Activity, Shelter Usage, Growth and Recruitment of Juvenile Red Hake *Urophycis chuss*

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ABSTRACT: Juvenile red hake *Urophycis chuss* (Walbaum) live in symbiotic association with sea scallops *Placopecten magellanicus,* immediately following the hake's descent from the planktonic post-larval stage to the benthos. Feeding behavior, activity rhythms, shelter preference and growth of juvenile fish were observed in the laboratory. Monthly field collections of juvenile red hake were used to study daily rhythms of shelter usage, size relationships between hake and scallops, recruitment patterns of hake from the plankton to the benthos, and growth rates. In the laboratory, hake activity, which included swimming and agonistic encounters, was predominantly nocturnal. Hake, ranging in size from 23 to 116 mm (TL), inhabited scallop shelters more often by day than by night in the field. Mean size of hake inhabiting scallops increased with larger scallops. Small scallops (< 100 mm) contained predominantly small hake (25–65 mm), but large scallops (> 120 mm) contained a wide size range of juvenile hake (26–116 mm). In shelter preference tests, juvenile hake chose non-living shelters over living scallops. Recruitment of hake from the plankton to the benthos lasted from September to December. Recruits in September ranged from 23 to 30 mm, while recruits in November were as large as 46 mm. Rates of recruitment were highest during October to November. Most hake emigrated from the scallop bed by February, at sizes of approximately 90 to 100 mm (TL), but a few individuals remained until May. Growth rates (length) of juvenile hake in the laboratory averaged from 0.61 % d^{-1} to 1.00 % d^{-1}, increasing with increasing average daily temperature. Growth (length) in the field during November to December was 0.93 % d^{-1}. Results suggest that shelter is an important resource for juvenile red hake. Variable growth rates and a prolonged recruitment period of hake to the benthos may result in overlap in size between different year classes of red hake. The abundance of juvenile red hake may be a better predictor of future year-class strength than planktonic eggs and larvae.

INTRODUCTION

There are certain stages in the life history of marine fishes that are considered critical in large measure due to their increased vulnerability to environmental pressures. The environmental factors which exert strong pressures are commonly identified in principle, for example, predation, food resources, temperature stress, but the precise interactions of any of these factors and the animal's response to them are often obscure. For benthic species which have planktonic eggs and larvae, the early juvenile stage immediately following descent to the bottom is one of these critical stages. Habitat requirements for newly descended juveniles change markedly, necessitating a wide range of behavioral and ecological adaptations. Definition of the precise role that various factors may play in these adaptations will lead directly to a better understanding of the habitat requirements of a species, necessary for the development of any rational resource management scheme.

Our aim in this study was to examine various aspects of the behavior of early benthic juvenile red hake *Urophycis chuss* (Walbaum) recently descended from the plankton, in relation to selected environmental factors. Whether an organism responds under natural conditions as it does in the laboratory ultimately can only be answered by verification under natural conditions. We, therefore, endeavored to compare and verify laboratory findings with measurements made from monthly field collections.

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The red hake, one of three *Urophycis* spp. common to the western North Atlantic Ocean, is found on the continental shelf from southern Nova Scotia to North Carolina (Musick, 1974). Spawnings take place from April to October (Musick, 1969; Wilk and Morse, 1979). Eggs and larvae are planktonic for approximately 1–2 mo until the larvae reach a size of 23 to 49 mm, at which time they descend to the bottom and remain benthic throughout the rest of their lives (Musick, 1969). Following their descent from the plankton, juvenile hake are commonly found within the mantle cavities of sea scallops *Placopecten magellanicus* (Gmelin) (Goode, 1884; Musick, 1969). They appear to maintain this association until reaching a maximum size of 136 mm (Musick, 1969).

In this work we have examined under laboratory conditions: (1) feeding behavior; (2) daily rhythms of activity and agonistic encounters; (3) shelter selectivity and usage; and (4) growth rates; under field conditions: (1) differences in the number of fish found in scallops between day and night; (2) size relationships between hake and their scallop hosts; (3) recruitment patterns from plankton to scallops; and (4) growth rates.

MATERIALS AND METHODS

Field Collections

A monthly sampling program of juvenile *Urophycis chuss* associated with *Placopecten magellanicus* was conducted from June 1980 to May 1981. The scallop bed was designated Location 1: 40°15′N, 73°50′W (30 m depth). Once a month, and on two occasions twice a month, a sample of at least 100 scallops greater than 80 mm in length was taken from the bed with a 1.21 m scallop dredge aboard the NOAA/NMFS vessel RV 'Kyma'. (One sample, 23 September, contained only 75 scallops greater than 80 mm). The sampling gear rarely captured scallops less than 80 mm. All tows were conducted between 1100 and 1400 h.

Once aboard ship, the scallops were immediately divided into 3 size categories: less than 100 mm, 100–120 mm, and greater than 120 mm, and placed in separate coolers with ambient sea water and returned to the laboratory. The juvenile red hake that had been trapped inside the scallops emerged, were collected and measured for total length (TL), and then placed in aquaria for observation and experimentation. In the majority of instances, it was not possible to determine the exact scallop with which an individual hake had been associated. Occasionally, a hake was found still within a scallop, and the sizes of both hake and scallops were noted. A ratio of the number of hake to the

number of scallops (H/S) was calculated to estimate the relative numbers of hake present in the scallop bed.

A second, continuous 24-h sampling program was conducted from 12 to 17 January 1981 aboard a commercial fishing vessel. Hourly (or bi-hourly) samples of 10 randomly selected scallops greater than 80 mm were taken from the boat's commercial catch. The boat fished continuously, day and night, and samples were taken from catches immediately after retrieval of the dredges. Each scallop was measured, then cut open and examined for the presence of entrapped juvenile red hake. All fish collected were measured (TL) and preserved. The sampling was conducted at Location 2: 40°08′N, 73°44′W (34 m depth); and Location 3: 40°08′N, 73°35′W (38 m depth).

Laboratory Observations

We observed and measured the behavior and growth of 3 separate groups of juvenile red hake held in the laboratory in association with sea scallops. All observations were made in an 1.5-kl aquarium, $2.48 \times 0.88 \times 0.96$ m, with a single viewing window, 2.29×0.81 m. The bottom was covered with a 5-cm thick layer of sand. Sea water was delivered via a network of pipes underneath the sand bottom and continuously circulated through a separate gravel, sand and oyster shell filter and recycled to the tank. The aquarium was surrounded by blinds and recessed into a small room to reduce both visual and acoustic interferences. Light intensity, as measured at the surface, was 5×10^3 lux in daytime and 2.5 lux at night and photoperiod was adjusted weekly to simulate the natural cycle.

All fish were fed live sand shrimp *Crangon septemspinosa* and diced muscle of the clam *Spisula solidissima*. The sand shrimp are an important part of the hake's natural diet (Langton and Bowman, 1980), while clam is also readily accepted by the chemically sensitive hake (Pearson et al., 1980). The sand shrimp were introduced to the tank in quantities of greater than 200 per introduction, at least once a week, except in times of low shrimp availability. Between introductions the fish fed on the shrimp *ad libitum*. During times of shrimp shortage, diced clam was introduced to the tank.

The fish were monitored for 20 min each hour over a 24-h cycle with a video tape recording system (Panasonic NV-8030 recorder unit, Sony Video Camera and RCA TC1030/H night camera). Video observations were made over periods of 3 to 9 d. Video tapes were reviewed to determine levels of activity and shelter usage. We obtained an activity score by counting the

total number of times any fish passed either of two points 1.24 m apart, within the 20-min observation period. Such a measure reflected several types of activity: foraging, prey capture, and agonistic encounters. We also counted the number of agonistic encounters between the juvenile red hake during each 20-min observation period.

Group 1

Group 1 consisted of fish which were of the same size range as fish commonly found inhabiting scallops. Initially, 8 hake (60–110 mm TL) and 14 scallops (80–140 mm length) were introduced into the tank on 5 February 1980. The scallop density was based on the field density estimates derived by Caddy (1970). We intended to introduce only 7 fish, but later realized that 1 of the scallops contained an additional fish that had not yet emerged at the time of introduction into the tank. On 2 March, 7 additional fish (62–125 mm TL) were introduced into the tank along with 14 scallops (80–140 mm) to provide additional shelters. On 8 May 1980, all 15 fish were removed and measured.

Temperature ranged from 7.1 to 11.7 °C, gradually increasing throughout the study. Relative rates of change in laboratory temperatures mirrored that of the field, but absolute temperatures were, on the average, 4.0 C° higher than the field. Salinity ranged from 22.7 to 25.0 ‰ S; pH, from 7.2 to 7.9; dissolved oxygen, from 6.5 to 7.7 mg l^{-1}.

Group 2

Juvenile red hake in Group 2 were of the same size range as fish which have recently emigrated from scallop beds. Seven fish (89–140 mm TL) and 14 scallops (> 120 mm) were introduced into the tank on 13 May 1980, and observed through 30 June 1980. Temperature ranged from 10.1 to 13.1 °C, averaging 0.8 C° colder than field temperatures; salinity ranged from 22.7 to 25.0 ‰ S; pH was 7.2; dissolved oxygen ranged from 6.5 to 6.7 mg l^{-1}.

Group 3

Fish in Group 3, as in Group 1, were of the same size range as fish commonly inhabiting scallops. Seven fish (50–93 mm) were introduced into the tank on 30 December 1980, along with 15 scallops (> 120 mm) for shelter. Initial temperature was 7.4 °C; it dropped to as low as 4.9 °C on 3 February, and rose to 7.7 °C by 9 April 1981. Rates of change in laboratory temperatures

reflected field conditions, but absolute temperatures averaged 1.8 C° higher than field temperatures. Salinity ranged from 22.4 to 27.5 ‰ S; pH, from 7.8 to 8.0; dissolved oxygen, from 7.0 to 7.5 mg l^{-1}. Each individual fish was remeasured after 16 d (15 January 1981) and every 21 d thereafter until 9 April 1981, the final day of the experiment.

Growth

Growth rates, in length, were calculated using the formula $G_L = 100 (1n L_2 - 1n L_1)/(t_2 - t_1)$ and expressed as percent growth d^{-1}, where L_1 and L_2 equal total lengths at time t_1 and t_2, respectively (Ricker, 1975).

We estimated an average growth rate for juvenile hake in the field using mean lengths of selected monthly samples for L_1 and L_2. An average growth rate was also calculated for Group 1 fish in the laboratory using mean initial and final lengths for L_1 and L_2 since we did not have a simultaneous initial length for all 15 fish, and hence, could not measure the exact amount of growth for each individual fish during the experiment. (The original 8 fish were not remeasured when the additional 7 fish were introduced to the tank). In Groups 2 and 3 growth rates were calculated for each individual fish and a mean calculated for each group.

Shelter Preference Experiments

Two shelter preference experiments were performed in three 264-l aquaria (1.21 × 0.53 × 0.50 m) with a 5-cm thick sand bottom and a continuous flow-through seawater system. Temperatures ranged from 6.2 to 7.2 °C. Salinity was 26.0 ‰ S; dissolved oxygen, 7.0 mg l^{-1}; pH ranged from 7.6 to 7.8. Fish were fed live sand shrimp and diced clam.

In Experiment 1, 3 fish (60–90 mm TL) were placed in an aquarium and given a choice of 3 live scallops (100–135 mm) and 3 empty bivalve shells, 1 horse mussel *Modiolus modiolus* (115 mm) and 2 ocean quahogs *Arctica islandica* (75–80 mm), from which to choose shelters. The fish were observed 4 times daily (every 2 h from 1000–1600 h) over a 14-d period, and their positions recorded. All fish not seen either in empty bivalve shells or in the open areas of the aquarium were considered to be occupying a live scallop cavity. All observations were made from behind a black plastic blind to prevent observer influence on the fish.

In Experiment 2, 7 fish (69–78 mm TL) were given a shelter choice of 3 live scallops (120–135 mm) versus 3 empty scallop shells (112–140 mm) artificially propped open with a white plastic peg. Two tests were run, 4

fish in one test, 3 fish in the other. Observations were made as noted above.

RESULTS

General Behavior

Urophycis chuss showed a clear association with *Placopecten magellanicus*, using them for shelter by either resting within the scallops' mantle cavities, or more commonly, beneath the scallops in a depression dug by the fish between the lower valve of the scallop and the sand substrate. The entrance of a fish into a scallop was through the excurrent opening, essentially as originally described by Musick (1969). Typically, a fish entered a scallop by first slowly circling a number of scallops, occasionally touching a scallop's velar mantle fold with its pelvic fins. Then, after what appeared to be an inspection of several scallops, the hake would approach a particular scallop and when within 1 to 2 cm, quickly dart into the excurrent opening. The scallop would respond to a hake's entrance by immediately closing its valves, often followed by rapid opening and closing of the valves several times in succession. The rapid clapping of the valves sometimes caused a shift in position of the scallop of several centimeters. Entrance of the hake and reaction of the scallop lasted no longer than 30 s. Depending on the orientation of the scallop to the observer, it was possible at times to see the fish undulating slowly, headfirst, against the excurrent flow of the scallop. In some instances, the tail of the fish was visible outside the velar mantle fold of the scallop.

Fish sought shelter beneath scallops by first digging a depression in a highly stereotyped manner. A hake would approach a scallop headfirst and then turn so that its tail was resting against the sand and edge of the bottom valve. Then with vigorous side-to-side movements of the posterior half of its body coupled with backing movements, the hake would displace sand from under the scallop, creating a depression. If movement of the scallop caused a partial collapse of the depression, the hake would repeat the digging sequence. If the opening to the shelter depression was large enough so that digging was unnecessary, the hake entered headfirst, and then immediately turned and faced out from the shelter.

Foraging behavior by the hake differed according to the food present. When pieces of clam were introduced, the fish displayed food searching behavior normally associated with chemical detection of food (Bardach and Case, 1965; Pearson et al., 1980). The hake swam approximately 1 cm above the bottom, lightly touching the substrate with their modified pelvic fins

and responded to the presence of possible food items by stopping and attempting to ingest them. With live prey items such as sand shrimp, visual cues played a more dominant role in prey search. Fish still searched the bottom in a manner which typified chemical search behavior. When a hake touched a shrimp with its pelvic fins, the shrimp reacted by quickly jumping from the substrate into the water column and immediately swimming. The hake would then either pursue the shrimp through the water column, orienting visually to the shrimp or would continue to search the bottom for other prey. Prey capture and ingestion has been described elsewhere in greater detail (Luczkovich and Olla, in prep.).

Agonistic encounters occurred frequently between individual red hake foraging and swimming in the open, and between hake occupying shelters beneath scallops and intruders attempting to enter the shelters or forage just outside a shelter. We did not observe any hake attempting to enter a scallop already occupied by another hake and do not know if internal scallop cavities are actively defended. On occasion, a fish too large (> 130 mm) to reside within or under scallops would occupy and defend a specific space next to a wall or tank corner. The intensity of agonistic encounters ranged from a simple intention movement whereby a larger fish merely turned toward a smaller fish, causing it to flee, to long vigorous chases about the tank lasting as long as 10 to 15 s. The most common agonistic encounter was a simple chase, lasting 1 to 2 s. Initiation of encounters appeared to be dependent on the relative size of the respective fish, the larger fish being the aggressor more than 90 % of the time. However, prior possession of a shelter sometimes took precedence over size so that a smaller fish was able to defend its shelter against a larger fish.

Daily Patterns of Activity

Laboratory

Activity of the juvenile hake, which included foraging, prey capture and agonistic encounters among fish, was greater at night than during the day. Mean night scores were significantly greater than day scores in 33 out of 35 instances for Groups 1 and 2 combined (Student-t test; $\alpha < 0.05$, df = 22) (Fig. 1). On 3 occasions large weekly introductions of shrimp coincided with videotape observations (14 February, 12 March and 7 April). In all 3 instances activity decreased markedly for at least 24 h following the initial burst of heavy feeding by the hake (Fig. 1).

The number of agonistic encounters was strongly correlated with the overall levels of activity. In all
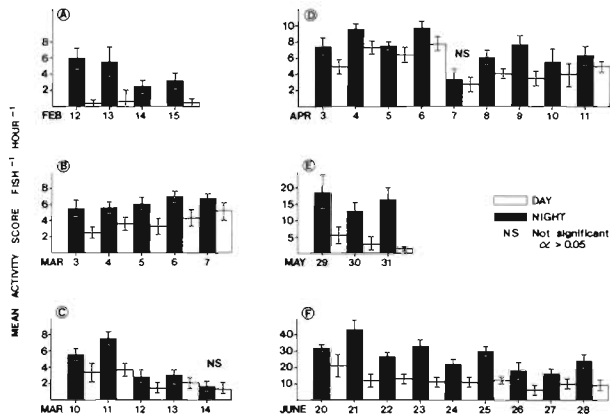
Fig. 1. *Urophycis chuss*. Mean activity score fish^{-1} h^{-1} over day and night for juvenile hake in Group 1 (A–D) and Group 2 (E–F). Bars around means indicate 2 standard errors

cases, the number of agonistic encounters was greater at night than during the day. Mean number of agonistic encounters ranged from 0.3 to 2.9 fish^{-1} h^{-1} at night, and from 0 to 1.1 fish^{-1} h^{-1} during the day. The correlation coefficient derived from a linear regression of number of agonistic encounters to activity scores was $r = 0.86$ (df = 33).

Field

Based on our laboratory observations, we predicted that there should be fewer fish inhabiting scallops during the night when fish were most active than during the day when they were least active. Comparing the mean number of hake found in a random sample of 10 scallops taken either hourly or bi-hourly
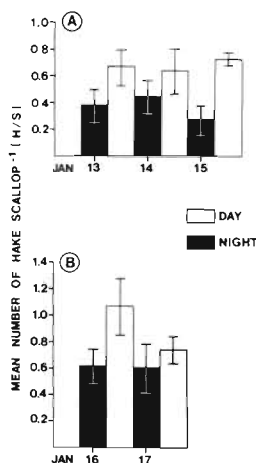

Fig. 2. *Urophycis chuss* and *Placopecten magellanicus*. Mean number of juvenile hake scallop^{-1} collected during day and night from 2 scallop beds. (A) Location 2 (40°08′N, 73°44′W); (B) Location 3 (40°08′N, 73°35′W). Bars around means indicate 2 standard errors

by a commercial boat over 5 night and day periods in 2 different scallop beds, we found that the number of hake in scallops during the day was greater than the number of hake in scallops at night in all instances (Fig 2). In Location 2, $\bar{x}$ (day) = 0.64 fish scallop^{-1}; $\bar{x}$ (night) = 0.33 fish scallop^{-1} (Student-t test, $\alpha < 0.005$, df = 49). In Location 3, $\bar{x}$ (day) = 0.88 fish scallop^{-1}; $\bar{x}$ (night) = 0.61 fish scallop^{-1} (Student-t test, $\alpha < 0.005$, df = 22). The finding of fewer fish inhabiting scallops during nighttime in the field confirmed our prediction and supported the laboratory results of greater activity at night.

Scallop-Hake Size Relationship

Our regular monthly scallop-hake collections did not allow us to associate individual hake with their scallop hosts, since the need for live specimens for laboratory experiments precluded opening and sacrificing scallops to obtain inhabitant hake. Thus, to examine the size relationship between hake and scallops, we segregated scallops into 3 size categories (< 100 mm, 100–120 mm, and > 120 mm) in separate containers and measured the fish after they emerged from their scallop hosts.

Juvenile red hake collected from scallops ranged in size from 23 to 116 mm. The length of an individual hake was never greater than the length of its scallop host, although on occasion, the length of a hake approached that of its host (Figs. 3, 4). The size range
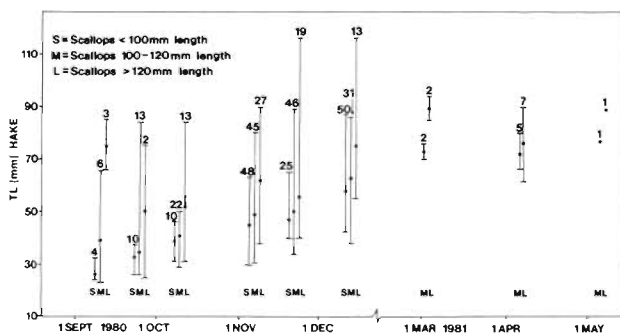

Fig. 3. *Urophycis chuss* and *Placopecten magellanicus*. Mean and ranges of total lengths of juvenile hake taken from small, medium, and large scallops in field study site: Location 1 (40°15′N, 73°50′W). Numbers above bars indicate number of hake in each category

of hake found inhabiting the small (< 100 mm) scallops was consistently less than the range of fish in the two larger scallop size categories (Fig. 3). In general, the small scallops contained only small fish, but the large scallops contained all possible sizes of fish, from the smallest to the largest fish of any given sample (Fig. 3). Despite the overlap in ranges of inhabitant fish
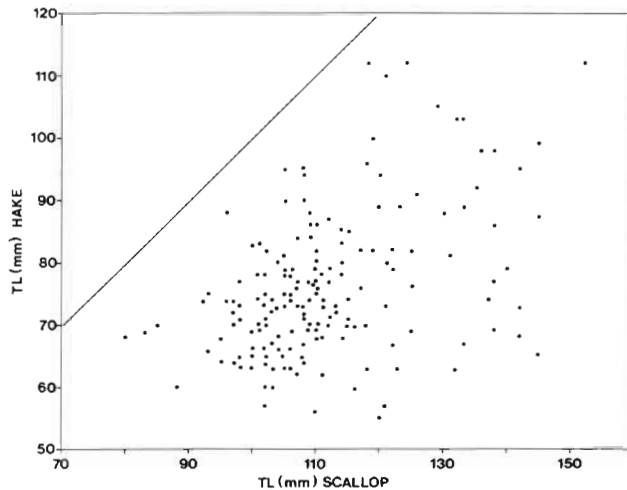
Fig. 4. *Urophycis chuss* and *Placopecten magellanicus.* Plot of total length (TL) of individual juvenile hake versus length of respective scallop host collected 13 to 15 January 1981 at Location 2 (40°08'N, 73°44'W). Diagonal line indicates 1:1 ratio of hake length:scallop length

taken from the 3 scallop size categories, the mean size of inhabitant fish increased with increasing size of scallops (Fig. 3). Examining the data seasonally, the mean sizes of inhabitant fish within each scallop size category increased from September onwards. For example, the mean size of fish from the < 100 mm scallops increased from 28 mm on 28 September to 54 mm on 11 December, and by March, there were no fish in the smallest scallops.

The sampling program from 12–17 January 1981 aboard the commercial scallop fishing boat was conducted, not only to study the 24-h rhythm of hake shelter usage, but also to more precisely measure the size relationships between individual hake and their scallop hosts. The results agreed with the general trends noted above for the monthly samples. The small scallops contained only small fish, while large scallops contained a wider range of fish (Fig. 4). When we lumped the data into 3 scallop size categories, to correspond with the monthly data above, the mean size of fish again increased with increasing scallop sizes: $\bar{x}$ hake size = 70 mm (< 100 mm scallops); $\bar{x}$ hake size = 72 mm (100–120 mm scallops); $\bar{x}$ hake size = 82 mm (> 120 mm scallops).

Shelter Selectivity in the Laboratory

Our observations of juvenile hake in the laboratory indicated that the fish were not limited to shelter within living scallop cavities, but also used depressions in the sand under scallops, recently dead scallops with partially opened valves, and pieces of PVC pipe

placed in auxillary holding aquaria to provide shelter. This suggested to us that the shelter relationship between juvenile hake and scallops might be faculative rather than obligatory, and the primary goal of the fish was to seek any object that provided shelter. To examine this question, we performed experiments testing the shelter preference of juvenile hake by giving them a choice between live sea scallops and other non-living objects that might serve as shelter.

In Experiment 1, the fish were given a choice of 3 live scallops and 3 partially opened empty bivalves. Of the 58 instances when fish were observed in shelters, scallop cavities were occupied 2 times (3 %), empty bivalves 54 times (94 %), and depressions underneath live scallops 2 times (3 %). In Experiment 2, where fish were given a choice of 3 live scallops and 3 empty scallops, live scallop cavities were occupied 26 times (17 %), empty scallop shells 92 times (62 %), and depressions underneath live scallops 31 times (21 %). The results indicated that the relationship between juvenile hake and scallops is apparently not obligatory.

Recruitment

Our aim in this portion of the study was to examine recruitment of post-larval red hake from the plankton to the population of juvenile red hake in the scallop bed. We used 2 criteria to estimate the relative rates and times of major recruitment: (1) changes in the relative abundance of the hake population associated with scallops, as indicated by the ratio of the number of hake to the number of scallops (H/S); and (2) the identification of new recruits in each sample using morphological tratis.

The second criterion, the identification of new recruits in each sample, was determined by the coloration and size of hake in each sample. New recruits had silver coloration below the midline of their lateral surfaces and on the ventral surface anterior to the anal pore. This was a residual coloration from their planktonic post-larval stage which is characterized by a blue dorsum and silver coloration of the head, laterally compressed sides, and ventral surfaces (Bigelow and Schroeder, 1953; Musick, 1969). Musick (1969), during incidental observations in the laboratory, found that this residual silver coloration may fade in as few as 12 h after settlement of a post-larva to the benthos. New recruits to the bottom were limited to lengths ranging from 23 mm (smallest juvenile found in scallops in this study) to 49 mm (largest post-larval red hake found to date in plankton; Musick, 1969). We concluded that there were no new recruits in any sample of benthic juveniles which did not include any

individuals less than 49 mm, nor any individuals with silver coloration.

The size distribution of scallops did not vary significantly among the monthly samples. A representative distribution is shown in Fig. 5. Therefore, the following
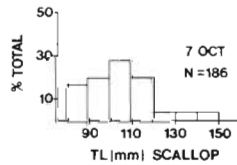

Fig. 5. *Placopecten magellanicus*. Representative length-frequency distribution of scallop population at field study site: Location 1 (40°15'N, 73°50'W)

results are based on changes in the hake population itself, and not an artifact of differential sampling.

The inhabitation of scallops by juvenile red hake was a distinct seasonal phenomenon. Recruitment of planktonic post-larvae to the benthos was protracted over a period of several months. Scallops collected June through August contained no hake. On 8 Sep-
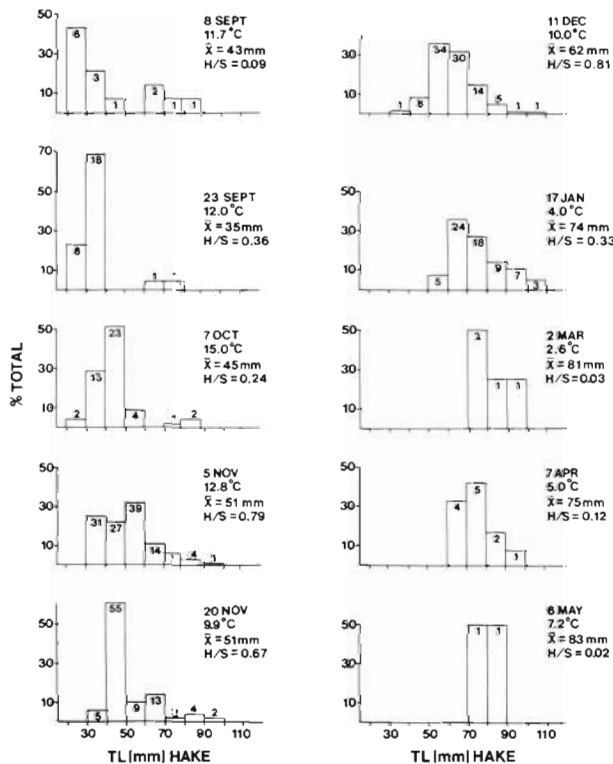

Fig. 6. *Urophycis chuss* and *Placopecten magellanicus*. Length-frequency distributions of juvenile red hake taken in monthly and bimonthly samples from field study site: Location 1 (40°15'N, 73°50'W). Numbers within bars: number of hake in each size category. Temperature was taken within 1 m of the bottom. H/S: ratio of number of hake collected to number of scallops greater than 80 mm in each sample

tember 1980, the first recruits of the new year class were collected. This sample was dominated by fish less than 30 mm, with the smallest being 23 mm (Fig. 6). All of the fish less than 30 mm were silver along their lateral and ventral surfaces, indicating that they were the most recent recruits of the sample. The next sample, taken 23 September, was dominated by fish in the 30 to 40 mm size range. These larger fish also showed the residual color of newly descended planktonic post-larvae. Along with the increase in the size of new recruits, there was an increase in the overall number of juvenile hake in the scallop bed, as indicated by the increase in the H/S ratio (Fig. 6). By November, the modal size of fish now settling to the scallop bed had increased even further. Of the 39 fish with silver coloration on 20 November, 85 % were greater than 40 mm with the largest being 46 mm. The number of fish on the scallop bed increased markedly from October to November with the H/S ratio increasing to levels as high as 0.79 on 5 November (Fig. 6).

By 11 December, only 9 % of the fish collected were less than 49 mm, none of which had any residual silver coloration. We concluded from this that recruitment had effectively ceased. The H/S ratio remained high through the December sample. There were no fish less than 50 mm in the 17 January 1981 sample, nor any fish with silver coloration. In addition, the H/S ratio had decreased precipitously. The H/S ratio continued to decrease through the spring months, with the last two fish being collected on 6 May 1981 (Fig. 6).

Growth

Field

In order to estimate growth rates from our monthly field samples, we had to choose a sampling interval during which there was both limited recruitment of small fish into the scallop bed and limited emigration of larger fish away from the bed. Such conditions, adapted from Ricker (1975), minimize the difference between the calculated apparent population growth and the true growth rate. Otherwise, the calculated growth rate would be an underestimate.

The interval that best fits the above criteria was 20 November to 11 December 1980 (Fig. 6). The 20 November sample was the last to contain significant numbers of newly descended recruits. Between 20 November and 11 December there was little emigration, as indicated by the continued high H/S ratios. After 11 December, large-scale emigration occurred, as indicated by the drop in the H/S ratio from 11 December to 17 January 1981. The mean total length

(TL) of individuals in the sample rose from 51 mm on 20 November to 62 mm on 11 December (Fig. 6). This 11 mm increase over 21 d corresponded to an average growth rate of 0.93 % d^{-1}.

Laboratory

We determined growth rates for 3 separate groups of fish. Group 1 fish, maintained from 5 February to 8 May 1980, had an average growth rate of 0.81 % d^{-1} (Table 1). Since we did not have simultaneous initial lengths, we do not have individual growth rates. Group 2 fish, maintained from 13 May to 30 June 1980, had individual growth rates which ranged from 0.82 to 1.22 % d^{-1}, with an average of 1.00 % d^{-1} (Table 1). Group 3 fish, maintained from 30 December 1980 to 9 April 1981, had individual growth rates which ranged from 0.36 to 0.70 % d^{-1}, with an average of 0.61 % d^{-1} (Table 1).

It was obvious that growth rates varied among the 3 groups of fish. Although our experimental procedure was not designed to specifically test the relative contribution of various factors that might contribute to variability in growth, there was a clear suggestion that temperature affected growth rates, i. e. growth

increased with increasing average daily temperature (Table 1). In further support of the role of temperature on growth, we calculated growth rates of Group 3 fish during intervals of 16–21 d and found that those growth rates correlated positively with average daily temperatures (Fig. 7).
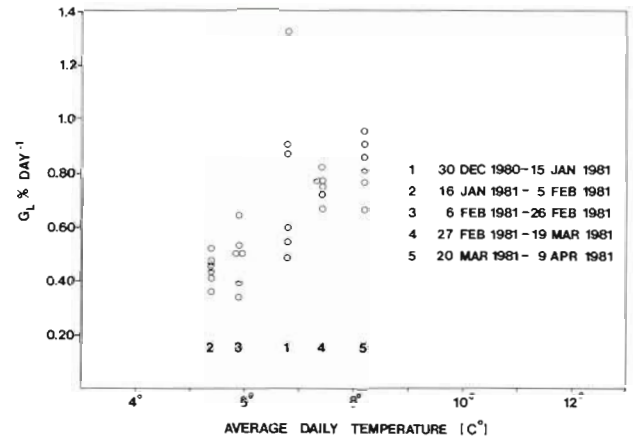

Fig. 7. *Urophycis chuss.* Plot of growth rate d^{-1} (G$_L$) versus average daily temperature for 6 fish in Group 3 over 5 intervals of 16 to 21 d

Table 1. *Urophycis chuss.* Initial and final total lengths (TL) and growth rates (G$_L$) for juveniles in Groups 1, 2, and 3

Group 1		Group 2			Group 3		
Initial TL (mm)	Final TL (mm)	Initial TL (mm)	Final TL (mm)	G$_L$ % d^{-1}	Initial TL (mm)	Final TL (mm)	G$_L$ % d^{-1}
60	86*	89	156	1.17	50	72	0.36
60	123	97	174	1.22	61	115	0.61
62	126	112	178	0.97	63	126	0.69
65	131	112	193	1.13	72	145	0.70
68	140	132	200	0.87	83	159	0.65
72	141	138	205	0.82	90	163	0.59
72	147	140	209	0.83	93	177	0.64
				$\bar{x}$ G$_L$ = 1.00 % d^{-1}			$\bar{x}$ G$_L$ = 0.61 % d^{-1}
73	150						
78	164	$\bar{x}$ Daily temperature = 11.5 °C			$\bar{x}$ Daily temperature = 6.7 °C		
80	168	Range = 10.1–13.1 °C			Range = 4.9–9.8 °C		
80	172	$\bar{x}$ Daily fluctuation = 0.41 C°			$\bar{x}$ Daily fluctuation 0.31 C°		
110	180						
117	180						
125	190						
	201						

$\bar{x}$ G$_L$ = 0.81 % d^{-1}
$\bar{x}$ Daily temperature = 8.6 °C
  Range = 7.1–11.7 °C
$\bar{x}$ Daily fluctuation = 0.34 C°

* Fish were not individually marked. Initial and final lengths are listed in order of increasing size and do not represent growth increments for individual fish. One fish was not measured initially

DISCUSSION

Laboratory observations and field collections both demonstrated that juvenile hake, associated with sea scallops, were primarily active at night. However, the fact that fish were active to varying degrees during the daytime in the laboratory, and fish in the field were found in scallops during nighttime, demonstrated that each individual hake did not exhibit a strict on-off activity rhythm controlled solely by light-dark conditions. Other factors such as availability of food and competitive interactions for resources may affect the length and amplitude of hake activity. We suspect that much of the activity that occurs is related to feeding. For example, following intensive bouts of feeding which occurred immediately after introductions of prey, activity decreased precipitously for 24 h or more. Gradually, fish once again increased activity.

The sizes of juvenile red hake associated with the scallop bed were limited, in part, by the sizes of the scallops. This is illustrated by the fact that the size distributions of both the scallops (Fig. 5) and the hake inhabiting them (Fig. 6) had relatively few larger individuals, i. e. there were few scallops greater than 120 mm and few fish greater than 90 mm. The relative scarcity of larger scallops limited the available shelter for larger hake. However, the smaller hake were not restricted to only smaller scallops. This was illustrated by the fact that small-sized fish were found in all size categories of scallops. Thus, the trend for larger fish in larger scallops was probably more a result of larger fish being forced to take larger scallops and smaller fish randomly choosing all-sized scallops; than a competition *per se* between large and small fish for large scallops.

The smallest scallop suitable for habitation by hake is probably determined on a volumetric basis. We noted that a hake was never found in a scallop which was shorter in length than the hake itself, although several times a ratio close to 1:1 was found. However, it is not likely that scallops as small as 23 mm ever contain hake as small as 23 mm (smallest hake found in scallops), since volume in the scallop decreases at a greater rate than does linear dimensions. Thus, there is probably an absolute lower limit to the size of a scallop that can host a hake. This lower limit remains to be determined.

All our evidence suggests that shelter is a critical resource for juvenile red hake. Laboratory observations of hake utilizing both internal cavities of scallops and depressions underneath scallops, and observations of hake defending shelters, along with field evidence of a high incidence of hake inhabiting scallops attest to the importance of shelter to the hake. However, the laboratory experiments on shelter selection by juvenile red hake showed clearly that the fish will utilize many objects other than living scallops, if available. This suggests that the use of live sea scallops may not be obligatory. It is possible that other areas of ocean bottom may provide sufficient relief to attract and maintain populations of juvenile red hake. Nevertheless, we must presently assume that scallops are still the most common form of shelter available to juvenile hake. Thus, a decline in the scallop population, which may be caused by any number of factors, both natural and man-induced, would reduce the habitat available for juvenile hake. This, in turn, could result in a reduction of the hake population. Commercial scalloping not only reduces the available habitat for hake, but directly contributes to hake mortality during those times of the year when hake reside within scallops.

Based on data obtained on recruitment, as well as field and laboratory growth rates, we surmise that juvenile red hake in the study area were spawned in August and September. Recruitment of benthic juvenile hake from the planktonic stage occurred from September to December, with the main peak occurring from mid-October to mid-November. Recruits in September were primarily 23 to 30 mm in length. Given a 2-d hatching period (Miller and Marak, 1959), and larval growth rates as high as 1 mm d^{-1} (Luczkovich and Olla, unpubl.), we estimate that these fish were spawned approximately 1 mo prior to recruitment to the benthos, i. e. early August. Later recruits in mid-November were longer than 40 mm. We estimate that these fish were spawned approximately 2 mo prior to settlement, i. e. mid-September

Historical records indicate that red hake spawn in Atlantic coastal waters from April to as late as October in various locations ranging from the New Jersey coast to Nova Scotian waters (Musick, 1969). The 2 main spawning grounds are south of Block Island and the southwest portion of Georges Bank (Musick, 1969). The highest concentrations of red hake eggs were taken in ichthyoplankton cruises from Georges Bank and the Mid-Atlantic Bight region during August and September, while the highest concentrations of planktonic larvae in the same areas were taken during October and November (M. Fahay, pers. comm.). These findings correlate well with both our estimated times of spawning and our observed peak times of recruitment, suggesting that red hake in our study come from 1 of the 2 major spawning grounds.

We derived estimates for growth rates of juveniles from field and laboratory studies. The field estimate for growth in November and December at temperatures of approximately 10 °C was 0.93 % d^{-1}, while a similar rate of 0.81 % d^{-1} was derived from laboratory tests at slightly lower temperatures (Group 1). Estimates of growth from both field and laboratory indicate that

juveniles should reach 90 mm or more, the size at which most fish leave the scallop bed (Fig. 6), within 2 to 3 mo. Thus, since last recruitment occurred in late November or early December, we would predict that most hake would emigrate from the scallop beds by late February or March. This, in fact, corresponds with our field data which shows that very few hake remained with the scallops after January.

After leaving scallops, growth of juvenile hake would depend on temperature and availability of food. Our laboratory observations of growth at temperatures which simulated field conditions of January–April (Group 3) and May–June (Group 2) showed growth rates of $0.61\% \, d^{-1}$ and $1.00\% \, d^{-1}$, respectively. These results demonstrated that hake are capable of reaching lengths of greater than 20 cm by late spring, if food is available in adequate amounts. Assuming growth continues at comparable or greater rates during the warmer summer months, we estimate that red hake which were originally recruited to the benthos in the fall, are capable of reaching sizes greater than 25 cm and possibly close to 30 cm by the following fall, 1 yr after their initial spawning and hatching.

In contrast, although most juveniles emigrate from the scallop beds by February, a number of individuals remained through May, at sizes no larger than 100 mm. Thus, we conclude that the same year class of juvenile red hake will contain a very wide range of sizes, perhaps as great as two-fold. Furthermore, it is very possible that significant overlap in size may occur between late recruits of a given year class, and the fast growing early recruits of the following year class. This overlap may be compounded by different overall growth rates during the first year for different year classes as shown in red hake (Rikhter, 1973) and cod (Beacham, 1981).

Such overlap in the sizes of different-aged fish can cause error when an age/length distribution derived from a given year is applied to a length distribution in a subsequent year to calculate an age structure (Westrheim and Ricker, 1978). Therefore, it is important that future studies carefully address the question of variable growth rates in red hake and establish an accurate age/length key, with particular attention to overlap between different age fish.

Previous literature on the growth of red hake is limited. Musick (1969) estimated that juvenile red hake associated with scallops on Georges Bank grew $10 \, mm \, mo^{-1}$, from 51 to 80 mm, between September and December 1959, and $2.5 \, mm \, mo^{-1}$, from 80 to 92 mm, between December and May 1960. These rates are equivalent to rates of $G_L = 0.49\% \, d^{-1}$ and $G_L = 0.09\% \, d^{-1}$, respectively. These values, particularly the rate for December to May, are lower than our field and laboratory estimates, probably because the mean

sizes in Musick's study were not adjusted to reflect the effects of prolonged recruitment. Rikhter (1973) reported that mean lengths of $1 +$ yr old red hake, in successive year classes from 1967 to 1971, ranged from 19 to 24 cm, which falls within the range of first year growth estimated in our study.

The success of attempts to predict year-class strength solely through the abundance of planktonic eggs or larvae has varied widely from species to species (see Blaxter, 1974, for pertinent articles). For red hake, the relative abundance of juveniles associated with sea scallops may be a more reliable indicator of future year-class strength, since: (1) the juveniles have all successfully passed through the potentially highly vulnerable periods of eggs, larvae, and the hazardous descent to the benthos, and hence the abundance of juveniles should be more closely correlated with year-class strength than any planktonic form; (2) the spatial distribution of juveniles is coincident with that of sea scallops, which is relatively stable, and hence the sampling program can be devised to exploit specific, known scallop concentrations; and (3) information on the life history of the hake can be utilized to pin-point specifically the time of year when juveniles are most abundant, and even the time of day when hake are most likely to be inhabiting the scallops.

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