between *H. jenkinsi* and *Neoclinus stephensae*. Here competition was avoided by preferences for pholadid clam burrows of different shapes corresponding to differences in body morphology of the fishes.

It is evident that for *H. ionthas*, interspecific competition for space and shelter sites is much more important than competition for food.

SUMMARY

Freckled blennies, *Hypsoblennius ionthas*, are abundant residents of oyster reef habitats in the northern Gulf of Mexico. Both sexes maintain territories around gaping oyster shell refuges. Territories of males are permanent, whereas those of females may be abandoned during the breeding season. Males fertilize and guard eggs deposited within their refuges by females until hatching.

Spawning season is protracted in *H. ionthas*, which ensures larval settlement on oyster substrate during much of the year. In this manner larvae are more apt to locate unoccupied substrate generated by the death or movement of former residents. Juveniles must compete among themselves and against larger, established blennies for available living space.

A definite size-dominance hierarchy exists, with a less distinct trend for male domination over females. The hierarchical social structure allows subordinates to hold pseudo-territories within the territorial boundaries of dominants. In this way all available space is more efficiently utilized. Larval settlement, expansion of pseudo-territories, and spatial encroachment by neighboring blennies ensures rapid reoccupation of vacant space. Availability of shelter sites appears to be a critical resource which sets a limit to the maximal or optimal population density of *H. ionthas*.

Freckled blennies are opportunistic feeders. By volume, their diet consists mainly of algae-detritus, yet considerable numbers of common oyster reef invertebrates are also eaten. As such, freckled blennies are important consumers in the oyster reef community. The available food resource is abundant, however, and there appears to be little intra- or interspecific competition for food.

Trophic niche breadth for *H. ionthas* shows a pattern of seasonal variation, being wider in the winter months and narrower in the summer months. Trophic niche overlap with other oyster reef fish species is low. Although the different fish species have a limited number of available food items, they select each item in different proportions.

Laboratory studies reveal several patterns of resource utilization in *H. ionthas*. As population density decreases, individual blennies use significantly greater amounts of habitat surface area. At low population density, large, socially dominant blennies utilize greater amounts of habitat space than smaller, subordinate blennies. At higher population density, size advantage in space utilization is lost, probably due to greater energy demands for territorial defense.

As food abundance decreases, individual blennies use significantly less habitat surface area. This phenomenon has not been demonstrated in other taxa. Results indicate that under stress, freckled blennies retreat to the protection of their shelters to await the return of more favorable conditions. At mid-population density, large, dominant blennies in laboratory colonies are able to outcompete subordinates for a rationed amount of food.

During the spawning season, space utilization by large males is reduced as a consequence of egg-guarding activities. At the same time, females increase their space utilization, thereby ensuring availability of mates. After cessation of spawning, males tend to utilize greater amounts of habitat surface area than equal-sized females.

Hence, space utilization in *H. ionthas* has been demonstrated to be influenced by population density, food abundance, sexual behavior, and social dominance. Territory size in this species has been shown to be largely a function of body size. The spacing pattern of territories on oyster reef substrate determines the population density level in each locality inhabited by *H. ionthas*, while rapid reoccupation of vacated space serves to maintain a stable population size.

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APPENDIX 1

Statistical Analyses

Analyses of Variance for Individual Regression Lines

Experiment 3. Regression of space utilized on total length.
Conditions: 7.1 fish/sq. m, high food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.327	0.327	43.29
Deviation from Regression	44	0.333	0.008	
Total	45	0.660		

P<0.001

Experiment 2. Regression of space utilized on total length.
Conditions: 14.3 fish/sq. m, high food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.229	0.229	56.06
Deviation from Regression	56	0.229	0.004	
Total	57	0.458		

P<0.001

Experiment 6. Regression of space utilized on total length.
Conditions: 21.4 fish/sq. m, high food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.002	0.002	0.43
Deviation from Regression	88	0.384	0.004	
Total	89	0.386		

P>0.5 NS

Experiment 5. Regression of space utilized on total length.
Conditions: 7.1 fish/sq. m, low food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.040	0.040	5.34
Deviation from Regression	53	0.399	0.008	
Total	54	0.439		

P<0.025

Experiment 7. Regression of space utilized on total length.
Conditions: 14.3 fish/sq. m, low food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.006	0.006	1.80
Deviation from Regression	75	0.264	0.004	
Total	76	0.270		

P>0.184 NS

Experiment 4. Regression of space utilized on total length.
Conditions: 21.4 fish/sq. m, low food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.057	0.057	24.35
Deviation from Regression	59	0.139	0.002	
Total	60	0.196		

P<0.001

Experiment 1. Regression of space utilized on total length.
Conditions: 14.3 fish/sq. m, spawning, high food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.057	0.057	11.68
Deviation from Regression	66	0.323	0.005	
Total	67	0.380		

P<0.005

Experiment 8. Regression of space utilized on total length.
Conditions: 14.3 fish/sq. m, non-spawning, high food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.118	0.118	25.40
Deviation from Regression	73	0.338	0.005	
Total	74	0.456		

P<0.001

Experiment 7. Regression of space utilized on condition factor.
Conditions: 14.3 fish/sq. m, low food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.034	0.034	12.13
Deviation from Regression	38	0.107	0.003	
Total	39	0.141		

P<0.005

Experiment 7. Regression of condition factor on total length.
Conditions: 14.3 fish/sq. m, low food abundance.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.197	0.197	18.77
Deviation from Regression	131	1.377	0.011	
Total	132	1.574		

P<0.001

Field Samples. Regression of condition factor on total length.

Source of Variation	DF	SS	MS	F
Attributable to Regression	1	0.000	0.000	0.03
Deviation from Regression	76	0.956	0.013	
Total	77	0.956		

P>0.75 NS

Analyses of Variance for Comparisons Between Regression Lines

Comparison of regression lines for experiments at low food abundance and at three population densities (7.1, 14.3, and 21.4 fish/sq. m).

Source of Variation	DF	SS	MS	F
Between Groups	4	0.137	0.034	7.97
Within Groups	187	0.802	0.004	
Total	191	0.939		

P<0.01

Comparison of regression lines for experiments at high food abundance and at three population densities (7.1, 14.3, and 21.4 fish/sq. m).

Source of Variation	DF	SS	MS	F
Between Groups	4	0.766	0.192	38.06
Within Groups	188	0.946	0.005	
Total	192	1.712		

P<0.001

Comparison of regression lines for experiments at low food abundance and at population densities of 14.3 and 21.4 fish/sq. m.

Source of Variation	DF	SS	MS	F
Between Groups	2	0.034	0.017	5.63
Within Groups	134	0.403	0.003	
Total	136	0.437		

P<0.01

Comparison of regression lines for experiments at a population density of 7.1 fish/sq. m and at high and low food abundance.

Source of Variation	DF	SS	MS	F
Between Groups	2	0.255	0.128	16.90
Within Groups	97	0.732	0.008	
Total	99	0.987		

P<0.001

Comparison of regression lines for experiments at a population density of 14.3 fish/sq. m and at high and low food abundance.

Source of Variation	DF	SS	MS	F
Between Groups	2	0.191	0.095	23.35
Within Groups	131	0.493	0.004	
Total	133	0.684		

P<0.001

Comparison of regression lines for experiments at a population density of 21.4 fish/sq. m and at high and low food abundance.

Source of Variation	DF	SS	MS	F
Between Groups	2	0.026	0.013	3.66
Within Groups	147	0.523	0.004	
Total	149	0.549		

P<0.05

APPENDIX 2

Surface salinities measured at the times of field collections.

Year	Date	Salinity (PPT)	
1976	15 March	8	
	28 September	22	
	26 October	24	
	27 November	21	
1977	28 April	3	
	18 May	14	
	10 June	19	
	5 July	24	
	25 July	25	
	18 August	24	
	8 September	24	
	25 September	16	
	27 September	22	
	4 October	16	
	6 October	16	
	8 October	22	
	10 October	19	
	15 October	9	
	18 October	(0800 hrs)	21
		(1100 hrs)	14
		(1400 hrs)	13
	(1700 hrs)	14	
	3 November	14	
	17 November	6	
	23 November	8	
	14 December	6	
1978	30 January	2	
	20 February	7	
	23 March	2	
	8 April	10	

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