Spawning Ecology of Anadromous Wakasagi, *Hypomesus nipponensis* inhabiting Hei River in Iwate, Japan

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(Accepted June 5, 2003)

**Abstract:** Spawning ecology of Anadromous Wakasagi, *Hypomesus nipponensis* was investigated from 1995 to 1998 in the Hei River during the spawning season. Upstream migration began when water temperature rose to about 10°C. Peak upstream migration always began after the snow thaw disappeared. After that, upstream migration peaks were confirmed to occur in a semi-lunar spawning cycle. For four years, the sex ratio of upstream migration of *H. nipponensis* was biased toward males. Females increased on the day before or after a new moon. The longer the spawning period progressed, the greater the decrease in body size of *H. nipponensis* was in every year; body size changed from year to year with even years being large and odd years small. On the contrary, the upstream migration period changed from year to year: even years were short; odd years were long. The female body size was larger than the male's when individual growth was promoted during the year. On the other hand, few sex-correlated body-size differences existed when individual growth was inhibited during the year.

**Key words:** *Hypomesus nipponensis*; Anadromous; Spawning ecology; Lunar cycle

Anadromous Wakasagi, *Hypomesus nipponensis* (McAllister), is a member of Osmeridae, Salmonoidei1. Two other species of *Hypomesus* are distributed in Japan: *H. olidus* and *H. japonicus* (Pallas). *H. olidus* in Japan are landlocked, while in other countries they are anadromous. *H. japonicus* inhabits brackish or coastal waters. *H. nipponensis* are now distributed throughout Japan in more than 100 lakes and rivers due to artificial propagation of eggs2. Eyed eggs of *H. nipponensis* were exported to California in 1950s3 and have established a spawning population in the Sacramento-San Joaquin estuary, threatening the endangered and endemic Delta Smelt, *H. transpacificus*4.

*H. nipponensis* are separated into a landlocked type and anadromous type5. Biologies of anadromous type populations, which inhabit brackish lakes, and landlocked type populations were widely investigated because they comprise an important resource for both commercial and recreational fisheries2,5-9.

However, there has been no investigation on the river spawning population of anadromous type except for a few studies conducted at the Ishikari River in Hokkaido10,11. Upstream spawning migration has never been studied in detail because there are multiple year classes and different body sizes at maturation in the same year class, making such study extremely difficult to conduct8,11,12.

In this study, timing of spawning migration is documented and discussed in connection with environmental factors, change in sex ratio, and body size as well as the reproductive strategy of anadromous *H. nipponensis* in the Hei River, Iwate Prefecture.
Materials and Methods

The Hei River extends 73.5 km west to east from its source located in the Kuzakai Highlands; it flows into Miyako Bay, situated on the Eastern seaboard of Iwate Prefecture, Northern Japan (Fig. 1). The width at the river mouth is 200 m. Akanuma Dam, with total width of 300 m, is located 3.0 km upstream of the river mouth. The waterway through its length is 182 m with two fish-ways in the center. Dam height is 0.9 m, the crown width is 1.65 m, and the apron length is 5.9 m. Water velocity is 2.0 m/sec in the fish-ways (at 15:00 on May 20, 1996). Most fish cannot swim upstream beyond this dam and are retained below it. Sampling was conducted at the downstream area of this dam. *H. nipponensis* were captured from 1995 to 1998 by cast net (3 m diameter, mesh size: 5 mm × 5 mm) in the spawning area from April to July.

Changes in water volume, influx of snow thaw, and surface water temperature were observed at 17:00 every day at the study site. A 24-hour survey conducted on May 20, 1996 revealed that upstream spawning occurred just before and after sunset. Based on this finding, both sampling and surveys were conducted daily from 17:00 to 20:00 in the spawning area during the spawning season: April to June from 1995 to 1998. During the survey period, water level (depth), amount of flow and suspended matter increased due to thawing of snow in the upper reaches. This is referred to as ‘snow thaw’ in the present paper.

We defined spawning school size as the maximum number of individuals caught per cast of a cast net (1: less than 20 fish caught, 2: 20-40 fish, 3: 40-70 fish, 4: 70-100 fish, 5: more than 100 captured). We also defined water volume by measuring water depth using a 1-m-long pole installed at the top of the dam (1: less than 0.2 m, 2: 0.2-0.4 m, 3: 0.4-0.6 m, 4: 0.6-0.8 m, 5: more than 0.8 m).

Sex of captured individuals was determined by examining gonads. Standard length (SL) was measured to the nearest 0.1 mm using vernier calipers. Specimens were fixed and preserved in 10% fresh water formalin. A total of 4,937 individuals were measured. The abdominal area of individuals was pushed to ascertain if the specimen had matured. Because we confirmed that more than 90% of samples matured, we assumed the migration to be for upstream spawning. Age determination of *H. nipponensis* using scales was conducted on populations inhabiting Lake Ogawara, Ishikari River, and Lake Abashiri. However, results were inconsistent and were unsatisfactory. *H. nipponensis* in spawning period, inhabiting Lake Abashiri, Lake Suwa, Lake Kasumigaura were treated as 0+ year old fish for analysis. Age determination of *H. nipponensis* using otolith was established in Lake Ogawara. However, Katayama’s technique, when used on *H. nipponensis* inhabiting Lake Abashiri, Lake Sagami, Lake Kasumigaura, and the Hei River obtained unsatisfactory results. Therefore, reliability of age determination of *H. nipponensis* using otolith is
doubted by researchers. In this paper, all individuals were treated as 0+ year old fish for analysis.

Results

Changes in water temperature

The relationship between water temperature and spawning school size is shown in Fig. 2. In all four years, upstream spawning migration commenced once water temperature exceeded 8°C; it terminated when temperature exceeded 18°C. The peak of upstream spawning migration occurred between 9°C and 17°C each year.

In 1995 and 1997, the spawning period was short; upstream spawning migration terminated when temperature exceeded 16°C. In 1996 and 1998, when the spawning period was long, upstream migration terminated when temperature exceeded 18°C.

Changes in snow thaw and water volume

Table 1 shows average water temperature and average water volume of the Hei River during the survey period. The survey period is divided into three periods: the starting period, from the onset of the upstream migration; the snow thaw period, from the end of snow thaw to spawning period termination. (1) Upstream migration began when the temperature (four years average temperature ± SD) reached 9.9 ± 0.4°C. (2) The snow thaw period began subsequently. During this period, mean temperature was 8.9 ± 0.1°C; mean water volume was 3.4 ± 0.2. Upstream migration to the spawning area decreased. (3) After snow thaw ended, water temperature increased to 11.3 ± 0.3°C and water volume decreased to 2.2 ± 0.7, followed by the upstream migration peak.

Spawning school size

Figure 3 shows daily changes in spawning school size and period of snow thaw during the four-year study period. Even years exhibited small spawning school size and short spawn-

<table>
<thead>
<tr>
<th>Year</th>
<th>Start of upstream migration</th>
<th>Period of snow thaw</th>
<th>Period of the first peak of upstream migration</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Temperature</td>
<td>Water volume</td>
<td>Temperature</td>
</tr>
<tr>
<td>1995</td>
<td>Apr. 22 ~ Apr. 26</td>
<td>9.0 ± 0°C</td>
<td>3.8 ± 0.84</td>
</tr>
<tr>
<td>1996</td>
<td>Apr. 23 ~ Apr. 25</td>
<td>9.7 ± 0.58°C</td>
<td>2.0 ± 0</td>
</tr>
<tr>
<td>1997</td>
<td>Apr. 19</td>
<td>Apr. 20 ~ Apr. 24</td>
<td>2.0 ± 0</td>
</tr>
<tr>
<td>1998</td>
<td>Apr. 7</td>
<td>Apr. 12</td>
<td>11.0 ± 0°C</td>
</tr>
<tr>
<td>Average</td>
<td>9.9 ± 0.37°C</td>
<td>2.0 ± 0</td>
<td>8.9 ± 0.14°C</td>
</tr>
</tbody>
</table>

*4 Personal communications.
Fig. 3. Daily changes in spawning school size and period of snow thaw during the four year study period.

Fig. 4. Changes in spawning school size from 1995 to 1998 at each date of lunar calendar. The first day is the day of a new moon. Total spawning school sizes were pooled for all years from 1995 to 1998.

The new moon always occurred on Day 120. Although the new moon occurs twice during the two-month period from April to May of the solar calendar, Day 120 is the new moon day, on which school size is the largest (Fig. 4). In respective years, Day 120 occurred on the following dates (1995: April 30; 1996: May 17; 1997: May 7; 1998: May 26). The adjusted date was termed the “synchronized lunar day”.

During all four years, the sex ratio (female/male) was biased toward males (1995; female/male = 0.18, 1996: 0.41, 1997: 0.47, 1998: 0.51). Changes in the daily sex ratio were significantly different during all four years (1995, $\chi^2 (8) = 47.32, p<0.001$; 1996, $\chi^2 (14) = 392.72, p<0.001$; 1997, $\chi^2 (10) = 237.10, p<0.001$; 1998, $\chi^2 (12) = 185.71, p<0.001$). Results of dispersion analysis show the sex ratio to be biased toward males during the early days of upstream spawning migration, while females gradually increased until the day before or after synchronized lunar day 120. However, as the upstream spawning migration period progressed, the sex ratio again became biased toward males ($p<0.001$).

Body size

1) Daily changes in body size

Figure 6 shows daily changes in the mean standard length – hereafter referred to as “body size” – during spawning periods from 1995 to
1998. Body sizes were small in the early days of upstream spawning migration, but it gradually increased and attained a maximum size on the following dates: Apr. 29, 1995; May 8, 1996; 1997 - not significant; May 8, 1998. After these dates, body size decreased as the spawning season progressed.

Body size differed significantly from day to day in all four years (1995 - F (7, 909)=16.85, p < 0.01; 1996 - F (15, 1582)=13.34, p < 0.01; 1997 - F (10, 1037)=8.02, p < 0.01; 1998 - F (12, 1177) =50.17, p < 0.01).

2) Annual changes in body size

Figure 7 shows the body size (mean standard length) distributions of *H. nipponensis* captured in the spawning area from 1995 to 1998. Body size fluctuated greatly from year to year (F (3, 4749)=1298.49, p<0.0001). Body size (± SD) of each year was: 1995 - 102.2±8.2 mm. 1996 - 86.8±10.6 mm; 1997 - 96.2±8.9 mm; 1998 - 78.0±10.1 mm. In odd years, body size was large; in even years, it was small. The largest body size occurred in 1995, while the smallest size was in 1998.

3) Sexual difference in body size

Body size of females was larger than that of males in 1995, 1996 and 1997 (Mann-Whitney U-test, 1995-z=-9.56, p<0.01; 1996-z=-2.84, p<0.01; 1997-z =-2.74, p<0.01). However, in 1998 no sexual difference in size was found (Mann-Whitney U-test, z=-0.96, n.s.).

Biological minimum sizes for males and females over the four year study period are as follows (1995: male-78.4 mm, female-88.2 mm; 1996: male-61.2 mm, female-62.5 mm; 1997: male-75.2 mm female-73.6 mm; 1998: male-55.4 mm female-61.0 mm).

**Discussion**

**Environmental factors**

The upstream spawning migration peak always occurred after disappearance of snow thaw. In other words, snow thaw is a limiting factor of upstream spawning migration in *H. nipponensis* (Fig. 4). In addition, after the water cleared, peaks in upstream spawning migration were observed; they were synchronous with the semi lunar spawning cycle (Figs. 4, 5). During this season, high tide of new or full moon occurs at sunset. The lunar tidal cycle also affects upstream migration peaks. From the
above, it is clear that *H. nipponensis* select not just specific water temperature, water volume and snow thaw, but also the lunar cycle as factors in determining upstream migration for spawning.

**Comparison of spawning periods from other sites**

In the Hei River, the spawning period fluctuated from year to year. In all four years, the period is from the beginning of April to the end of June, with the peak period occurring during the period from the end of April to the end of May (Fig. 4). Table 2 shows spawning periods of *H. nipponensis* inhabiting lakes and rivers in Japan. There is a clear geographical cline in the spawning period, earlier in the south and later in the northern regions. In Lake Ogawara, the spawning period extends from the end of March and to the beginning of April, when the temperature exceeds 5°C. A peak is visible at the beginning or middle of April when the temperature is 6°C.

The spawning period of Lake Abashiri is similar to that of the Hei River. Still, the spawning period of Lake Ogawara commences much sooner than in the more northern Hei River. Further environmental and genetic factors must be investigated because this phenomenon remains unexplained.

**Spawning strategy and lunar cycle**

Intersexual differences in fitness cause variations in patterns of maturation and reproductive behavior. Because male gametes are smaller than female gametes and generally require less investment to produce the necessary amounts

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**Fig. 6.** Daily changes in the mean standard length during spawning periods from 1995 to 1998. Body size differed significantly from day to day in all four years (1995 - $F(7, 909) = 16.85, p < 0.01$; 1996 - $F(15, 1582) = 13.34, p < 0.01$; 1997 - $F(10, 1037) = 8.02, p < 0.01$; 1998 - $F(12, 1177) = 50.17, p < 0.01$). An asterisk indicates significant difference from the first day ($p < 0.01$).
of male gametes, more ingested energy can be funneled to individual maintenance and activities to enhance overall fitness of the individual. This causes intra-sexual selection and intense competition among males by having to stay in the spawning area. In contrast to males, females select a strategy to migrate upstream to the spawning area when environmental conditions are more suitable for the survival of offspring.

Our four-year study also found new evidence in the Hei River indicating an increase in females on the day before or after synchronized lunar day 120. Synchronized lunar day 120 is the day of the new moon (Fig. 6). After the new moon, the time of high tide coincides with sunset in this season. This condition is advantageous for upstream migration of females because water volume and temperature are stable and coincide with the cessation of snow thaw.

These inter-sexual differences in migratory behavior explain the annual observation that the sex ratio is skewed towards males at the spawning ground. Males migrate upstream at the onset of the spawning season, creating intense competition among males. Females migrate upstream when the tidal condition is favorable for such migration, at the high tide of the full moon: synchronized lunar day 120.

Similar phenomena are observed between spawning behavior and the lunar cycle in numerous aquatic organisms\(^{(16,19)}\). For example, in the damselfish, *Pomacentrus coelestis*, the semi lunar cycle rhythm is seen in maturing
females; also, spawning behavior is observed frequently during new moons and the full moons. From the above, the anadromous population of *H. nipponensis* exhibits a relationship between female spawning migration and the lunar cycle.

### Body size

1) **Daily and annual changes in body size**

The *H. nipponensis* body size decreased as the spawning period progressed (Fig. 6). Similar phenomena are also observed in Lake Abashiri and Lake Ogawara. This is because larger individuals mature and enter the spawning ground earlier than smaller individuals.

However, in the Hei River, there is a tendency for body size to increase with onset of the spawning season. The same pattern can be seen in upstream migration of Ayu, *Plecoglossus altivelis altivelis*. Initially, body size is small and gradually increases with the onset of the spawning season. Not only investigation of biotic factors such as growth rate, age composition etc., but also that of environmental factors such as temperature or day length, are necessary to further our understanding in the future.

2) **Density effect**

A biannual pattern in fish body size was observed whereby even years engendered large body size and odd years showed small body size. There was also a biannual pattern in the upstream migration period: even years were shorter, while odd years were longer. Thus, in even years when the body size is large, the upstream spawning migration period is short; the opposite is true in odd years. Similar phenomena are also observed in Chum salmon, *Oncorhynchus keta*, and Shirauo, *Salangichthys microdon*.

An inverse relationship between the number of individuals and growth, indicating a "density effect", was confirmed in Lake Suwa. *H. nipponensis* in the Hei River may also show an inverse relationship between the number of individuals and growth. The underlying mechanism of this annual variability in growth, spawning stock size and spawning season duration may be the following. In even years, population size was small, as indicated by the smaller spawning stock size. This affects the growth of individuals through a density effect. Growth is good, yielding a few large individuals. Post-spawning mortality of *H. nipponensis* is high. Therefore, the spawning period is short, with fewer individuals participating in spawning. In odd years, the large population size stunts growth through a density effect. The larger stock size lengthens the spawning season duration.

It was difficult to detect annual changes in environmental factors during the four-year study period from data of the Miyako Meteorological Observatory (Fig. 8). If environmental factors were stable, then growth of *H. nipponensis* in the Hei River would be density-dependent. Although we have constructed a life history model using population size, growth and spawning behavior of anadromous *H. nipponensis* of Hei River based on the density effect as the underlying determinant, it is necessary to elucidate the whole life history of this unique population in the Hei River-Miyako Bay area in order to further strengthen this hypothesis. Especially, the horizontal distribution of juvenile and young *H. nipponensis* during its oceanic life and the food conditions requires further study.

3) **Sexual Differences in Body Size**

In general, female body size was larger than males (Fig. 7). This sexual difference was observed strongly in 1995, when mean body size was the largest. On the other hand, there was limited sexual difference observed in the body size during 1998 when body size was the

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### Table 2. Spawning periods of *H. nipponensis* lakes and rivers of Japan

<table>
<thead>
<tr>
<th>Sampling Site</th>
<th>Spawning Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. Abashiri</td>
<td>Apr. E - June E</td>
</tr>
<tr>
<td>R. Ishikari</td>
<td>May - June</td>
</tr>
<tr>
<td>L. Ogawara</td>
<td>Mar. L - June E</td>
</tr>
<tr>
<td>R. Hei</td>
<td>Apr. E - June L</td>
</tr>
<tr>
<td>L. Hachiro</td>
<td>Mar. L - Apr. E</td>
</tr>
<tr>
<td>L. Haruna</td>
<td>Mar. M - Mar. L</td>
</tr>
<tr>
<td>L. Suwa</td>
<td>Feb. E - Mar. L</td>
</tr>
<tr>
<td>L. Kahoku</td>
<td>Jan. E - Apr.L</td>
</tr>
<tr>
<td>L. Iruka</td>
<td>Feb. M - Feb. L</td>
</tr>
</tbody>
</table>

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Sato (1954)
smallest. Moreover, the percentage of small individuals in females is higher than in males. With this evidence, we may say that the body size of a female is larger than a male when individual growth during the year is promoted. Inter-sexual differences in body size are less pronounced or nonexistent when individual growth during the year is inhibited. Therefore, females are more strongly affected by annual variability in environmental conditions such as food, temperature and density effect.

There is a latitudinal cline in the type of diadromy selected by Teleosts\(^{26}\). At higher latitudes, anadromy prevails, while in lower latitudes, catadromy is more abundant. Amphidromy is found in mid-latitudes. It is interesting to note that the monthly mean temperature of Iwate Prefecture is the lowest along the Pacific coast of Honshu: lower than Aomori Prefecture. Iwate is also home to the anadromous population of \(H.\) nipponensis. Further efforts to elucidate the whole life history of this unique population of \(H.\) nipponensis will provide a very interesting model case to study the evolutionary process of selection for diadromy in Teleosts. Also, if a positive method for age determination of this population of \(H.\) nipponensis can be developed, a life history model of trade off between longevity and reproductive fitness can also be studied. We have just reached a starting point of elucidating selective pressure and phenomena which evolved this very unique population of \(H.\) nipponensis.

Acknowledgments

We appreciate English correction by our colleagues, Ms. Gemma Knight and Ms. Mari Inoue. Also, aquaculture course students at Iwate Prefectural Miyako Fisheries High School, especially Mr. Masashi Taguchi, are appreciated for their cooperation. We also thank Dr. Yoshinobu Tokita for advice on educational practice study there and Dr. Masahiko Nakamura of the Joetsu University of Education for statistics advice, Dr. Sinji Tsuchida in Japan Marine Science Technology Center for his critical opinion, and members of Hei River Fisheries Cooperative, especially Mr. Yuichi Nakamura and Mr. Yoshitami Kikuchi, for their kind cooperation. This study was supported in part by a JSPS Grants-in-Aid for Scientific Research, Encouragement of Young Scientists (A) No. 10760114 for fiscal years 1998 and 1999 awarded to Saruwatari as well as by an Aid in Grant for Environmental Research from Sumitomo Foundation for 1997 awarded to Saruwatari and Sasaki.

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岩手県閉伊川に生息する週回遊型ワカサギの産卵生態

佐々木剛・猿渡敏郎・渡邊精一

週回遊型ワカサギの産卵生態を調べたために、1995年から1998年の産卵期間に閉伊川において調査を実施し、河川の水温、水量等の環境要因、体サイズ、性比に関して考察した。調査の結果、水温が約10度を超えると週上が開始し、週上のピークは常に雪解けによる湧き水に治まってから始まった。

その後、半月周期的にピークが確認された。4年間にわたり、性比は雄に偏っているが、雌が多くなるのは新月の前後であった。体サイズは年変動し奇数年は大きく、偶数年は小さい。これに対し、週上期間は奇数年が短く、偶数年は長い。また、体サイズが大きい年は雌、体サイズが小さい年は雄、差は認められなかった。