Original Article

Spawning time and place of the Japanese eel 
Anguilla japonica in the North Equatorial Current of the western North Pacific Ocean

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ABSTRACT: The location and timing of spawning of the Japanese eel Anguilla japonica was studied during two research cruises of the R/V Hakuho Maru and R/V Suruga Maru in the North Equatorial Current of the western North Pacific Ocean during June–September 1998. There were 38 A. japonica leptocephali (10.0–43.2 mm in total length (TL)) collected in three areas: 24 specimens around the Arakane and Pathfinder Seamounts in June (approx. 16°N and 143°E) and five specimens at the southernmost station (13°N) and nine specimens at the northernmost station (17°N) of a transect along 137°E in September. The average total lengths of the leptocephali were significantly different among the three areas, with those around the seamount being smallest, those at the northern station being largest, and none being collected along the easternmost 144°E transect. This and the currents in the region suggested that spawning of A. japonica occurred near some of the seamounts in the West Mariana Ridge. Back calculated spawning dates indicated that most leptocephali were born during the new moon, supporting the hypothesis that A. japonica spawns around the new moon. Analysis of otolith daily rings found a strong correlation between total length and age \((r=0.97)\), and the average daily growth rate was about 0.5 mm/day.

KEY WORDS: Anguilla japonica, New Moon Hypothesis, otolith, Seamount Hypothesis, spawning date.

INTRODUCTION

The spawning area of the Japanese eel, Anguilla japonica, was discovered to be within the North Equatorial Current west of the Mariana Islands in

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accepted and is essentially the same pattern that has been observed in the American eel Anguilla rostrata in the western North Atlantic Ocean.4

Tsukamoto et al.5 have analyzed the otolith microstructure of the Japanese eel leptocephali collected near the estimated spawning area and found evidence of lunar periodicity of spawning. Together with more detailed analyses using scanning electron microscope observations (Lee et al. unpubl. data, 1995), the ‘New Moon Hypothesis’ has been developed to explain the timing of eel spawning.2,5 This hypothesis proposes that spawning eels may use the new moon period of the lunar cycle to synchronize the timing of the final stage of maturation and the initiation of spawning behavior.

However, neither matured adults nor eggs have been collected or observed anywhere around the estimated spawning area, and the number of leptocephali used for otolithe analysis has been limited, so these two hypotheses need additional verification. Therefore, detailed data on the distribution of leptocephali around the inferred spawning area and additional otolithe samples are needed to verify the two hypotheses.

In this study, we carried out research cruises on the R/V Hakuho Maru and the R/V Suruga Maru to sample for A. japonica leptocephali around the West Mariana Ridge and in the North Equatorial Current during June–September 1998. We report the distribution and size of the leptocephali collected during these two cruises, and analyze the growth rates of these leptocephali based on counts of the daily growth rings in their otoliths and use these data to evaluate the two hypotheses about the location and timing of spawning of A. japonica.

MATERIALS AND METHODS

During the cruise on the R/V Hakuho Maru (from 22 May to 2 July 1998) of the Ocean Research Institute, the University of Tokyo, A. japonica leptocephali were collected around the Arakane and Pathfinder seamounts using an Isaacks Kidd Midwater Trawl (IKMT) with an 8.7 m² mouth opening and 0.5 mm mesh. Tows were either oblique from the surface to depths of 300 or 500 m, or horizontal step tows, with the depth strata of the step tows being selected based on the location of the halocline observed in the CTD (conductivity, temperature, depth measurement system; Sea-Bird Electronics, Inc., Washington DC, USA) casts at each station. Two or three depth strata were sampled at either 50, 75, 100, 150, 250 or 300 m depths during each step tow. The sampling stations were located within 1.2–5 km from the top of each seamount, except for three stations between the two seamounts (Fig. 1).

During the cruise on the R/V Suruga Maru of the Shizuoka Prefectural Fisheries Experimental Station (from 17 August to 14 September 1998), A. japonica leptocephali were collected using an IKMT with a 2.8 m² mouth opening and 0.5 mm mesh. All tows were oblique from the surface to a depth of 300 m. Ten tows were made in a transect between 13°–18°N along the 144°30’E line, seven tows were made between 13°–17°N along the 137°E line, six tows at three stations at 13°25’–14°N and 138°E–141°18’E, and two tows were made around a seamount located at 14°13’N and 142°56’E, which we called the Suruga Seamount (Fig. 1).

All leptocephali collected during the two cruises were identified using myomere counts made on board and their total length (TL) measured. After identification using morphological features, the leptocephali were preserved in 99% ethanol. The identifications of leptocephali were confirmed in the laboratory using a mitochondrial DNA method.6 Out of 38 A. japonica leptocephali collected during two cruises, 17 specimens were subsampled for otolith analysis, with five from the Hakuho Maru cruise and 12 from the Suruga Maru cruise being used (Table 1).

Sagittal otoliths were extracted from the leptocephali and mounted in Euparal (Schmidt GmbH, Koengen, Germany) on a glass microscope slide. Grinding and polishing were not required because the otoliths were thin and transparent. Increments were traced on paper using a light microscope with a drawing system at 1000×. The ages in days after...
hatching were estimated based on the number of daily increments outside the hatch check. The spawning date (date of fertilization) was estimated for each individual using the sampling date and the estimated age plus 2 days, because the eggs from artificially induced spawning of captive *A. japonica* have been shown to hatch 36 h after fertilization.\(^8,9\) The equation of the linear regression line between age and *TL* was calculated by the least square method and the value of its slope was regarded as an overall growth rate for *A. japonica* leptocephali. In addition, the growth rate of each individual was calculated as \((TL - 3)/age\), assuming that the size at hatching was about 3 mm\(^10,11\).

### RESULTS

#### Distribution of leptocephali

A total of 38 *A. japonica* leptocephali ranging from 10.0 to 43.2 mm were collected in three areas.
during June and September, 1998 (Table 1). Twenty-four specimens were caught around the seamounts in June. Along the 137°E line, five and nine specimens were caught at the southernmost station and at the northernmost station in September, respectively (Table 1; Fig. 1). The five leptocephali collected at 16°4′19″N and 143°14′56″E were the easternmost specimens of *A. japonica* ever recorded. No *A. japonica* leptocephali were collected along the easternmost 144°E line, or around the Suruga Seamount.

The largest of the specimens (43.2 mm *TL*) was collected at 17°N and 137°E during the *Suruga Maru* cruise, and the smallest (10.0 mm *TL*) was collected at 15°39′N and 142°45′E during the *Hakuho Maru* cruise. The average total length and standard deviation (± SD) of *A. japonica* was 16.6 ± 4.9 mm near the seamounts, 23.6 ± 2.3 mm at the southern station on the 137°E line, and 36.2 ± 3.2 mm at the northern station on the 137°E line. The average total lengths of the leptocephali collected at these three sampling areas were significantly different (ANOVA, *P*<0.05).

**Age**

The estimated ages of the 17 specimens showed a wide range of 12–73 days (Table 1). The average ages were significantly different among the three sampling areas (ANOVA, *P*<0.001) with no overlap in their ranges. The specimens around the seamount were the youngest (12–25 days), those at the southern station on the 137°E line were the second youngest (36–42 days), and those at the northern station on the 137°E line were the oldest (62–73 days).

**Spawning date**

The leptocephali collected during the two cruises could be divided into three groups: (i) May born (including one specimen born in June); (ii) June born (including some specimens born in July); and (iii) July born. The inferred spawning dates of the specimens collected around the seamounts ranged from 15 May to 2 June 1998, those of the specimens from the northern station on the 137°E line ranged from 22 June to 3 July 1998, and those of the specimens from the southern station on the 137°E line ranged from 21 to 27 July 1998. The new moon dates from May to July in 1998 were 26 May, 24 June, and 23 July. Therefore, the spawning dates of these three groups were distributed around the new moon dates of each month (Fig. 2).

**Growth**

The *A. japonica* leptocephali that were collected during the *Hakuho Maru* and the *Suruga Maru* cruises showed a strong linear relationship between total length (*TL*) and age (*D*) with the following linear regression equation (Fig. 3):

\[
TL = 0.46 \times D + 2.39 \quad (r = 0.97, n = 17),
\]
where $r$ is the correlation coefficient and $n$ is the number of specimens.

The overall growth rate for *A. japonica* leptocephali ranging in length from 10.0 to 37.0 mm $TL$ was 0.46 mm/day.

The individual growth rates ranged from 0.45 to 0.68 mm/day (Table 1). The average and SD of the individual growth rates for all the specimens examined was 0.53 ± 0.07 mm/day. The average individual growth rate of the specimens collected around the seamounts was 0.59 ± 0.06 mm/day (range 0.53–0.68 mm/day, $n=5$), that of the specimens from the southern station on the 137°E line was 0.53 ± 0.07 mm/day (range from 0.45 to 0.59 mm/day, $n=5$), and that of the specimens from the northern station on the 137°E line was 0.50 ± 0.05 mm/day (range from 0.45 to 0.59 mm/day, $n=7$). There were no significant differences in the average individual growth rates among the three sampling areas (ANOVA, $P>0.05$, Table 1).

## DISCUSSION

### Spawning place and timing

Presently, the only successful method of estimating the spawning areas of anguillid eels is to examine the distribution and size of their leptocephali in the ocean. In the present study, we reported the easternmost record of an *A. japonica* leptocephalus around the Pathfinder and Arakane Seamounts at 143°E, and simultaneously observed the absence of *A. japonica* leptocephali at all the sampling stations between 13 and 18°N along the 144°E line to the east of the seamounts. The total lengths of the leptocephali that were collected during this study were smallest at the sampling stations between 13 and 18°N along the 144°E line to the east of the seamounts. The total lengths of the leptocephali that were collected during this study were smallest at the sampling stations in the east (Fig. 1). This was consistent with the results of the previous studies,2,3 and supported the hypothesis that *A. japonica* spawns around the seamounts on the West Mariana Ridge (Seamount Hypothesis).2,4

Almost all leptocephali were born around the period of the new moon, indicating *A. japonica* consistently spawns during a several-days period around the new moon (New Moon Hypothesis, Fig. 2).2,5 The relatively wide range of spawning dates around the new moon dates may have been a result of errors in the aging of the specimens, and the actual range of spawning dates might coincide more closely with the new moon dates. From March 1997 to March 1998, a large-scale El Nino occurred, and its influence would have remained until May 1998.18,19 Therefore, the specimens collected during the *Hakuho Maru* cruise included leptocephali born under the influence of El Nino. However, these leptocephali also were born around the time of the new moon, so the influence of El Nino on the synchronization of spawning to the new moon is still unclear.

This study verified that *A. japonica* spawns near the seamounts of the West Mariana Ridge during the new moon lunar phase within their April–November spawning season.20 Therefore, the two hypotheses, the Seamount Hypothesis and the New Moon Hypothesis, were supported by the distribution and aging data from the *A. japonica* leptocephali collected during this study. Further detailed studies of the distribution and spawning dates of more leptocephali from a wider geographic area in relation to hydrographic features will enable a more complete evaluation of the two hypotheses, but the collection of eggs, even smaller leptocephali or matured adult eels at the spawning place will be necessary to finally resolve the question of the exact spawning place of the Japanese eel.

### Larval transportation

In the North Equatorial Current area, there is relatively fast westward flow (20–40 cm/s) in the surface layer in the south (from 10 to 16°N) and slower flow (10–20 cm/s) in the north (>16°N).21,22 In the deeper layers in the North Equatorial Current, slower velocities of 10–20 cm/s in the south and approximately 10 cm/s in the north have been observed.22 Considering the vertical migration of the leptocephali of *A. japonica*, which were found in the surface layer at night-time and in deeper layers during the daytime,23 the maximum velocities of passive transportation of the leptocephali may be approximately 30 cm/s in the southern area and approximately 15 cm/s in the northern area if it is assumed that the durations of daytime and night-time are approximately the same. Therefore, the leptocephali could arrive at the 137°E line from the seamounts of the West Mariana Ridge after 23 days in the southern area and after 46 days in the northern area. The average age of the leptocephali collected at the southern and northern stations on the 137°E line were 39 days and 67 days, respectively. The 16- or 21-day difference between the calculated period of transport days and the ages of leptocephali would suggest that they were not transported directly from the West Mariana Ridge. In fact, some eastward counter flows have been observed in the North Equatorial Current area, and even around the Pathfinder seamount.22 In addition, Argos satellite-tracked buoys showed the existence of complex eddies around the Arakane and...
Pathfinder seamounts (Inagaki et al. unpubl. data, 1998). Therefore, most of the *A. japonica* leptocephali that were spawned near a seamount during a new moon period would be generally transported westward, but sometimes part of the cohort may be transported by eastward countercurrents or trapped in eddies around the seamounts. Thus, even though some relatively large *A. japonica* leptocephali (10.0–26.0 mm TL) have been caught at the estimated spawning area near the seamounts, and the ages of some leptocephali have exceeded the calculated period of transport days, the physical oceanographic conditions in the area indicate that these observations do not conflict with the hypothesis that *A. japonica* spawns around the West Mariana Ridge.

The *A. japonica* leptocephali collected during the two cruises could be categorized into three groups, based on when they were spawned and the different oceanographic conditions that they experienced, to explain the distribution and ages of leptocephali during this study: (i) leptocephali born in May and caught by the eddies surrounding the seamounts; (ii) leptocephali born in June and transported through the slow flow area in the northern part of the North Equatorial Current; and (iii) leptocephali born in July and transported through the fast flow area in the southern part of the North Equatorial Current. The majority of May-born and June-born fish would have been transported further west by the North Equatorial Current and would have been outside of the area surveyed in this study.

**Growth of leptocephali**

There was a strong relationship between TL and age over a wide range of lengths in the leptocephali examined in this study and in previous studies of the age and growth of *A. japonica* leptocephali. The average individual growth rate (0.53 ± 0.07 mm/day; mean ± SD) obtained for *A. japonica* leptocephali ranging from 10.0 to 37.0 mm TL in this study was not significantly different (ANOVA, P > 0.05) from those in the previous studies that had specimens ranging from 19.5 to 45.9 mm TL.24,25 Similarly, the overall growth rate (0.46 mm/day) obtained from the regression between TL and age (Fig. 3) was not significantly different (ANOVA, P > 0.05) from the growth rates of 0.56–0.59 mm/day that had been previously reported.24,25 Therefore, because the total number of leptocephali that have been analyzed for growth rates are still relatively small, the best estimate of the overall growth rates of leptocephali should be obtained by combining the data from the different studies.

When the data from previous studies were combined,24,25 the relationship between TL and age (D) was estimated by the following equation:

\[
TL = 0.52 \times D + 5.49 \quad (r = 0.96, n = 32), \quad (2)
\]

where \( r \) is the correlation coefficient and \( n \) is number of specimens.

When Eqns 1 and 2 were compared, the slopes were not significantly different from each other (ANOVA, \( P > 0.05 \)), but the second terms (y-intercepts) were different (ANOVA, \( P < 0.05 \)). The second terms of these equations indicate the total length of leptocephali at hatching and were smaller in Eqn 1 and larger in Eqn 2 than the 2.9 mm hatching length observed in leptocephali produced from artificial maturation and spawning experiments.9 When the data from two previous studies\(^{24,25} \) are combined with those of the present study, the relationship between TL and age (D) was estimated by the following equation:

\[
TL = 0.51 \times D + 2.09 \quad (r = 0.96, n = 49), \quad (3)
\]

where \( r \) is the correlation coefficient and \( n \) is number of specimens.

Thus, the strong relationship between TL and age of a substantial number of specimens (49) over a wide range of lengths in equation 3 indicated that the best estimate of an overall growth rate of *A. japonica* leptocephali is approximately 0.5 mm/day.

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