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Life History Style of the Threespine Stickleback, *Gasterosteus aculeatus* (L.), in Lake Ogawara, Japan

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To reveal the life history style of the threespine stickleback, *Gasterosteus aculeatus* (L.) in Lake Ogawara, Japan, its external features, growth and migration pattern were examined by investigating external body morphology, age in year and seasonal changes in body size, and trace elements of otoliths. The fish have 30 or more lateral plates, which completely covered the body trunk, but the dorsal fin membrane did not reach the top of the fin rays, representing anadromous common characteristics. All fish caught in the lake were identified as 0+. The seasonal occurrence suggested a migrating pattern that the stickleback hatching in May–June emigrated from the lake in summer and returned in the next spawning season in spring. Sr/Ca ratios were remarkably low in the center of otoliths and high in the outer region, respectively, representing life in the lake and in the sea. The life history style of stickleback inhabiting Lake Ogawara is discriminated to be anadromous.

Key words: threespine stickleback, life history style, otolith microchemistry

Introduction

The threespine stickleback, *Gasterosteus aculeatus* (L.), occurs around the north Atlantic and north Pacific in a wide range of aquatic habitats (Wooton, 1976, 1984). It has a large range of phenotypic plasticity of life history corresponding to the various habitats, and has at least three general lifestyles, marine, anadromous, freshwater (Wootton, 1984). The freshwater style is subdivided variously into two forms, including typical and unusual black (Moodie, 1972), limnetic and littoral (or benthic) (Lavin and McPhail, 1985; Schluter and McPhail, 1992), and lake and stream (lacustrine and stream-dwelling) (Reimchen *et al.*, 1985; Snyder, 1991; Baker, 1994), based on morphological or ecological difference.

The life history style has been determined from the number of lateral plates (Wootton, 1976) and the existence of a dorsal fin membrane (Nakabo, 1993). Marine and anadromous fish are almost always completely plated (Wootton, 1984), although some populations consist largely of partially plated fish (vanMullem and vanderVlugt, 1964; Aneer, 1973; Bell, 1979; Crivelli and Britton, 1987). While freshwater populations may be sparsely or partially plated*, some populations are completely plated (Münzing 1963; Igarashi, 1970; Baumgartner, 1992; Baker, 1994). These facts suggest that the life history style can not be revealed only by observation on the external characteristics. It is therefore necessary to carry out field investigations and examine the environmental history of individuals.

In Japan, the threespine stickleback is distributed in northern Honshu and Hokkaido (Ikeda, 1933; Honma, 1987). Surprisingly few studies have so far been made of its life history, including migration patterns, although genetic and morphological characteristics have been reported (Higuchi *et al.*, 1996; Mori, 1987, 1990). Study techniques used include temporal changes over time in fish distribution and the pursuit of tagged and released individuals. Recent progress in analysis of trace elements in fish otoliths has made it possible to learn the nutritional and environmental history of individual fish. Otolith Sr/Ca ratios can be confidently used to distinguish freshwater and marine life phases of individual fish (Halden *et al.* 1995; Tzeng *et al.* 1997; Otake and Uchida, 1998; Radtke, 1995; Radtke and Shafer, 1992; Secor *et al.*, 1998).

In this study, we aimed to reveal the life history style of stickleback inhabiting Lake Ogawara. The external fea-

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* Nakabo (1993) considered partially plated stickleback to be another species, *Gasterosteus microcephalus* (Girard). Furthermore, Honma (1987) and Mori (1991) suggested that anadromous and land-locked forms should each be separate species because of genetic differentiation (Taniguchi *et al.*, 1990; Honma and Tamura, 1984).

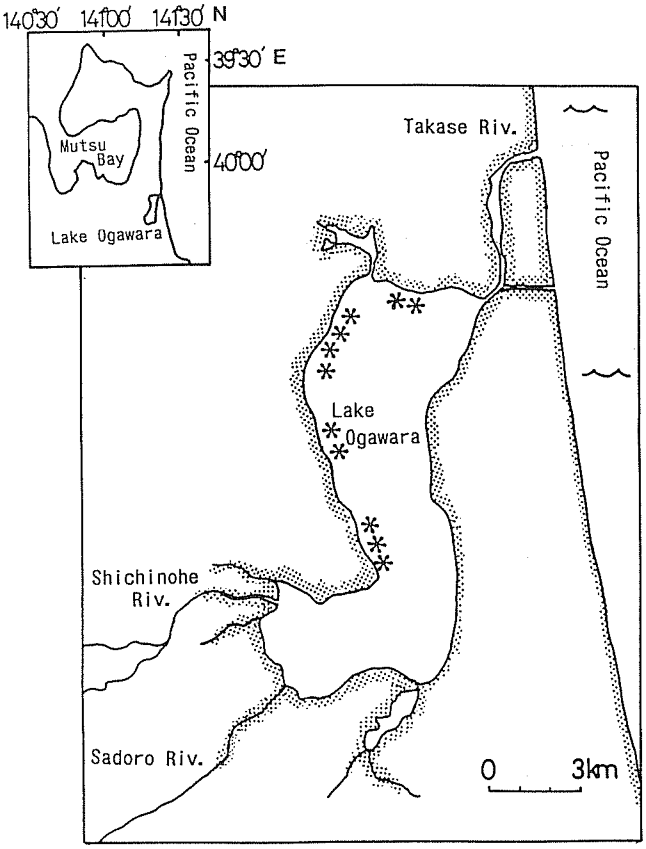

Figure 1. Map showing sampling locations (*) in Lake Ogawara.

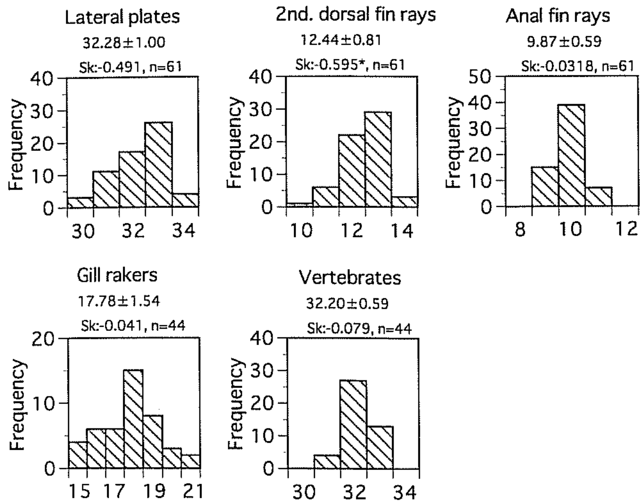

Figure 2. Morphorogical characteristics of stickleback in Lake Ogawara. Mean±standard deviations are denoted for each graph with skewness and sample size. *: Significant skewness at $0.01<p<0.05$.

tures, growth of fish and migration patterns were examined, by investigating external body morphology, age in year and seasonal changes in body size, and trace elements in otoliths.

Material and methods

Lake Ogawara is a brackish lake on the Pacific side of the northernmost part of Honshu, Japan. It is 11.0 m deep on an average and its deepest area lies at 24.4 m. The northernmost part of the lake is connected to the Pacific Ocean by the 6-km-long Takase River. The lake is meromictic and permanently stratified . The chemocline, separating the circulatory, surface layer form the stagnant, deep layer, lies at 15–20 m. The surface aerobic layer of the lake fills water far less saline (chlorinity, 0.5–0.6 g/l) throughout the year and in all over the layer. The deep water is consistently about on order of magnitude as rich in chlorinity as the surface water, and is always anaerobic (Sato, 1953; Kawasaki and Ito, 1995). Stickleback were caught by 11 set nets located on the west and north coasts of Lake Ogawara about every 20 days from August 1993 to December 1994 (Fig. 1). Specimens were fixed and preserved in 10% formalin solution. Total body length and sex were recorded for all specimens. For fish caught in March–May and December in 1994, the existence of a dorsal fin membrane was noted, and dorsal fin rays, vertebrates, lateral plates, and gill rakers were counted. Age in year was determined by using an otolith phase method (Jones and Hynes, 1950; Allen and Wooton, 1982).

For chemical analysis of otoliths, the stickleback were collected in April 1998 and frozen for preservation. Sagittae of three specimens (TL: 74.3 mm, 76.6 mm, and 76.9 mm) were mounted in Petropoxy 154″ (a heat-setting resin; Palouse Petro Products, Palouse, WA, USA) and grounded to reveal their central cores. They were polished with 0.3 μm alumina paste and then coated with carbon.

Strontium and calcium were measured quantitatively with an X-ray wavelength dispersive electron microprobe (JEOL, JXA-8900). The electron beam was focused to 1 μm diameter for mapping and 10 μm for quantitative analysis, using accelerating voltage of 15 kV and a beam current of about 4×10^{-7} A. X-ray intensities were corrected and computed with the ZAF method (Reed, 1975). Final elemental concentrations are presented as ratios of the weight percentage.

Results

Morphological characteristics

Fig. 2 shows frequency distributions of the number of lateral plates, second dorsal fin rays, anal fin rays, gill rakers, and vertebrae together with the mean, standard deviation, and skewness. Each characteristic shows a unimodal distribution. The skewness was not significant (it was slightly skewed in the second dorsal fin rays), which suggests that all distributions are normal. Lateral plates numbered 30 or more and covered the whole body trunk. All fish were completely plated. The first dorsal fin membrane did not reach the top of the fin rays.

Seasonal occurrence of the fish in Lake Ogawara

Fig. 3 shows the seasonal changes in stickleback numbers which are pooled of 11 set net catches, in order to examine the seasonal occurrence pattern in Lake Ogawara. Hardly fish of the 1993 year class were caught from August to January. Catches numbered <10 in March–April and 20–30 in May, reaching a minimum after July. Catches of the 1994 year class numbered 130 in June and 128 in early July, re-

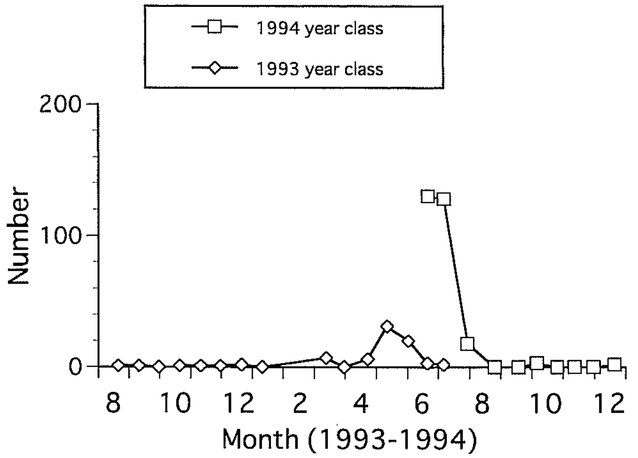

Figure 3. Seasonal change in the number of stickleback catches by year class in Lake Ogawara.

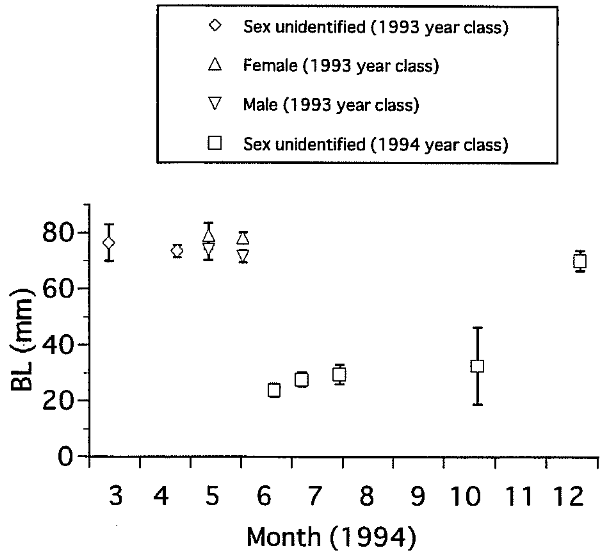

Figure 4. Seasonal change in mean and standard deviation ($\pm 1\sigma$) of the total body length of stickleback in Lake Ogawara.

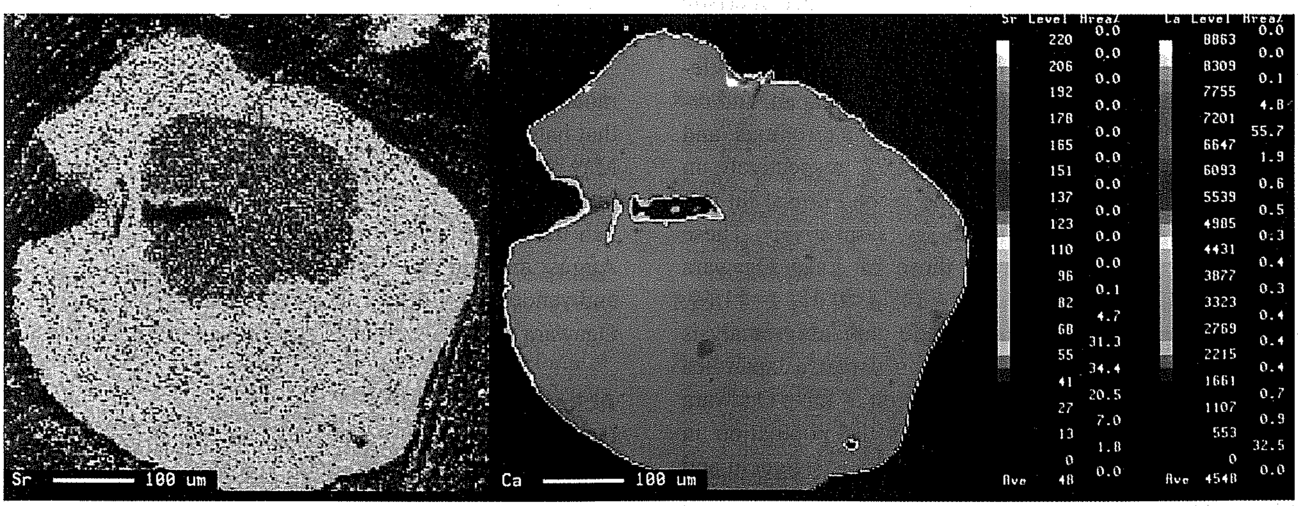

Figure 5. Sr and Ca distributions on the section of sagittal otolith (TL 76.6 mm, April, 1998).

Table 1. Morphorogical characteristics of stickleback in Lake Ogawara.

	N. of Lateral plates	N. of 2nd. doral fin rays	N. of anal fin rays	N. of gill rakers	N. of vertebrates
Agerage	32.28	12.44	9.87	17.78	32.20
S.D.	1.00	0.81	0.59	1.54	0.59
Range	30–34	10–14	9–11	15–21	31–33
n	61	61	61	44	44

spectively, but decreased approximately to zero after August. The fish disappeared in summer and reappeared the next spring.

Growth

All stickleback caught were 0+ fish. In samples of the 1993 year class caught on 11 May and 1 July, the females were significantly larger than the males ($t=2.51$, $p<0.05$, $t=6.78$, $p<0.01$). Body lengths of the 1994 year class caught in June were 20–30 mm (Fig. 4). These fish grew to about 70 mm by December. The 1993 year class remained at approximately 70 mm during March–June.

Otolith microhemistry

Distribution images of strontium and calcium are shown in Fig. 5. Ca levels varied little all over the otolith (the central blue part is the incision). Sr levels changed obviously, from low in the center to high around the outside. All three otoliths measured showed a similar distribution pattern. The Sr/Ca ratios (mean±SD, $n=3$) were 1.78 ($\pm0.38)\times10^{-3}$ in the center and 6.92 ($\pm1.94)\times10^{-3}$ around the outside, showing significant difference ($p>0.05$).

Discussion

Morphological characteristics

The number and distribution of lateral plates and the short dorsal fin membrane of the stickleback in Lake Ogawara are anadromous common characteristics. Other meristic characteristics ranged within species-specific limits (Nakabo, 1993). However, Mori (1990) studied the stickleback population in Lake Harutori, Hokkaido, Japan, and reported meristic characteristics of large anadromous and small resident groups of 33.80 and 33.22, respectively, in lateral plates, 11.89 and 11.82 in the second dorsal fin ray, and 8.51 and 8.80 in the anal fin ray, respectively. These values differ significantly from those of Lake Ogawara ($t=8.23$, 6.45, $p<0.01$; $t=3.61$, 4.24, $p<0.01$; $t=11.69$, 8.58, $p<0.05$, respectively). A genetic population analysis suggested the existence of two groups in Japan, a Japan Sea group and a Pacific group. The population in Lake Ogawara belongs to the Pacific group, whereas the population in Lake Harutori belongs to the Japan Sea group (Higuchi and Goto, 1994). However, the relationships of morphological traits with this genetic population structure and with the intra-group variation in the morphological traits are unknown.

Migration pattern

The seasonal occurrence pattern suggests that the stickleback disappear in August and appear again around April. This pattern is interpreted as anadromous migration: the stickleback after hatching in May–June emigrate in summer, and return to the lake in the next spawning season in spring. The Sr concentration increased drastically from the otolith core toward the edge. The Sr/Ca ratios were 1.78 in the center and 6.72 in the outer region. The Sr/Ca ratios determined for the stickleback tended to be slightly higher than the previous studies (1.5–5.2 marine, 2.3 estuarine, and 0.3–1.5 in freshwater, Secor *et al.* 1995; Radtke and Kinzie, 1996). We have no information to distinguish whether higher ratios are associated with the specific metabolism rate of stickleback or geophysical characteristics, but the increase of Sr/Ca ratio is a similar to that displayed for the anadromous pond smelt, Hypomesus nipponensis, inhabiting Lake Ogawara (Katayama *et al.*, 2000). Although many factors as temperature, body size, ontogeny, stress and so on can effect differential incorporation of Sr into otolith carbonate (Radtke & Shafer, 1992), the drastic increase in Sr shown in Fig. 5 is interpreted to reflect differences in environment salinity. Salinity in the surface layer displays almost same in the horizontal distribution throughout the year. The deep layers water has consistently high salinity, but always anaerobic (Sato, 1953; Kawasaki and Ito, 1995). Therefore, the low and high Sr/Ca phases represented life in the lake and the sea, respectively. Though the edge of otolith did not display low Sr concentration, this was because the sample fish seemed to be just after immigrating into the lake. We concluded that the life history style of stickleback inhabiting Lake Ogawara was discriminated as anadromy, which spend most of their lives in the sea and which migrate to fresh water to breed, defined by McDowall (1988).

There are a few reports of the life history of anadromous stickleback. In Mediterranean wetlands, young fish that hatch in freshwater migrate to brackish water in April–May and return to freshwater in January–February to breed in March (Crivelli and Britton, 1987). In the Netherlands, fish that hatch at the end of April appear in the sea after August and migrate upstream in March–April (vanMullem and vanderVlugt, 1964). The stickleback population in Lake Ogawara shows a similar migration pattern to these.

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小川原湖におけるイトヨの生活史

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青森県小川原湖におけるイトヨ *Gasterosteus aculeatus* (L.) の生活史を明らかにするために，湖内において採集されたイトヨの外部形態，年齢，体長の季節的変化，耳石の微量成分を調べた．採集された全ての個体は，体側の鱗板数が30以上で体幹部を覆い，第2背鰭の鰭膜が鰭条の先端に届かず，降海回遊型の外部形態の特徴を有していた．耳石の年輪を観察した結果，年齢は全て0+であった．湖内における出現状況も降海回遊パターンを示し，5–6月に孵化したイトヨは8月にはほとんど採集されなくなったが，翌年4月に再び湖内に出現した．耳石のSr/Caは，耳石の中央部では著しく低かったが外縁部は有意に高く，生息域が各々湖内，海洋域であったことが示された．したがって、小川原湖のイトヨは孵化後，夏季に外海に移動し，翌年春の産卵期に湖内に来遊するという降海回遊型の生活史であることが明らかとなった．

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