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Research article

Loss of *Coilia nasus* habitats in Chinese freshwater lakes: An otolith microchemistry assessment

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ABSTRACT

Loss of valued diadromous fishes and their habitats is one of the most critical problems in aquatic habitat connection and resource management worldwide. In China, the Poyang, Dongting, Gaobao, Gucheng, Dongping, and Taihu lakes were known to be historical migratory spawning sites of the anadromous estuarine tapertail anchovy *Coilia nasus*. However, except for Poyang Lake, it is believed that these lakes are no longer used by anadromous fish owing to overfishing, water pollution, and loss of connectivity. To confirm this assumption, we used an electron probe microanalyzer to analyze elemental strontium (Sr) and calcium (Ca) microchemical patterns in the otoliths of *C. nasus* individuals sampled from these lakes, in accordance with our previous analysis of the otolithic patterns of the same species sampled from habitat areas characterized by different salinity gradients. The results of line transect analysis of Sr/Ca ratios and Sr X-ray intensity maps of the otoliths indicated that all individuals from Dongting, Gaobao, Gucheng, Taihu, and Dongping lakes were characterized by a freshwater-resident life history. In contrast, individuals from Poyang Lake exhibited both freshwater-resident and anadromous life histories. The findings of this pilot study suggest that anadromous *C. nasus* can be found in Poyang Lake but are unlikely to be found in Dongting, Gaobao, Gucheng, Dongping, or Taihu lakes, despite these lakes being historical distribution areas or even spawning sites. This anchovy can possibly be used as a good model species for understanding the aforementioned global problem. Given that *C. nasus* is a commercially important species, restoration of its natural habitats and maintenance of their connections are recommended for its management and conservation.

1. Introduction

The estuarine tapertail anchovy *Coilia nasus* Temminck et Schlegel, 1846 (junior synonym *Coilia ectenes* Jordan et Seale, 1905) is an anadromous clupeid fish found in the Northwest Pacific, including the marine areas of China, Korea, and Japan [1, 2, 3]. In China, *C. nasus* inhabits major rivers, coastal estuarine zones, and their connected large lakes, including the Yangtze River, the Yellow River, Poyang Lake, Dongting Lake, and Dongping Lake [4, 5]. At approximately 2 years of age, *C. nasus* make an anadromous migration for spawning. The migratory season for this species is within a large window of time, from February to October, depending on early or late upstream populations from sea areas. During this period, there is a rapid development of sexual maturity, with individuals breeding annually in the lakes and some backwater bays along rivers [6]. After hatching, young-of-the-year (YOY) anchovies move downstream and enter estuarine brackish or seawater habitats where they spend a year growing and maturing [7]. Anadromous *C. nasus* is a species of high commercial value [8], fetching prices up to $1000 USD/kg [9], with a distinctive aroma, intense umami taste, and high nutritional value [10]. Previously, sea-going high-value anadromous *C. nasus* spawned naturally in the Dongting Lake in Hunan Province, Poyang Lake in Jiangxi Province, Gaobao Lake and Gucheng Lake in Jiangsu Province, Taihu lake, mainly in Jiangsu Province along the middle and lower reaches of the Yangtze River, and the Dongping Lake in the lower reaches of the Yellow River (all of which are important traditional fishing grounds for *C. nasus*), which are connected with the Yangtze or Yellow River throughout the year [6, 11]. Moreover, until the 1980s, anadromous *C. nasus* was reported as a common or main fishery species in Dongting [6, 12], Poyang [6], Gaobao [11], Gucheng [11], Taihu [13], and Dongping lakes [14], and coexisted with

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freshwater-resident *C. nasus* in Dongting [15] and Taihu lakes [13] when the above lakes were still connected to the Yangtze or Yellow River.

Historically, the middle and lower reaches of the Yangtze River were covered with the largest freshwater lake cluster in East Asia [16], characterized by numerous freely river-connected lakes [17, 18] including the Dongting, Poyang, Gaobao, Gucheng, and Taihu lakes surveyed in the study. Since the 1950s, most lakes have been disconnected due to the construction of embankments or sluice gates [18, 19]; for example, 321 such lakes were reported in a recent literature review by Xie et al. [16]. To date, only the medium-sized Shijiu Lake and the large-sized Dongting and Poyang lakes are believed to be connected with the Yangtze River [18, 19]. Today, due to the construction of a water gate, Gucheng Lake [20], Gaobao Lake [21, 22], and Taihu Lake [23] are not able to retain free connection with the Yangtze River. Moreover, all the lakes have suffered eutrophication, ecosystem degeneration, and water quality deterioration because of land reclamation, wastewater discharge, and other anthropogenic impacts [21, 22, 24]. The loss of river-lake connectivity combined with aggravated water pollution, resource overexploitation, environmental degradation, and habitat shrinkage, has caused local extirpations of fish species, especially migratory clupeid, tetraodontid, anguillid, acipenserid [25], and cyprinid [19] fishes. Likewise, at least 140 lakes were located in the lower reaches of the Yellow River historically; however, the Dongping Lake is now the only remaining lake [26]. It has become a reservoir mainly for local flood control, and the waterways for the eastern route of the national South-to-North Water Diversion Project [26, 27], and can no longer freely connect with the Yellow River because of the water gate systems in place [28]. The Dongping Lake has also been eutrophicated, and its aquatic environment has become stressed by anthropogenic factors [29].

Due to overfishing, water pollution, and the construction of dike or sluice gates lacking fish passages, the distribution of *C. nasus* has contracted markedly, and it is now believed to be limited to the mainstream of the Yangtze River below the Anhui section [30]. No anadromous *C. nasus* individuals are believed to be found in the aforementioned lakes since the late 1980s [31,32,33,34], and only low-value freshwater-resident (including land-locked) ecotype stocks, unlike the aforementioned high-value anadromous *C. nasus* with a distinctive aroma, intense umami taste, and high nutritional value [10], are considered to inhabit the river and associated lakes in the middle and lower reaches of the Yangtze watershed [30]. However, due to the lack of effective discriminatory approaches, it is difficult to confirm whether these observations are indeed correct, even when using the traditional measurement of the length of the supermaxilla, since not all long supermaxilla (supermaxilla length/head length>1)-type *C. nasus*, which are traditionally treated as high-value anadromous individuals, migrate anadromously [35]; additionally, advanced molecular approaches (e.g., D-loop region sequences, AFLP markers) are also inadequate in this regard [36, 37]. In fact, the existence of anadromous *C. nasus* individuals with short supermaxilla (supermaxilla length/head length<1) was recently confirmed along the Yangtze River [38, 39].

Otoliths comprise hard tissues, and their elemental compositions have emerged as effective markers for examining life histories [40, 41, 42] and the corresponding chemical compositions of fish habitats [43, 44]. Otoliths develop during the larval stage of fish and continue to grow throughout life, with growth being expressed in terms of incremental bands representing short-term (even daily) durations. In addition, otoliths are acellular and metabolically inert [45, 46] and are not resorbed or otherwise chemically altered via biogenic processes. Consequently, otolith microchemistry provides reasonable timeline representations of the chemical composition of the waters in which fish live during the course of their lives [47, 48]. Otoliths have previously been used to determine fish natal habitats, population connectivity, and distribution areas [49, 50].

In *C. nasus*, the strontium (Sr) and calcium (Ca) microchemical fingerprint of otoliths can be used to distinguish anadromous and freshwater individuals [35], as freshwater Sr and Ca concentrations (ca. 60 μg/L and 1.5×10^4 μg/L, respectively) are reported to be considerably lower than those in seawater (8000 μg/L and 4.2×10^5 μg/L, respectively) [51]. Our previous studies of *C. nasus* otolith microchemistry in fish collected from the Yangtze River estuary and the Taihu Lake of China [31], the Chinese coast [1], the Changshu section of the Yangtze River [35] of China, and the Rokkaku River and Chikugo River estuaries of Japan [3], characterized by different levels of salinity, have made effective use of this technique. Here, we used this approach to confirm whether *C. nasus* recently collected in the Poyang, Dongting, Gaobao, Gucheng, Taihu, and Dongping lakes are anadromous or freshwater-resident individuals, and to assess whether these lakes are still among the distribution areas or spawning sites for anadromous *C. nasus* evaluated in this study.

The extirpation of valued diadromous fishes, which provide many vital ecosystem services throughout their life cycles, has become a critical problem for resource management worldwide; some examples include the loss of traditional populations of managed North American diadromous fish (e.g., alosine clupeids and sturgeon) within the North Atlantic basin [52], the disappearance of the highly valued Atlantic salmon (*Salmo salar*) from Lake Ontario [53], the development of the landlocked population of smelt (*Osmerus eperlanus*) in Lake Ijsselmeer of the Netherlands [54] (indicated by otolith microchemistry), and Chinook salmon (*Oncorhynchus tshawytscha*) in reservoirs of USA [41] (indicated by otolith microchemistry), because of extensive changes to aquatic habitats. The outcomes of the present study will highlight the potential dangers posed by anthropogenic-derived habitat changes to traditional anadromous fish resources and contribute to formulating more effective plans for resource management and natural habitat restoration of *C. nasus* in studied water bodies. Furthermore, we hope that the anchovy can be used as a model species for understanding the importance of the health of the network of connected aquatic habitats in the maintenance of the life cycle of fish and the consequences of the abovementioned critical global problem.

2. Materials and methods

2.1. Study area

The *C. nasus* used in this study were collected from the Poyang (around 116°5′5.43″E, 29°25′8.65″N), Dongting (around 113°0′35.80″E, 29°19′34.15″N), Gaobao (around 119°27′32.87″E, 32°37′0″N), Gucheng (around 118°55′3.51″E, 31°17′11.64″N), Taihu (around 120°10′17.61″E, 31°30′34.93″N), and Dongping (around 116°14′26.53″E, 35°58′47.25″N) lakes during the spawning season of anadromous *C. nasus*, i.e., between February and October. The sampling sites and the water gate barriers on the lakes are shown in Figure 1. There are no fishways or fish ladders in the water gates.

As aforementioned, the Dongting, Poyang, Gaobao, Gucheng, and Taihu lakes are situated in the middle and lower reaches of the Yangtze River, while the Dongping Lake is located in the lower reaches of the Yellow River. All these lakes are typical freshwater lakes and their year-round degree of mineralization is 0.048, 0.173, 0.189, 0.189, 0.200, and 0.211 g/L for the Poyang, Taihu, Dongting, Gucheng, Dongping, and Gaobao, respectively [55], which is far lower than that of saltwater lakes (1–35 g/L) and salt lakes (>35 g/L) [56]. The anthropogenic uses of these lakes include agricultural irrigation, flood protection, and industrial and domestic usage [57]. Notably, the Gucheng Lake is almost a closed, mesotrophic lake [20]; Gaobao Lake and Dongping Lake are eutrophicated [21, 29]; Taihu Lake is now characterized by the accumulation of industrial, residential, and agricultural pollutants, and is severely eutrophic [24]; Dongting Lake and Poyang Lake currently retain free connections with the main body of the middle and lower reaches of the Yangtze River [18]; however, Dongting Lake has been losing surface area heavily over recent decades because of human activities (e.g., reclamation, embanking) and is likely to shrink further, and in the near

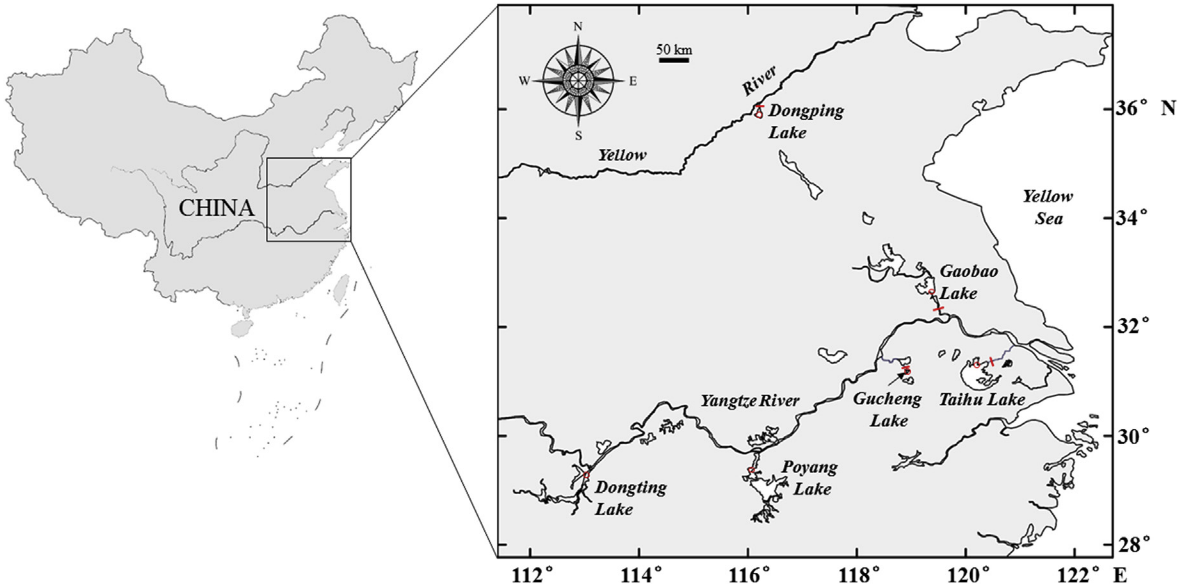

Figure 1. The locations of the Dongting, Poyang, Gucheng, Gaobao, Taihu, and Dongping lakes along the Yangtze River and Yellow River Basins of China. The sampling sites and barriers of water gate are marked with red open circles and lines, respectively.

future, may serve merely as a river channel during non-flood conditions [58]. It also suffers from serious water pollution [59, 60].

2.2. Fish collection and otolith preparation

Over two years (2016 and 2017), a total of 65 individuals of the anchovy were collected from the aforementioned six lakes (Poyang Lake: 16, Dongting Lake: 10, Gaobao Lake: 11, Gucheng Lake: 11, Taihu Lake: 6, and Dongping Lake: 12 individuals) during the spawning season of anadromous *C. nasus* between February and October (Figure 1, Table 1). All of them were obtained from commercial catches harvested using plastic set-nets (mesh size: 3 cm), which were set at selected sites in lakes during the evening and retrieved the following morning based on the experience of the local fishermen. Fish samples were frozen soon after collection and transported to the laboratory on ice. They were stored frozen again in the laboratory until processing. Table 1 provides the basic biometric information of the sampled fish, e.g., body weight, total length, estimated age, supermaxilla length/head length ratio, sex, and gonadal maturity, mainly following the measurement or determination methods of Jiang et al. [9]. All available information was used to evaluate life history stages to determine whether they corresponded to either the 'dispersing to sea' or 'spawner' stage. Because anadromous *C. nasus* was once a common or main fishery species in all of the lakes in this study, it will not be very difficult to collect the anadromous individuals in the former distribution areas of these lakes if they still contain anadromous *C. nasus*. As the long supermaxilla-type *C. nasus* individuals are traditionally treated as high-value anadromous individuals, but not all of them migrate anadromously [35], while the short supermaxilla-type *C. nasus* could possibly be anadromous migrants, like in the aforementioned cases [38, 39], the otoliths of all 65 sampled fish were analyzed for further confirmation by microchemical analysis, including the long supermaxilla (supermaxilla length/head length >1)-type fish collected from the Poyang (CE group), Gaobao, Gucheng, Taihu, and Dongping lakes, which were suspected of being diadromous individuals by local people.

The left sagittal otolith of each fish was weighed and then, the frontal plane was embedded in epoxy resin (Epofix; Struers, Copenhagen, Denmark), followed by grinding with an automated polishing wheel (LaboPol-35, Struers, Copenhagen, Demark) to expose the core. Next, the otoliths were cleaned in an ultrasonic bath and rinsed with deionized water. Finally, they were dried and carbon-coated using a high vacuum evaporator (JEE-420, JEOL Ltd Tokyo, Japan) [3, 61].

2.3. Otolith microchemical analysis

The analysis of otolith microchemistry was conducted according to Jiang et al. [9]: The otoliths of the fish were used for the microchemical analysis of life history based on Sr and Ca concentrations. A representative transect line was demarcated along the longest diametric axis from the core to the edge of each otolith. For the transect line analysis, we used a wavelength dispersive electron probe X-ray microanalyzer (EPMA, JXA-8100; JEOL Ltd, Tokyo, Japan) to take measurements with

Table 1. Comparison of parameters for *Coilia nasus* collected from the six sampled freshwater lakes.

Sampling sites	Sampling date	*n*	Body weight (mean ± SD g)	Total length (mean ± SD cm)	Estimated age (years)	Supermaxilla length/head length	Sex and gonadal maturity
Dongting Lake	2016/09	10	20.48 ± 18.42	18.21 ± 4.89	1+	0.72 ± 0.10	♀III-IV; ♂II-III
Poyang Lake	2017/08	10 (CB*)	44.83 ± 8.76 (CB)	24.89 ± 1.36 (CB)	1+ ~ 2+ (CB)	0.76 ± 0.07 (CB)	♀III-IV; ♂III-IV(CB)
		6 (CE**)	45.29 ± 6.01 (CE)	25.78 ± 1.78 (CE)	2+ (CE)	1.19 ± 0.07 (CE)	♀IV; ♂III (CE)
Gucheng Lake	2016/10	11	30.58 ± 11.05	21.93 ± 2.71	1+ ~ 2+	1.33 ± 0.06	♀III-IV; ♂III
Gaobao Lake	2016/06	11	5.32 ± 1.75	9.49 ± 1.32	0+ ~ 1+	1.42 ± 0.11	♀I-II; ♂I
Dongping Lake	2016/03	12	8.71 ± 3.69	14.83 ± 1.74	0+~1+	1.40 ± 0.32	♀I-II; ♂I-II
Taihu Lake	2017/09	6	56.61 ± 7.50	26.58 ± 0.73	2+	1.36 ± 0.17	♀IV-V; ♂IV

* CB: group of fish with short supermaxilla; ** CE: group of fish with long supermaxilla.

accelerating voltage and beam currents of 15 kV and 2×10^{-8} A, respectively. The electron beam was focused on a point 5 μm in diameter, and measurements were taken from points spaced at 10-μm intervals along the transect. Moreover, to visualize Sr and Ca compositions two-dimensionally in a whole cross-core section of the otolith, X-ray intensity maps of the contents of these elements were developed for each representative otolith using the same microprobe in accordance with the aforementioned transect line analysis. Subsequently, using an accelerating voltage of 15 kV, beam current of 5×10^{-7} A, counting time of 30 mS, and pixel size of 6×6 μm, the electron beam was focused on a 5-μm-diameter point. Measurement quality was validated using calcium carbonate ($CaCO_3$) and strontium titanate ($SrTiO_3$) standards purchased from the Chinese Academy of Geological Sciences.

2.4. Otolith age determination

Having conducted EPMA microanalysis, all otoliths were re-polished to remove the carbon coating and then etched with 5% ethylenediaminetetraacetic acid (EDTA) to reveal the annulus marks [61] so as to determine individual age.

2.5. Habitat history determination and statistical analysis

Statistical analysis of data was performed using Excel 2016 (Microsoft, Seattle, WA, USA) and IBM SPSS Statistics v. 21.0 (IBM Corp., Armonk, NY, USA). The Sr/Ca ratios of concentrations were customarily calculated and expressed as Sr/Ca×1000 [61]. The Sr/Ca ratios and X-ray intensity maps of Sr content were used to define the habitat phases in the otolith by comparing them with known patterns of various salinity exposure phases in *C. nasus,* based on our previous analysis results [31, 62], where a Sr/Ca ratio of ≤3 is considered to be indicative of a freshwater phase and is colored blue (salinity: < 5); a ratio of 3–7 is considered indicative of a brackish water phase (salinity: 5–25) and is colored green-yellow; and a ratio >7 is considered indicative of a fully sea water phase (salinity: >25) and is colored red. Compared with the phase patterns of the Sr/Ca ratio transects, the color map patterns of otolith Sr can provide more objective and intuitive insights into the environmental salinity history and migratory patterns of fish [1, 3, 31, 35]. The typical patterns of the otolith X-ray Sr intensity maps for anadromous (with both freshwater and seawater habitat histories in the whole life cycle), freshwater-resident (with a single freshwater habitat history in the whole life cycle), and sea-resident (with a single seawater habitat history in the whole life cycle) *C. nasus* are presented in Figure 2 based on our previous otolith microchemistry results obtained from the anchovies sampled from lake, river, estuary, and marine habitats of different salinities [1, 3, 31, 35]. These patterns can provide comparative references or "cut-offs" to distinguish anadromous, sea-resident, and freshwater-resident *C. nasus* individuals from each other objectively and intuitively by producing alternating bluish/greenish colors, alternating greenish/reddish colors, and a constant bluish color, respectively (Figure 2).

If differential color fluctuation phases were observed in the otolith, the *t* test was used to assess the significance of the differences in Sr/Ca ratios between the phases characterized by Sr/Ca ratio data groups of the corresponding low and high ratio level phases (according to the different colored areas) in the otoliths measured with the abovementioned Sr and Ca life-history transect analysis of EPMA in 10-μm intervals along the longest axis of each otolith from the core to the edge [3]. Differences of $P < 0.05$ were considered statistically significant.

3. Results and discussion

In the fish collected from the lakes of Dongting, Gucheng, Taihu, Gaobao, and Dongping, the values for Sr/Ca ratios measured from the otolith core to edge were consistently low (i.e., 1.25 ± 0.66, 1.65 ± 0.74, 1.66 ± 0.75, 1.88 ± 0.76, 2.08 ± 0.83, respectively, mean ± SD, similarly hereinafter) across the sampled individuals (Figure 3). For the samples collected from all five lakes, bluish color patterns were visible in the X-ray intensity maps of Sr contents (Figure 4). These results indicate that the anchovies from the lakes have only a freshwater habitat signature or phase in their otoliths (Figure 2) and have no habitat history of brackish or sea water. Especially, the results were rather unexpected for the long supermaxilla-type (i.e., supermaxilla length/head length>1) fish from the Gucheng, Taihu, Gaobao, and Dongping lakes (Table 1) since this fish type is traditionally treated as anadromous *C. nasus* as aforementioned. The specimens from Gaobao Lake and Dongping Lake had slightly higher Sr/Ca ratios (i.e., 1.88–2.08) (Figure 3) and Sr content (relatively bright bluish color) (Figure 4) patterns. This phenomenon may be related to the degree of mineralization among freshwater lakes; the degree of mineralization of Gaobao Lake and Dongping Lake are 0.211 and 0.200 g/L are slightly higher than those of Dongting, Poyang, Gucheng, and Taihu (≤0.189) [56]. Therefore, there is a need for future research to reveal the exact reasons for this occurrence. Nevertheless, the otolith microchemical elemental ratio and color patterns for the anchovies from Gaobao Lake and Dongping Lake belong to those of freshwater, as the

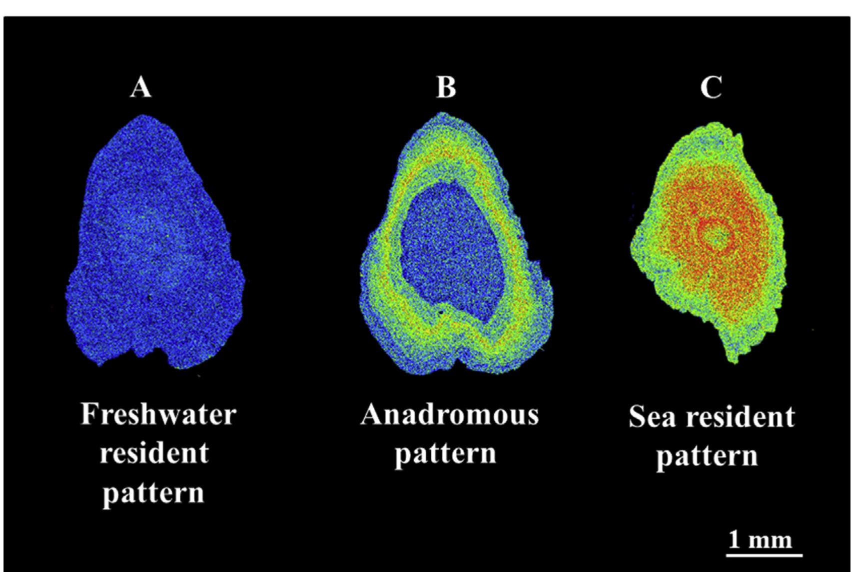

Figure 2. The typical patterns of the otolith X-ray strontium (Sr) intensity maps for freshwater-resident, anadromous, and sea-resident *C. nasus* based on our previous otolith microchemistry results obtained with the anchovies sampled from different salinity habitats, i.e., lake, river, estuary, and marine habitats [1, 3, 31, 35]. Freshwater-resident, anadromous, and sea-resident patterns can be distinguished from each other by (A) a constant bluish color, (B) alternating bluish and greenish colors, and (C) alternating greenish/reddish colors, respectively.

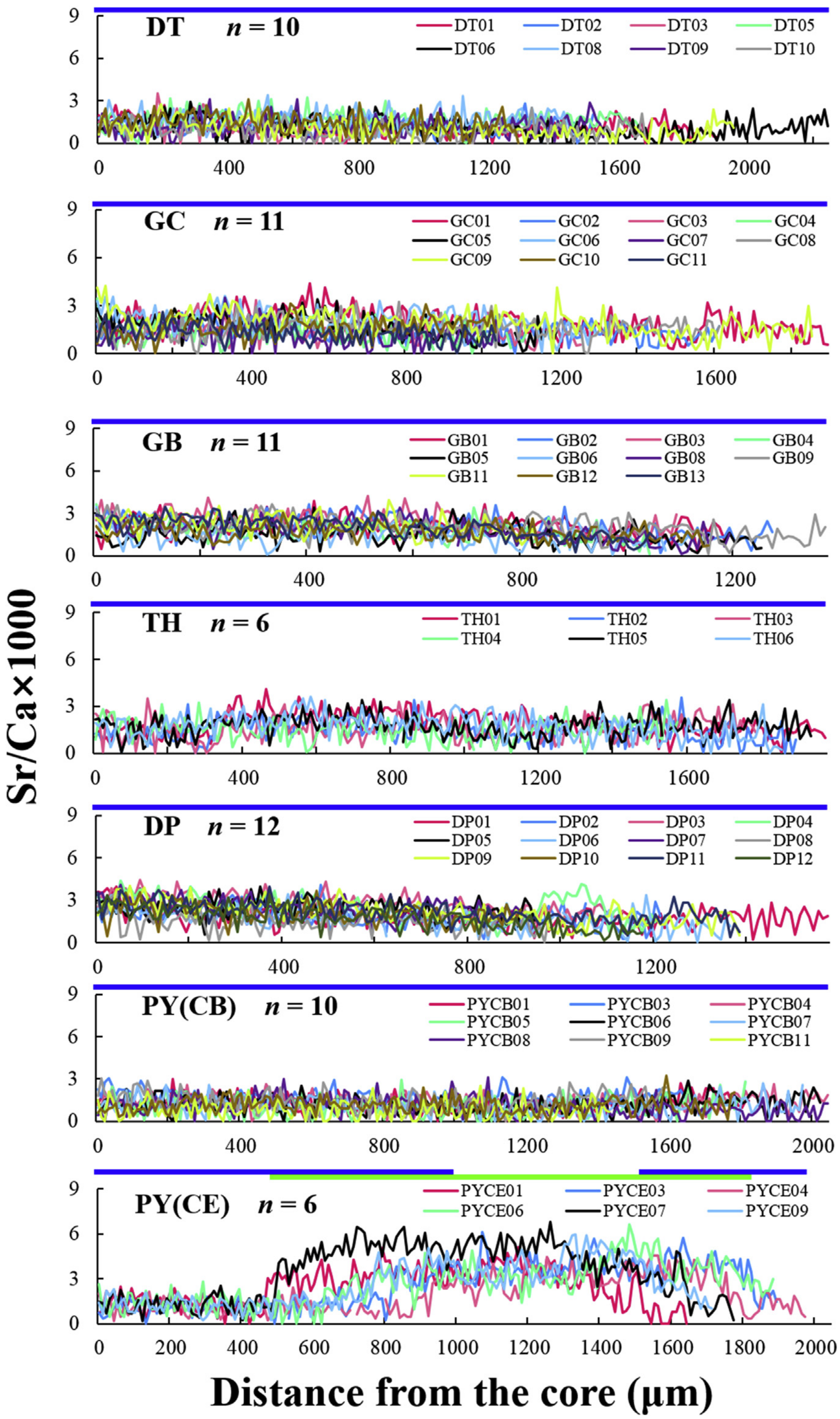

Figure 3. Fluctuation of otolith strontium/calcium (Sr/Ca) concentration ratios along line transects from the core to edge in the sagittal plane of the otoliths of *Coilia nasus* individuals collected from Dongting Lake (DT), Poyang Lake (PYCB: non-anadromous type; PYCE: anadromous type), Gucheng Lake (GC), Taihu Lake (TH), Gaobao Lake (GB), and Dongping Lake (DP). The blue and green lines above each figure for different lakes indicate the distance ranges of freshwater and brackish phases in the otoliths, respectively.

otolith ≤2.08 ratios are far less than that of 3 for freshwater habitat history determination of *C. nasus*, and less than 2.7 ± 1.5, which could be used as the marker ratio for freshwater habitat according to the ratio data of Clupeiformes, Salmoniformes, Anguilliformes, Mugiliformes, Perciformes, Gasterosteiformes, Cypriniformes, Gadiformes, Scorpaeniformes, Beryciformes, and Osmeriformes [62]. The otolith color patterns indicating Sr content in the fish of Gaobao and Dongping lakes are bright bluish, which indicated a lower Sr level than those of green-yellow for the brackish water habitat of *C. nasus* (Figure 2).

In contrast, the results obtained for the otolith microchemistry of fish collected from the Poyang Lake showed two different Sr/Ca ratios and Sr color map patterns. Ten anchovies (CB group in Table 1) showed consistently low Sr/Ca ratio phases (1.25 ± 0.60) (Figure 3) and bluish areas (Figure 4) throughout the otolith, like those obtained for fish sampled in the aforementioned five lakes. However, portions of the otolith samples obtained from the remaining six fish (CE group in Table 1) showed indications of variable Sr/Ca ratio phases. The color maps of the first phases were characterized by bluish central regions from the core to the point 470–1000 μm away from the core with low Sr/Ca

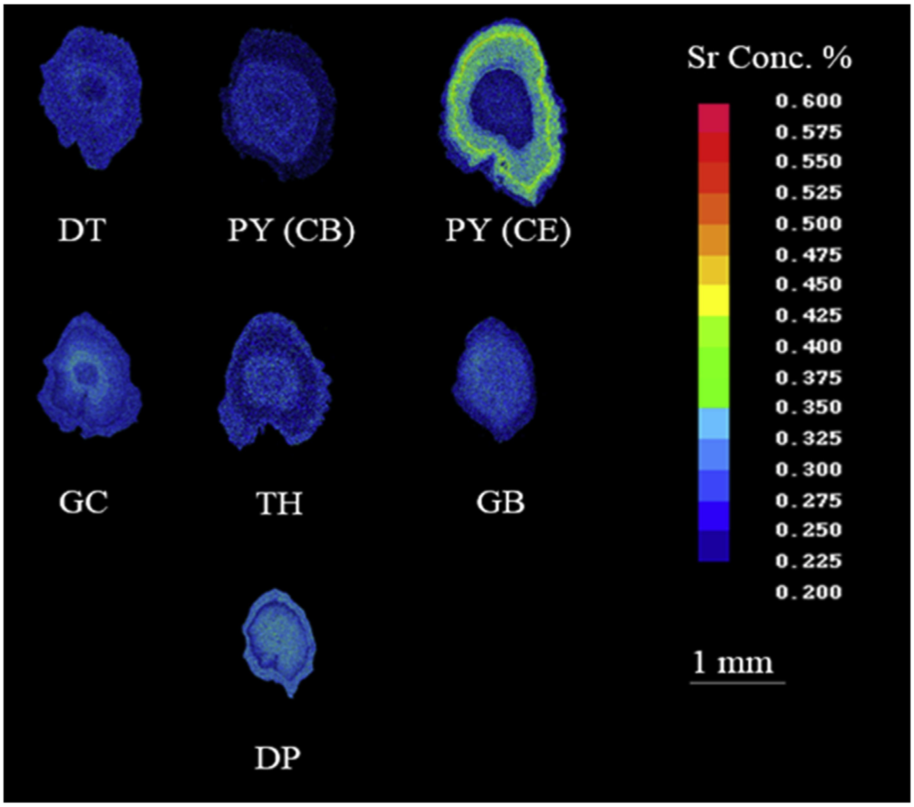

Figure 4. Strontium (Sr) concentrations in the sagittal plane of representative samples of *Coilia nasus* otoliths from specimens collected in the Dongting Lake (DT), Poyang Lake (PYCB: freshwater resident type, PYCE: anadromous type), Gucheng Lake (GC), Taihu Lake (TH), Gaobao Lake (GB), and Dongping Lake (DP) visualized using X-ray electron microprobe analysis in two dimensions. Different colors from blue (lowest) to green, yellow, and red (highest) indicate values corresponding to Sr concentrations.

ratio (1.46 ± 0.90) phases (first blue line range for PYCE, Figure 3). Following this were the second phases of greenish zones (Figure 4) between the points 470–1500 and 1000–1830 μm away from the core with significantly higher Sr/Ca ratio phases (3.71 ± 1.02, green line range for PYCE, Figure 3) ($P < 0.001$, values of *df* varied from 149 to 181 depending on the cases of different otolith samples). The subsequent third phases were distinguished by bluish areas (Figure 4) from the point 1500–1830 μm away from the core with significantly lower Sr/Ca ratio phases (1.60 ± 0.88) toward the otolith edges (second blue line range for PYCE, Figure 3) ($P < 0.001$, values of *df* varied from 93 to 112 depending on the cases of different otolith samples). These results indicate that all anchovies of the CE group from the lakes have alternating habitat histories with a freshwater–brackish water–freshwater habitat signature in their otoliths during their entire life cycle (Figure 2), which is the typical pattern of anadromous *C. nasus*.

For the otolith samples in the present study, the observed microchemical patterns relating to habitat salinity history among fresh-, brackish-, and seawater are fully consistent with those reported in the previous literature for *C. nasus* [1, 3, 31, 35, 60]. By a combined analysis of otolith annuli and microchemical profiles, Jiang et al. [7] reported that, for anadromous *C. nasus*, juveniles entering the Yellow Sea from the Yangtze River were less than 1-year old, and spawners in the Yangtze River migrating upstream from sea areas were generally 2-year old. Also, Chen et al. [35] reported an anadromous *C. nasus* with a total length of 18.5 cm (at 1-year old) and two anadromous *C. nasus* at only stage II of gonadal maturity from a river section in the lower reaches of the Yangtze River in Jiangsu Province. In fact, high stage (e.g., IV or more) of gonadal maturity is not necessary for this fish to start anadromous migration into the freshwater areas to spawn. Adult anadromous *C. nasus* individuals are usually less sexually mature in downstream reaches, developing gonadal maturity during their journey upstream [9]. Therefore, all fish at 1-year old and older, stage II gonadal maturity and higher, or total length around 18.5 cm and longer in the present study (Table 1) are believed to have reached the 'migrating to river' and 'spawner' stages, respectively.

Notably, the samples from all individuals collected from the Dongting, Gucheng, Taihu, Gaobao, and Dongping lakes during the spawning season of anadromous *C. nasus* exhibited low Sr bluish color and Sr/Ca ratio (average from 1.25–2.08) patterns (Figures 3 and 4), consistent with the patterns of otoliths obtained from land-locked *C. nasus* previously sampled in the Taihu Lake (average Sr/Ca ratio values of 1.33–1.79, bluish color pattern) [31]. This finding suggests that the *C. nasus* specimens in these lakes are most likely freshwater-resident and/or land-locked ecotypes, and that anadromous *C. nasus* may be unable to migrate into some localities lying within their historically reported distribution and spawning areas [6, 11, 14].

Human activities can radically alter or destroy lake environments through water conservancy or embankment construction, land reclamation, cultivation, and industrial development [20]. The loss of river-lake connectivity in the Yangtze River Basin combined with aggravated water pollution, resource overexploitation, environmental degradation, and habitat shrinkage, has caused local extirpations of fish species, especially migratory clupeid (including *C. nasus*), tetraodontid, anguillid, acipenserid [25] and cyprinid [19] fishes. In fact, human activities are suspected to contribute to the disappearance of anadromous *C. nasus* in the Taihu Lake around the late 1980s [17, 31]. Even for Dongting Lake that freely connects with the Yangtze River, it is unlikely that anadromous *C. nasus* are able to reach the lake, due to changes in annual flow attributable to the construction of the Three Gorges Dam [30]. The same case occurred for *C. nasus* of Dongping Lake in the lower reaches of the Yellow River. As aforementioned, there is most likely no way for the anchovies to enter Dongping Lake, as the lake has become a large reservoir because of the water gate systems and is mainly utilized for local flood control and as the waterways for the eastern route of the national South-to-North Water Diversion Project [26, 27]. Furthermore, this species has not been caught even in the whole lower Yellow River for decades because of intermittent flow [63].

This study suggests that both freshwater-resident and anadromous ecotypes of *C. nasus* can still be found in Poyang Lake, as indicated by the fluctuation of two significantly different Sr/Ca ratio phases and Sr color map patterns (i.e., low: around 1.50, bluish color pattern; high: around 3.70, greenish color pattern) (Figures 3 and 4). On the basis of *C. nasus* samples collected in 2014 and 2015, Jiang et al. [9] recorded the co-existence of freshwater-resident and anadromous *C. nasus* and identified a spawning area for the latter using the same otolith microchemistry approach. Notably, because our samples were collected in 2016, it is reasonable to assume that *C. nasus* is able to migrate annually into Poyang Lake even as far as 1000 km from the Yangtze River mouth, and that the spawning areas there are still important for reproduction and recruitment.

There is evidence that the long-distance upstream movement of diadromous fishes might lead to the development of strong homing migration for the successful reproduction [64]. *C. nasus* historically migrated more than 1300 km into Dongting Lake [11] and now migrates 1000 km into Poyang Lake [9] for spawning. We previously conducted a comparative study on element composition profiles of Na, Mn, Fe, Ni, Cu, Sr, Ba, and Ca in otolith cores of *C. nasus* from the Yangtze River, Yellow Sea, and Poyang Lake using LA-ICPMS analysis. The results of the study suggested a natal homing capability of this species; the Poyang Lake, Yangtze River, and Yellow Sea seemed to be the natal lake, migration pathway, and feeding ground, respectively, for this species [48]. As indicated by Arostegui and Quinn [65], based on studies of salmonid fish of the North American, Asian, European, and African ranges, lakes provide spawning, rearing, and refuge habitats and support life-history variants, reproductive ecotypes, and trophic morphs. Unfortunately, anadromous *C. nasus* individuals have not been found recently in the lakes of Dongting, Gucheng, Taihu, or Dongping. If *C. nasus* does indeed have natal homing behavior, the loss of spawning sites could lead to the extirpation of some of its populations, as exemplified by local extirpation of the alewife (*Alosa pseudoharengus*) along the Atlantic coast in North America, which was attributed primarily to dam construction [66]. A similar case is the extinction of *Macrura reevesi*, another valuable anadromous species of economic interest in the Yangtze River, due to overfishing and the loss of spawning sites as a consequence of dam construction and water pollution [67]. In this regard, it is noteworthy that a large dam across the northern end of Poyang Lake, 27 km from the Yangtze River [68], has been proposed by the Poyang Lake Water Conservancy Project, which would block the migration path for anadromous *C. nasus*. Our findings indicate that indispensable efforts should be made to maintain the connectivity between the lake and the river in future hydraulic development projects.

Overall, the findings of our investigation confirm that two *C. nasus* ecotypes currently exist in the studied lakes: Type I, with anadromous

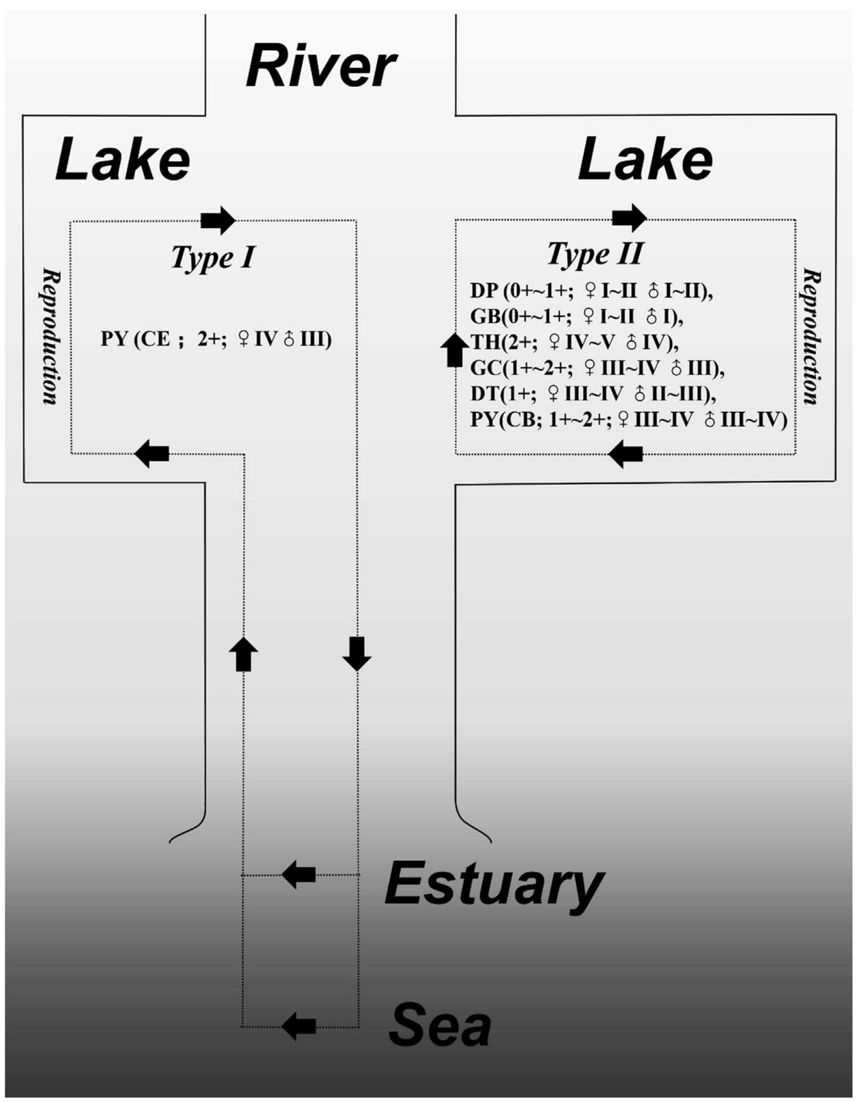

Figure 5. Diagram of the reconstructed life histories of *Coilia nasus* from the Dongting Lake (DT), Poyang Lake (PYCB: non-anadromous type; PYCE: anadromous type), Gucheng Lake (GC), Taihu Lake (TH), Gaobao Lake (GB), and Dongping Lake (DP) based on otolith strontium (Sr) content or strontium/calcium (Sr/Ca) ratio analysis along life history transects. The line with arrows represents possible dispersion.

behavior, and Type II, with a completely freshwater-resident habit (Figure 5). Among Type II populations, the individuals of the CE group from the Poyang Lake showed indications of anadromous migration into brackish water or seawater (Table 1, Figure 5). In contrast, for Type I populations, all individuals are land-locked in the Dongping, Gaobao, Taihu, and Gucheng lakes due to anthropogenic impacts; additionally, all individuals in the Dongting Lake and some individuals in the Poyang Lake (i.e., the CB group) are likely to be residents of a single freshwater habitat, but no part of their life history is spent in brackish water or seawater (Table 1, Figure 5).

The data obtained in this pilot study suggested that anadromous *C. nasus* were found in Poyang Lake, but are unlikely to be found in Dongting, Gaobao, Gucheng, Dongping, or Taihu, despite historic records of anadromous life histories in these lakes [11, 13, 14]. If the above-mentioned water conservancy project [68] is constructed in the future, even Poyang Lake faces very significant risks regarding the loss of diadromous *C. nasus* and their habitat. The disappearance of anadromous *C. nasus* in the lakes connected to the Yangtze and Yellow Rivers highlights the impact of anthropogenic activities on the life histories of diadromous fish species, such as becoming land-locked in Gucheng, Taihu, Gaobao, and Dongping lakes, and the loss of spawning and nursery habitats in Dongting Lake. Similar to the cases of other fish species in Europe [69] and North America [66], the disruption of habitat connectivity poses considerable challenges with respect to *C. nasus* resource management. The challenges are especially caused by the destruction of local lake ecosystem integrity, the effects of the altered ecological roles of different ecotypes on resource structure and ecosystem function, and the non-sustainability of high-value anadromous *C. nasus* fisheries in these lakes. These lessons of the *C. nasus* (as a model species) serve to highlight the potential dangers faced by traditional anadromous fish resources in other countries as a consequence of anthropogenic-derived habitat changes. Notably, for diadromous fish species (e.g., alosine clupeids, sturgeons, salmons, and eels), the effects of habitat loss and degradation are most profound, and therefore, require more attention in terms of restoration and conservation [70]. In reality, the decline of diadromous fishes, taken as a group, represents one of the greatest corruptions of the ecological connections in North American and European watersheds and the North Atlantic ecosystem [52]. Restoration of the connectivity between the rivers and their associated lakes can strongly facilitate the re-use of historical spawning sites and assist in the recovery of anadromous *C. nasus* resources, not only in these lakes but also in the rivers, estuaries, and even seas potentially inhabited by this fish throughout its entire life history. Consequently, it will be necessary to develop corresponding methodologies based on the present study, cooperating with more targeted otolith-based approaches. These include otolith shape-based population or ecotype discrimination [71, 72], multiple element-based spatiotemporal habitat reconstruction [44, 73], and heavy metal-based anthropological environmental impact/pollution monitoring [74, 75] that are designed to enable more accurate monitoring of the dynamics of different *C. nasus* ecotypes, the development of land-locked/freshwater resident population, the vulnerability of anadromous *C. nasus* to lacustrine pollutants (e.g., heavy metal) or habitat degradation. This will help in the more effective establishment of natural refugia and reserves in the lakes to conserve and enhance the populations of anadromous *C. nasus*. Moreover, China has instituted a 10-year ban on all commercial fishing in the Yangtze River, its tributaries and adjoining lakes since January 2020 [76]. Continuous work on this subject matter, with the use of the model species and a comprehensive otolith approach as used in the present study, will also help in re-inhabitancy monitoring of anadromous *C. nasus*, and stock/habitat restoration and effectiveness evaluation of other diadromous fish in the lakes.

4. Conclusion

The present study of otolith microchemistry assessment suggested that anadromous *C. nasus* can be found in the Poyang Lake but are unlikely to be found in the Dongting, Gaobao, Gucheng, Dongping, or Taihu lakes, despite these lakes being historical distribution areas or even spawning sites. Blockage of river-lake connectivity combined with aggravated water pollution, resource overexploitation, environmental degradation, and habitat shrinkage has resulted in habitat loss of anadromous *C. nasus* in the latter five Chinese freshwater lakes. Our study represents the first step toward validating and proposing *C. nasus* as a model species for understanding the health of the network between connected aquatic habitats and suggests that restoration of natural habitats of diadromous fish and maintenance of their river-lake connections are particularly important for resource re-inhabitation, management, and conservation. Future studies will be necessary to develop more targeted otolith-based approaches and corresponding methodologies based on *C. nasus* as a model species for more effective establishment of natural refugia and reserves in the lakes to conserve and enhance the populations of not only *C. nasus* but also other anadromous fish.

Declarations

Author contribution statement

Jian Yang: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Ly Sokta, Tao Jiang: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Hongbo Liu, Zhongya Xuan, Chen Qiu, Xiubao Chen: Performed the experiments; Contributed reagents, materials, analysis tools or data.

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Competing interest statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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