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Seasonal Migration of the Hagfish, *Eptatretus burgeri*, Girard

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ABSTRACT—The seasonal migration of the hagfish, *Eptatretus burgeri,* was studied in the sea near the Misaki Marine Biological Station of University of Tokyo during the period from October 1970 to October 1975. The hagfish was caught by a cylindrical trap (80 cm in length, 15 cm in diameter) with a funnel-shaped one way entry at both ends. Sardines were used for baits. The hagfish were found in water of 6 to 10 m depths in Koajiro Bay and Moroiso Bay near the Station from mid October to mid July of the following year, but they were absent from the bays at other times. On the other hand, they were found throughout the year in offshore water of 50 m depth, about 1,600 m west of the Station. Two hundred and nine hagfish caught in water of 50 m depth in October and November were marked by making a small triangle cut on the tail fin and releasing them at the original place of capture. Sixty five marked hagfish in total (31.1%) were recaptured in Koajiro Bay and Moroiso Bay. Among 1,323 hagfish marked in Koajiro Bay in April, May and June, 23 marked hagfish (1.7%) were recaptured in water of 50 and 100 m depths. The mean total lengths of the hagfish collected in Koajiro Bay and water of 50 m depth during November through April were 43.3±0.7 cm (±SEM, n=1,796), and 34.3±0.9 cm (±SEM, n=689), respectively. Data on monthly collections of the hagfish in both Koajiro Bay and water of 50 m depth indicated that when they migrate from shallow to deep water and the reverse, larger hagfish more than 39 cm in total length move first being followed by smaller ones, but many hagfish less than 35 cm in length remain in water of 50 m depth throughout the year. We failed to collect either fertilized eggs or juveniles by net sweeping of the bottom of water of 40 to 110 m depth. Furthermore, we could not find hagfish less than 20 cm in either shallow water or water of 50 m depth. It seems that the spawning ground of *E. burgeri* may not be at the 50 m depth but at a deeper place than 100 m depth. Finally, the present study demonstrated directly the seasonal migration of the hagfish, *E. burgeri*, between shallow and deeper waters of Sagami Bay by the marking experiments.

INTRODUCTION

Dean (1904) reported that the hagfish, *Eptatretus burgeri*, were found in shallow water of 6 to 10 m depths in Koajiro Bay and Moroiso Bay (see Fig. 1) near the Misaki Marine Biological Station (Fig. 1, MMBS), University of Tokyo, Kanagawa Prefecture, Japan, throughout the year except during the period from September to October; further that they exhibited seasonal changes in gonadal development. Dean's studies were detailed by Conel (1931). The findings by Dean on *E. burgeri* revealed that this Japanese species is different in ecological aspects from other hagfishes, such as *Myxine glutinosa* of the Atlantic Ocean and *Eptatretus stouti* of the eastern Pacific coast, in that both species live in deep water more than 50 m in depth and do not show seasonal synchronized gonadal development (Gorbman, 1983; Patzner, 1998). This raises the question as to where *E. burgeri* spends its life during September and October period. To explore this question, we considered to the following two earlier findings: 1) the Atlantic hagfish, *Myxine glutinosa*, is usually trapped at a depth of around 500 m, but there are reports that they can be caught in water of about 30 m (Adam and Strahan, 1963), and 2) Dean collected a total of 169 animals of *E. burgeri* in water of 36 m depth by three collections in June and August. Based on these findings, we thought initially that *E. burgeri* might be caught in water of 30 to 50 m depths during September and October, when Dean (1904) could not find the hagfish in shallower water. So, we tried first to trap *E. burgeri* in water of about 50 m depth, in an area about 1,600 m west to the Station during September and October. Three traps (see Materials and Methods), containing sardines as bait, were set, about 50 m apart, on September 30, 1970, at the depth of about 50 m. In the next morning the traps were raised. To our surprise, the traps were full of hagfish (more than 30 in each trap) (Kobayashi *et al.*, 1972). At this time we first were convinced

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The coauthors of this paper wish to dedicate it to the memory of late Dr. Tomoyuki Ichikawa, who wrote the draft of this manuscript.

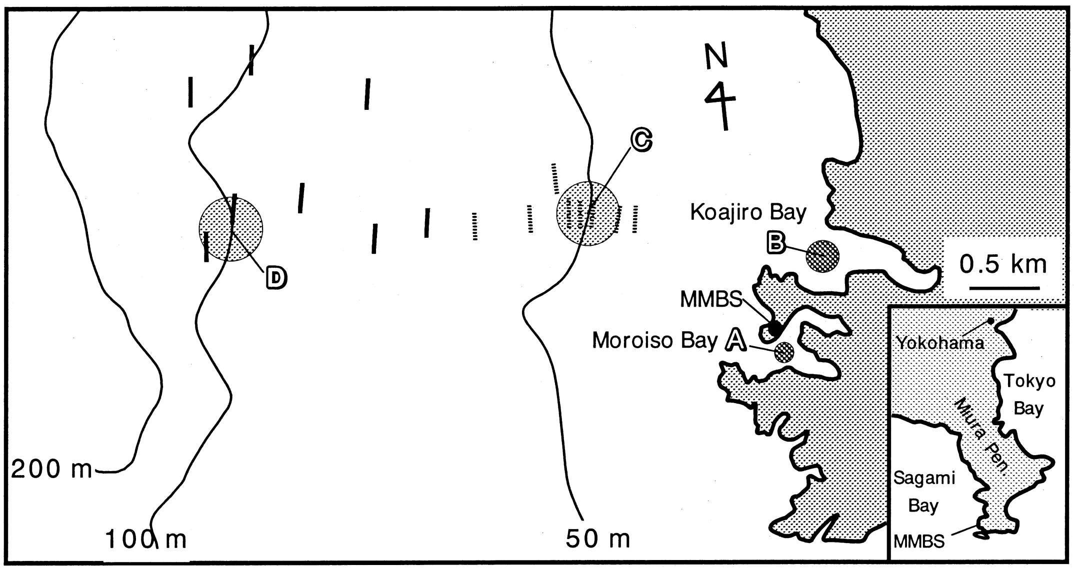

Fig. 1. Shaded circles (A to D) are areas where *Eptatretus burgeri* were collected. Thick lines and broken lines indicate traces of net sweeping in October 1973 and November 1975, respectively. Net sweeping was carried out for about 200 m each time. A and B, water of less than 10 m depth; C, water of 50 m depth; D, water of 100 m depth; MMBS, Misaki Marine Biological Station.

of the seasonal migration of *E. burgeri* (Kobayashi *et al.*, 1972).

This preliminary study on the migration of this species encouraged us to study further the details of their migration and seasonal changes in gonadal development throughout the year. Although Dean (1904) studied gonadal development, sex ratio and feeding habitats of *Eptatretus burgeri*, his observations were limited to only those living in shallower water.

In the present study, seasonal migration was further investigated in both shallow and deep water hagfish throughout the year. Furthermore, since hagfish are known to be benthic (Adam and Strahan, 1963), the nature of bottom type at a depth of 9 m in Koajiro Bay and water of 50 m depth in Sagami Bay (see Fig. 1) was studied. Seasonal gonadal development of this population will be described separately (Nozaki *et al.*, 2000).

MATERIALS AND METHODS

Collection of the hagfish

The hagfish, *Eptatretus burgeri* Girard, were trapped two to eight times a month at depths of 6 to 10 m in Moroiso Bay (Fig. 1, A) and Koajiro Bay (Fig. 1, B) near MMBS (35°09'18" N, 139°36'54" E), and at depths of 50 m (Fig. 1, C) and 100 m (Fig. 1, D) in Sagami Bay (Fig. 1, inset). Depths of 50 and 100 m are found at about 1,600 m and 4,800 m west to the MMBS, respectively. Collections were performed during October1970 to March 1973. Months of collections for each

Table 1. Experimental periods in respective experiments

Manthly collection of hagfish	
Moroiso Bay	October 1970 to November 1971
Koajiro Bay	November 1971 to March 1973
Water of 50 m depth	November 1971 to March 1973
Water of 100 m depth	August 1972 to March 1973
Additional collection of hagfish	
Koajiro Bay and/or water of 50 m depth	April 1973 to September 1973
Marking experiments	
Trapping and Marking in deeper water	October and November 1971
Recapturing in shallower water	Novembr 1971 to February 1972
Trapping and Marking in shallower water	April to June 1972
Recapturing in deeper water	May to September 1972
Sweeping of the sea bottom by net	
Water of 80 to 110 m depths	October 1973
Water of 40 to 80 m depths	November 1975
Habitat examination	
Koajiro Bay	November 1971 and May 1972
Water of 50 m depth	November 1971 and May 1972

Table 2. Dates of collection and number of hagfish caught in Moroiso Bay and Koajiro Bay

Year	Month	Moroiso Bay	Koajiro Bay
1970	October	15 (0)*, 25 (0), 29 (0)	–**
	November	1 (14), 3 (1), 4 (1), 7 (4), 12 (40), 19 (35)	–
1971	July	6 (6), 8 (2), 9 (0), 14 (4), 15 (11), 16 (11), 19 (0), 25 (0)	–
	October	19 (0), 26 (0), 30 (1)	–
	November	5 (2), 7 (3), 12 (19), 15 (3), 17 (3), 20 (3), 24 (20)	15 (59/20)***, 19 (142/39), 26(117/7)
	December	–	10 (69/7), 20 (62/7)
1972	Jan. to May		(Omitted)
	June	–	3 (65/6), 7 (35/6), 16 (11/11), 19(8/5), 22 (7/5), 27 (1/11)
	July	–	1 (2/11), 18 (0/6), 20 (0/6)
	August	–	19 (0/6), 31 (0/6)
	Septembr	–	14 (0/6)
	October	–	20 (1/6), 26 (18/18)
	November	–	2 (39/10), 11 (52/10), 26 (85/10)
	After Dec. 1972	–	(Omitted)

* Date and number of hagfish in parenthesis.
** Collection was not carried out.
*** Date and number of hagfish / number of traps in parenthesis.

experiments are listed in Table 1 and are described in the sections of respective experiments. Collection in Moroiso Bay was not carried out after December 1971, because of small size of the population of the hagfish there (Table 2).

For capturing the hagfish, a cylindrical trap (80 cm in length, 15 cm in diameter) with a funnel-shaped one way entry at both ends was used, baited with sardines. Before experiments, we confirmed twice that the hagfish could not be caught in daytime in shallow water, although we knew that they are nocturnal (Dean, 1904; Kobayashi *et al.*, 1972; Ooka-Souda *et al.*, 1985). Therefore, 6 to 39 traps in shallow water and 2 to 4 in deeper water, respectively, were placed at the sea bottom, separated by 10 to 100 m distances from each other, depending on the depth of the sea, in late afternoon, and picked up in the following morning. Incidentally, although hagfish could be caught during daytime in deeper water of 50 or 100 m, traps were placed in the late afternoon as well as in shallow water. Sardines were the best bait compared with mackerel, cod oil soaked in cotton and viscera of hagfish.

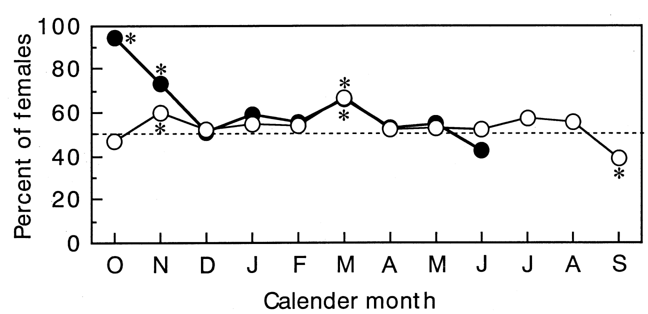

Fig. 2. Percent of females of all hagfish caught in Koajiro Bay (closed circles) and water of 50 m depth (open circles) in each month. The percentage was calculated from the hagfish caught in each month from November 1971 to March 1973. Numbers of animals in each month were listed in Figures 3 and 4, although the sex was not shown. *, $P < 0.05$.

Marking experiments for migration studies

Two hundred and nine hagfish more than 40 cm in total length, which were expected to migrate to shallow water (see Fig. 5), were trapped in water of 50 m depth (Fig. 1, C) in October and November 1971. One thousand three hundred and twenty three hagfish of all total lengths were caught in Koajiro Bay (Fig. 1, B) in April, May and June 1972. For the marking, a small triangular piece was cut off from the upper or lower margin of the tail fin. Immediately after the marking, the hagfish were released at the same place where they were caught. Months during which recapture of the marked hagfish occurred are described in Results. The mark remained visible for at least about 5 months.

Measurement of total length and observation of gonads

To examine the relationship between migration, body length and sex, total lengths of all hagfish caught were measured. All hagfish, except for those used in the marking experiments, were dissected and sex was examined.

Sweeping of the sea bottom by net

In an attempt to locate the spawning ground and to obtain fertilized eggs or juveniles, net sweeping was carried out in October 1973 at depths of 80 to 110 m and in November 1975 at depths of 40 to 80 m (Fig. 1). The sweeping device was a set of 7 to 10 layers of nylon nets, each of which was about 20 cm in width, 4.5 m in length and 1 to 3 cm in mesh size. It was weighed at the bottom by a lead-weighed steel tube (2 m in width and 8 cm in diameter) at one end. The device was drawn very slowly by a boat to sweep the bottom surface for about 200 m distance in each trial. Such a device is used to collect corals and other benthic animals at the Station.

Examination of habitat

Substrate samples were collected from the bottoms of Koajiro Bay (water depth of 9 m) and of Sagami Bay (50 m) with a SK type bottom sampler (Rigosha, Tokyo). The sizes of the particles therein were measured with a sieve (Marukawa Co. Ltd., Tokyo), whose pore sizes were 3.36, 1.00, 0.50, 0.21 and 0.053 mm. The contents of the intestine of the hagfish caught in 50 m in Sagami Bay were collected and the sizes of the particle therein were also measured.

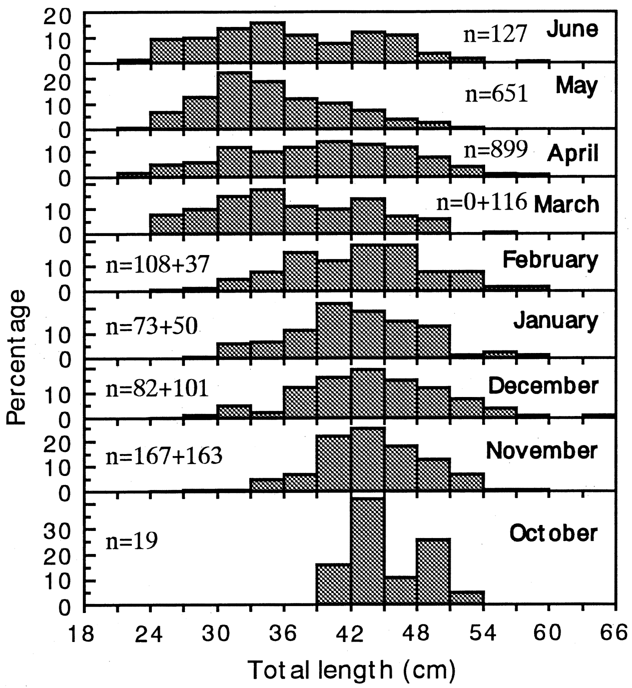

Fig. 3. Frequency distribution histograms of the total lengths of the hagfish caught in Koajiro Bay. Fishes caught each month from November 1971 to March 1973 were collected. Total lengths are expressed at 3 cm intervals. Numbers in each column indicate number of animals collected in the same months of the first and second years in order.

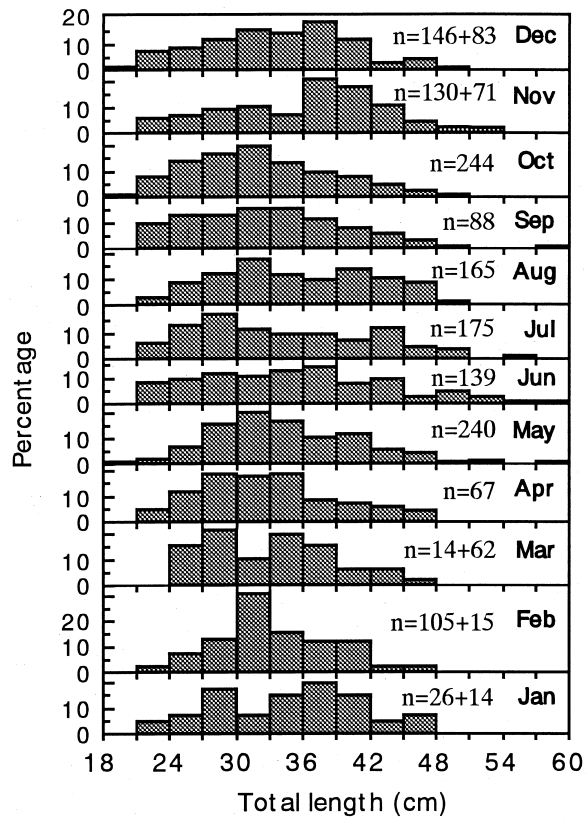

Fig. 4. Frequency distribution histograms of the total lengths of the hagfish caught in water of 50 m depth. Fishes caught each month from November 1971 to March 1973 were collected. Total lengths are expressed at 3 cm intervals. Numbers in each column indicate number of animals collected in the same months of the first and second years in order.

Statistics

Kolmogorov - Smilnov two-sample test was used to compare the frequency distribution histograms of the body length (1) of the hagfish caught in each month in Koajiro Bay, (2) of those caught in each month in water of 50 m depth, and (3) of the hagfish caught in Koajiro Bay and in water of 50 m depth. Student's t-test was used to compare the body length between males and females.

RESULTS

1. Collection in each month

In the shallow water of 6 to 10 m depths in Moroiso Bay and Koajiro Bay, the hagfish could be caught during a period from mid October to mid July of the following year, but not during any other period (Table 2). On the other hand, the hagfish could be caught throughout the year in water of 50 m depth (see Fig. 4). Number of hagfish collected per trap was relatively consistent in respective collection sites: it was 8.1±1.2 (±SEM, n=21 collections) in Koajiro Bay during November 1971 through May 1972, whereas it was 18.7±1.9 (±SEM, n=37 collections) in water of 50 m depth during November 1971 through March 1973. Mean numbers of the traps used in one collection were 10.0±1.0 (±SEM, n=47) in Koajiro Bay, and 3.3±0.2 (±SEM, n=37) in water of 50 m depth during November 1971 through March 1973.

2. Marking experiments

In the first experiment, 209 hagfish caught in water of 50 m depth in October and November 1971, were marked. Among

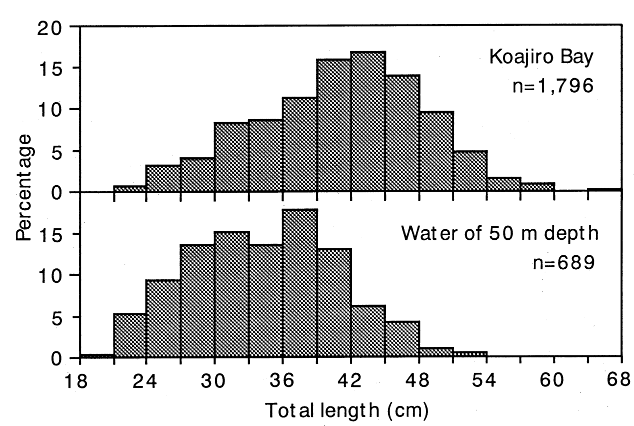

Fig. 5. Frequency distribution histograms of the total lengths of the hagfish caught during months from November to April in Koajiro Bay (upper panel) and in water of 50 m depth (lower panel).

764 hagfish caught during November 1971 to February 1972 in Koajiro Bay and Moroiso Bay, 65 marked hagfish were recaptured starting from November 1971. Recovery was 31.1%. In the second experiment, 1,323 hagfish caught in Koajiro Bay were marked in April, May and June 1972. Among 939 hagfish caught from May to September 1972, in water of 50 m depth, 22 marked hagfish were recaptured starting from

May 1972. Among 74 hagfish caught during the same period in water of 100 m depth, one hagfish with the mark was recaptured. Recovery in water of 50 and 100 m depths was 1.7%. These observations indicate that the hagfish exhibit seasonal migration between shallow water less than 10 m in depth and water of 50 to 100 m in depth.

3. Sex difference in total length and sex ratio

There was no significant difference in the mean total length between males and females in each month either in Koajiro Bay or in water of 50 m depth, respectively. However, in total, females (37.6±0.19 cm, n=1,564) were significantly larger than males (36.4±0.24 cm, n=1,221)($p<0.05$).

Based on 2,785 specimens caught in Koajiro Bay and water of 50 m depth during a period from November 1971 to March 1973, the ratio of males to females was 1:1.28; thus trapped females were significantly more numerous than males ($p<0.001$). However, in Koajiro Bay, almost all hagfish caught in October and most hagfish caught in November were females (Fig. 2). This indicates that females migrate first to Koajiro Bay during this period. From December to June, there was no difference in sex ratio except March in either Koajiro Bay or water of 50 m depth. The reason why number of trapped females is significantly larger than males in March is not explicable at the present time. Significant differences in sex ratio were also noted in November and September in water of 50 m depth, but such differences are not explainable at the present time. The patterns of the seasonal changes in the sex ratio observed in the present study are similar to those of Dean (see Conel, 1931).

4. Relationship between total length and migration

The largest trapped hagfish was 76.5 cm (male) in total length, which was caught in Koajiro Bay in April 1973. The smallest specimen was 9.3 cm (sex is not clear) caught in water of 100 m depth in September 1973.

(1) Koajiro Bay (Fig. 3)

As is shown in Figure 3, no hagfish less than 21 cm in total length was caught in Koajiro Bay. Only one male and 18 females were trapped in two collections in October 1972 (Table 2). The male was 39 cm in total length, and the 18 females were larger than 40 cm, indicating that larger females first migrate to the Bay. Among November, December, January and February, there was no difference in frequency distribution histograms of the total length except for the time between November and February ($p<0.01$). This difference is due to the fact that the hagfish about 30 to 40 cm in length increased in February in Koajiro Bay. Such an increase began from November, showing that these smaller hagfish migrate from deeper water to Koajiro Bay. The frequency distribution histograms in March, April, May and June differed significantly from each of those of previous months before March ($p<0.01$ in each). These differences are due to the facts that fish between 21 and 35 cm in length increased remarkably beginning from March. There was a significant difference in frequency distribution histograms between April and May ($p<0.001$). This difference is attributed to the decrease in larger hagfish (≥39 cm) in May, possibly due to their migration to deeper water. There was also a significant difference in frequency distribution histograms between May and June ($p<0.05$), which may be attributed to the fact that smaller hagfish (< 39 cm) also begin to migrate to deep water in June.

(2) Water of 50 m deep (Fig. 4)

As is shown in Figure 4, hagfish less than 21 cm in total length were rarely caught in water of 50 m depth. There was no significant difference in frequency distribution histograms among January, February, March, April and May. From January to April, hagfish larger than 48 cm could not be caught, which contrasted with data of Koajiro Bay. There were significant differences in histograms between February and those of June, July and August ($p<0.05$), and between March and August ($p<0.05$). The differences in the shape of histograms of June, July and August from those of February and March are attributed to the increase in larger hagfish (≥42 cm), and may result in the migration from the shallow water. There were significant differences in histograms between October and May ($p<0.05$), June ($p<0.01$), July ($p<0.05$) and August ($p<0.01$), which were characterized by the decrease in larger hagfish in October. Such decrease in larger hagfish in October may be explained by their moving to the spawning ground somewhere to deeper water, greater than 50 m depth, rather than by their migration to shallow water, since all females collected in Koajiro Bay in October were post-spawning ones (see Nozaki *et al.*, 2000). The frequency distribution histograms of November and December were different from those of other months ($p<0.01$ or $p<0.001$), which were characterized by the increase in relatively large hagfish (≥36 cm). A similar tendency was also observed in the frequency distribution histograms of January. Such increases in relatively large hagfish in November, December and January are apparently strange phenomena in the light of the earlier migration of larger hagfish to shallow water, and will be explained in Discussion.

(3) Comparison of the total length between Koajiro Bay and water of 50 m depth

To compare the total length between Koajiro Bay and water of 50 m depth, all hagfish collected during November through April were analyzed. However, it should be noted that the hagfish collected in water of 50 m depth might include both the migrating and the remaining populations, since the migration from deep to shallow water seemed to continue from October to March of the following year (see above). The mean total lengths (±SEM) of the hagfish collected in Koajiro Bay and water of 50 m depth during November through April were 43.3±0.7 cm (n=1,796), and 34.3±0.9 cm (n=689), respectively, and thus they were quite different ($p<0.001$). The frequency distribution histograms also differ significantly ($p<0.001$)(Fig. 5). This difference between the histograms comes from the facts that in Koajiro Bay more than half (63.6%) of the hagfish were larger than 39 cm in length, whereas in water of 50 m depth, 75.0% of the hagfish were less than 39 cm.

5. Failure to find the spawning ground or to collect fertilized eggs

Sixteen net sweepings in total, which were carried out at depths from 40 to 110 m in October and November (Fig. 1), failed to collect eggs or juveniles. As shown partly in Figure 1, the depth of water increases gradually toward 100 m, and then increases suddenly to about 700 m. Therefore, the spawning ground may be in water of more than 100 m depth, and juvenile hagfish may spend their life there until they grow to about 20 cm in total length.

6. Characteristics of the habitat

In Koajiro Bay, the surface of the bottom is covered with mud to a certain depth. The mean particle size in the mud layer is less than 53 μm. Under this mud layer, there seems to be a layer of sand with mean particle sizes of 53–210 μm. In water of 50 m depth, the bottom surface seems to be covered by a layer of sand of less than 53 μm particles mixed with sediments to certain depth, and beneath it there seems to be a layer of sand with 53–210 μm particles. The upper sand layer contains protozoa and dead plankton. In the intestines of the hagfish caught in water of 50 m depth, fine sands of less than 53 μm particle size, protozoa, plankton and others were found. Therefore, it is possible that these microorganisms could be utilized as food in the hagfish living in deep water. Shelton (1978) also reported that the hagfish, *Myxine glutinosa*, are carnivorous, carrion feeders, and/or scavengers.

DISCUSSION

Migration general

Dean (1904) found that the hagfish, *E. burgeri*, inhabit shallow water of 6 to 10 m depths of Koajiro Bay except during September and October. However, we could not find them during July, August in addition to September and October in Koajiro Bay (Kobayashi *et al.*, 1972; the present study). This difference which had occurred during 70 years is difficult to explain. Furthermore, we found that they live in water of 50 to 100 m depths in September and October and suggested that they engage in migratory behavior (Kobayashi *et al.*, 1972). These findings were extended considerably by the subsequent studies. Namely, Fernholm (1974), by SCUBA diving, observed many hagfish in Koajiro Bay during the period from late October through early June, but no hagfish were found there during the remaining period. Patzner (1977, 1978) reported annual changes in the testis and ovary using the hagfish collected in Koajiro Bay from October to June and in water of 50 or 100 m depth from July to September. In another study, Tsuneki *et al.* (1983) also observed the seasonal migration and seasonal gonadal changes of this species near the Oki Islands in the Japan Sea. Thus, *E. burgeri* seems to migrate generally between shallow water and water of at least 50 to 100 m depths. However, all these reports mentioned above were inferred from indirect evidence that the hagfish were absent from shallow water during months from July to September, and that they were collected in water of about 50 m depth. In the present study, we obtained direct evidence from recovery of marked hagfish at sites different from the place of marking. This is the first report which indicates directly that there is the seasonal migration of the hagfish, *E. burgeri*, between shallow water of Koajiro Bay and/or Moroiso Bay and deep water more than 50 m of Sagami Bay. A high percentage of the recovery (31.1%) recorded in the hagfish which were marked in water of 50 m depth and recaptured in Koajiro Bay or Moroiso Bay, suggests that most hagfish living in Koajiro Bay and Moroiso Bay come from water of 50 m depth. On the other hand, only 1.7% of recovery was recorded in the hagfish which were marked in Koajiro Bay and recaptured in water of 50 m or 100 m depth. This low percentage of recovery is considered to be due to the following complex of factors: 1) The number of the hagfish recaptured in water of 50 and 100 m depths was smaller (939 and 74, respectively) than those released (1,323), 2) the areas of water of 50 and 100 m depths were too wide to survey thoroughly, 3) collected hagfish included those stayed there throughout the year, and 4) it may also be likely that marked hagfish moved to water deeper than 100 m depth. Despite such a low percentage of the recovery, the present result clearly shows that migration of the hagfish from Koajiro Bay to water of more than 50 m depth occurs.

In the present study, number of hagfish collected per trap was more than two times greater in water of 50 m depth than in Koajiro Bay. However, the distances between traps were less than 10 m in Koajiro Bay, whereas they were about 50 m in water of 50 m depth. Thus, it is not clear whether the difference of number of animals collected per trap between two collection sites reflect the difference of the population density between two or not.

Migration, body length and gonads

From collection data and marking data, it is suggested that (1) larger hagfish (≥39 cm) migrate from water of 50 m depth to shallow water of Koajiro Bay and Moroiso Bay after mid October, whereas smaller hagfish (<39 cm) begin to migrate to shallow water after November, with peaks after March, and 2) larger hagfish (≥39 cm) begin to migrate to deep water from May, whereas smaller hagfish (< 39 cm) begin to migrate to deep water in June, and thus all hagfish complete the migration to deep water by mid July. In a separate study of this hagfish population (Nozaki *et al.*, 2000), most hagfish larger than about 40 cm in length living either shallow or deep water have maturing gonads, and most females larger than 40 cm, which migrated to Koajiro Bay during October and November, have post-ovulatory follicular capsules. Thus, it is possible, therefore, that the migration is initiated by reproductive populations of the hagfish larger than 40 cm in total length in both ways.

The present study also showed that in water of 50 m depth the percentage of larger hagfish (≥36 cm) increased during the months from November to January. However, such increases in larger hagfish in water of 50 m depth are difficulat to understand, since they should be decreasing in numbers due to the migration to shallow water. One possible explanation is that they came from other places of origin such as water of 100 or more than 100 m in depth. It is further likely that some specimens were trapped on their way to shallower water, since one hagfish marked in Koajiro Bay was recaptured in water of 100 m depth.

Spawning ground

In a previous study (Kobayashi *et al*., 1972), we could not find hagfish in October at Koajiro Bay or Moroiso Bay, but found hagfish in water of 50 m depth. We considered that the spawning ground may be located in water of 50 m depth (Kobayashi *et al*., 1972). However, in the present study, net sweeping of the bottom of water of 50 to 110 m depths failed to collect eggs or juveniles. Further, hagfish less than 20 cm in total length were rarely found at water of 50 m depth. Therefore, the spawning ground may not be located around 50 m depth. It seems possible that it is located at water deeper than 100 m.

Factors initiating migration

Since smaller hagfish (<36 cm) with immature gonads (Nozaki *et al*., 2000) also migrate to shallow water of less than 10 m, the adaptive significance of the seasonal migration between shallow and deep waters does not seem to be simply a reproductive requirement. Food requirement is another possibility for the motivation of migration. However, even this possibility may not be the primary factor for the migration for the following reasons: 1) In the 1970s, during the course of our study, there were large floating fish enclosures (ikesu), made of nets and containing anchovy for bait of tuna fishing in Koajiro Bay (see Fernholm, 1974). One enclosure contained about 10 tons of fish and the numbers of enclosures varied during the year from a few to about 100. During tuna fishing season, May, June and July, there were many fish enclosures, and many fish in the enclosures died because of the high water temperature and fell down to the bottom of the sea. Thus, food was most abundantly supplied and available for hagfish during May through July, when they migrate out of the Bay. 2) In a pioneer study, Dean (1904) collected hagfish in shallow water almost throughout the year except September and October. This means that hagfish lived in shallow water for a much longer period in the past than during our study, although there were no floating enclosures in days of Dean. Salinity and temperature are known to be limiting factors for all known species of hagfish (Martini, 1998). Indeed, Fernholm (1974) claimed that temperature may provide an important stimulus for migration of *E. burgeri*. However, temperature is more stable in deeper water, and thus migration from deep to shallow water would not seem to be initiated by temperature and/or salinity. Probably, the integration of several factors, such as food supply, water temperature, and population density, etc., may be the promoting factors for the migration of *E. burgeri*.

Finally, the present study has demonstrated directly that there are seasonal migrations of the hagfish, *E. burgeri*, between shallow water of Koajiro Bay and deep water of Sagami Bay, although initiating factors are not known. Spawning sites are considered to be in waters of more than 100 m depth.

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