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Shift towards Opportunistic Life-History of Sleeper in Response to Population Decline over Multi-Decadal Overfishing

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Citation: Xiang, M.; Rypel, A.L.; Cheng, F.; Qin, J.; Zhang, L.; Chen, Y.; Xie, S. Shift towards Opportunistic Life-History of Sleeper in Response to Population Decline over Multi-Decadal Overfishing. *Water* **2021**, *13*, 2582. https://doi.org/10.3390/w13182582

Academic Editor: Fernando Cobo

Received: 18 August 2021
Accepted: 17 September 2021
Published: 18 September 2021

Abstract: Understanding long-term changes in life-history traits is central to assessing and managing freshwater fisheries. In this study, we explored how life-history traits have shifted in association with long-term change in population status for a native fish species (freshwater sleeper, *Odontobutis sinensis*, a by-catch species of shrimp traps) in the middle Yangtze lakes, China. We assessed the life-history traits of the species from Honghu Lake in 2016, where abundance had been dramatically lower following about 60 years of high fishing pressure, and made comparisons to similar data from Liangzi Lake (1957), when fishing intensity was low and abundance was high, and Bao'an Lake (1993–1994), when about 10 years of intense exploitation had occurred and abundance had greatly declined. Modern Honghu Lake sleeper exhibit life-history traits that are substantially more opportunistic compared to both of the historical populations. Modern fish were larger at age-1 and had significantly faster growth rates, a higher prevalence of sexually mature individuals and increased fecundities. Fish from the historical samples were larger and had higher age class diversity and delayed sexual maturation. Combined, the data suggest that faster growth towards early sexual maturation and reduced body sizes are associated with destabilized populations and ecosystems. Similar life-history patterns are common in other declined fish populations under exploitation. Recovering historic fish life-history dynamics requires conservation management policies aimed at reducing harvest and improving floodplain habitats.

Keywords: fecundity; growth; life-history plasticity; overharvest; sleepers

1. Introduction

Life-history traits are a fundamental outcome of evolutionary processes [1–3]. Yet life-history traits also vary widely on an interspecific basis over space and time, which has implications for conservation management [4,5]. Several theoretical frameworks have emerged for understanding the life-history strategies of species in response to environmental conditions [6–8]. The r/K selection theory continues to be one of the most widely recognized frameworks, but it receives frequent challenges [9,10]. Alternatively, Winemiller and Rose (1992) proposed a semi-triangular surface model upon which the life-history of any fish species or population rests. The three endpoints were termed "opportunistic", "periodic" and "equilibrium". The opportunistic strategy combines low juvenile survival, low numbers of offspring, and early reproductive maturity [11]. This life-history is considered advantageous for colonizing in unpredictable environments across space and time.

Fishes utilizing the periodic strategy are often larger in body size, producing copious offspring with low survivorship. Finally, equilibrium strategists vary in body size and have moderated to late age at maturation, small clutches of large eggs, well-developed parental care and high offspring survivorship. Equilibrium fishes are normally associated with habitats exposed to low environmental variation [12]. Several aspects of the Winemiller and Rose system are attractive to ecologists and fishery biologists, especially the basis of classification upon fundamental aspects of population ecology (i.e., growth, survival, longevity). This system is also attractive because it can be applied to multiple levels of ecological organization. For example, life-histories can be mapped interspecifically (as is classically done) [13], but also intraspecifically.

Fish species can respond to short-term environment changes and shift their life-history traits in order to facilitate populations to successfully colonize a changed environment [14]. However, exploitation of fish populations also modifies life-history traits at the intraspecific level, which has been a major concern in fishery management and conservation [15–17]. For example, many over-exploited populations show life-history traits associated with reduced size, smaller average age, quickened maturation and elevated fecundity [18,19]. These shifts likely function in a compensatory fashion, stimulating contributions by survivors to enhance production while also preventing further population declines overall [20]. Furthermore, eutrophication and climate changes have also been important factors in inducing shifts in the life-history traits of many populations [21,22].

Fisheries resources in the Yangtze River basin, China, have been dramatically exploited and have declined since the 1970s [23]. The total annual landings of fish in the middle and lower reaches of the Yangtze River basin were 427,221 t in 1954, but by the 1990s, the annual landings declined by 80% to less than 100,000 t [24]. Associated with the decline in fish abundance, an erosion in fish size structure has been frequently reported at both the population and community levels [25–27]. Increasingly, small and resilient species dominate fish communities, and commercial fisheries catch includes only young and small individuals [28,29]. Meanwhile, the environment of these lakes has also dramatically changed, e.g., hydrological modification due to isolation from the river [30], eutrophication [21], and climate changes [22]. However, the way life-history traits shifting is associated with environmental changes has rarely been investigated and taken into account in fisheries management and conservation in the Yangtze River basin, as is the case in other water bodies [31].

The sleeper (*Odontobutis sinensis*) is endemic to the lakes of the Yangtze basin and is an important commercial species with a high market value (the price is about 15 USD/500 g) [32]. It is usually a by-catch species of shrimp traps and occurs in the harvest during spawning season of this species in March and June [33]. This species exhibits parental care behavior by males to fertilized eggs during the breeding period, which is a typical feature of the equilibrium strategy [11]. Yet beginning in the 1970s, the population declined sharply, presumably due to intense over-exploitation. As a result, the species is now rarely captured [34]. Two historical surveys were conducted on this species (both collecting life-history data) in Liangzi Lake in 1957 [32] and in the Bao'an Lake from 1993–1994 [33]. These periods, respectively, represent contrasting dynamics of low and initially high harvest rates according to the development stages of fisheries in the Yangtze River basin [23,35]. Currently, the sleeper has become so rare that a broad-scale study in multiple lakes is simply not feasible. Changing life-history traits associated with population declines has been suggested in some fishery-focused species, such as *Coilia mystus* [19] and *Siniperca kneri* [36] in the Yangtze basin. However, in all of these cases, historical life-history data are lacking to adequately document change.

Here, we have provided the first formal investigation of long-term shifts in life-history traits on the sleeper in the Yangtze basin. We documented data on the body size, growth, fecundity and sexual maturation of the sleeper and compared modern life-history traits with those recorded in historical surveys. We tied temporal changes in life-history parameters to the fish life-history classification system and discussed the implications of our findings on the sustainable conservation of fisheries in the Yangtze River basin and similar fisheries throughout the world.

2. Materials and Methods

2.1. Study Area

Modern fish were sampled in Honghu Lake (29°49′ N, 113°17′ E) while two historical surveys were conducted in Liangzi Lake (30°3–19′ N, 114°26–38′ E) and Bao'an Lake (30°15′ N, 114°23′ E), respectively (Figure 1). All three lakes are typical shallow lakes belonging to the Jianghan lake clusters [37]. The three lakes have similar climate conditions and community compositions (e.g., species abundance and trophic structure), and have undergone the same process of fisheries exploitation development [38,39]. These shallow lakes were historically connected to the Yangtze River via floods. Extensive diking and hydrologic management isolated the lakes from the river beginning in the 1950s, creating an altered and isolated regime that persists today. Fish communities have changed dramatically over this period, typically with reduced numbers of migratory species and an increased dominance of lake resident species [37].

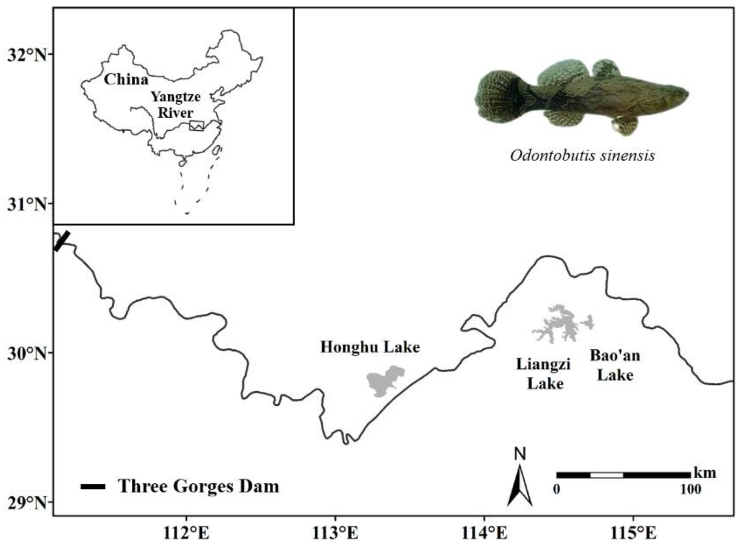

Figure 1. Map of the middle Yangtze River, China, showing the locations of Honghu Lake (the present-day studied population) and Bao'an Lake and Liangzi Lake (the two historical populations) where life-history traits of *Odontobutis sinensis* were compared.

2.2. Fish Sampling and Processing

To minimize the potential for gear size selectivity of life-history traits, we used the same sampling technique and study design as the historical data obtained in the other two lakes. All samplings were collected from the commercial harvest of fishermen using shrimp traps during the spawning season, March and April 2016. The shrimp trap is a kind of fyke net which is usually about 15 m long and 0.6 m wide with a 4 mm mesh size. Each net contains about 20 trap cases, and each case has three entrances that shrimp and fish could enter but not exit [40]. Sleeper is a by-catch species of the shrimp traps, which mainly occurs in the harvest in near-shore areas with a water depth of about 1 m [38]. All specimens were placed on ice and brought into the laboratory for analysis. Each fish was individually measured for standard length (SL, 0.1 mm) and weighed for body weight (BW, 0.01 g). For age estimation, scales were removed from each fish near the terminus of the pectoral fins. Age was determined by the first author alone. Three independent readings were made with a minimum period of 2 weeks between each reading [32,33]. Each fish was dissected, and sex was determined through a visual inspection of the gonads.

Both gonads were removed from each female and weighed (GW, 0.01 g). As preliminary observations showed no difference in developmental stage or fecundity between the left and right ovaries, fecundity was determined using only the right ovary of mature females (gonads at stage IV or V). Approximately 0.3 g of oocytes were removed from the middle and each of the two ends of the ovary, mixed, weighed (RW, 0.01 g) and preserved in a 5% formalin. We later counted the eggs (n) from each fish under a dissecting microscope. The absolute fecundity (AF) of a fish was calculated by AF = n × GW/RW, and relative fecundity (RF) was calculated by RF = AF/BW.

2.3. Statistical Analysis

The data on the age composition, size at age and fecundity of the sleeper population in Honghu Lake which were obtained in this study were compared with the data on available historical populations in lakes of the middle Yangtze River, i.e., the population in 1957 in Liangzi Lake [32] and the population in 1993–1994 in Bao'an Lake [33]. Fish size data from Hao [32] were reported in total length; therefore we converted these data to SL using the function TL = 1.133SL + 0.729 (R^2 = 0.98) developed by Cao et al. [41]. Growth differences among populations were compared using Analysis of Covariance (ANCOVA). In this model, SL was the dependent variable, $\log_{10}$(age) was an independent variable, and the population was a blocking variable. Differences in growth rate were assessed by examining differences of $\log_{10}$(age) × population interaction term using Tukey post hoc tests. Due to the low amount of replication (only 3 age classes with 10 SL–age data points overall), the p-value was relaxed in the analysis to $p < 0.10$ = significant [42,43].

Finally, we used principal component analysis (PCA) to illustrate how life-histories have shifted over time in the Yangtze River basin. Inputs into the PCA included size at age-1, growth rate, RF and percent of age-1 individuals in the catch of each population, and we expected to reduce to two principal components by PCA. Selected life-history parameters were based on the classic life-history framework and PCA from Winemiller and Rose [11]. All life-history data were $\log_{10}$-transformed prior to conducting the PCA.

3. Results

A total of 145 individuals were collected from Honghu Lake in 2016. SL ranged from 62.1 to 127.1 mm and BW ranged from 5.25 to 46.53 g (Figure 2). There were three age classes in the population. Individuals of age-1 and age-2 accounted for 54.5% and 43.4% of the population, respectively; age-3 fish were uncommon. In contrast, age-3 and older fish accounted for 43.6% and 42.2% of all fish in the 1950s and 1990s samples, respectively (Table 1). Thus, older fish have become rare, especially in recent years.

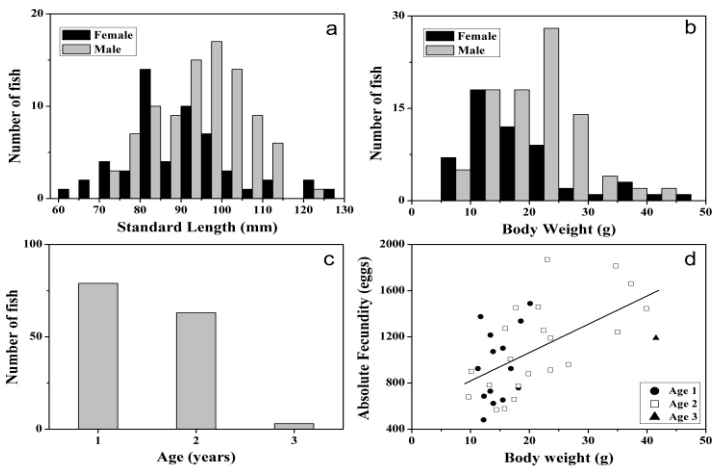

Figure 2. Distribution of standard length (**a**), body weight (**b**), age (**c**) and relationship of fecundity to body weight (**d**) of *Odontobutis sinensis* collected from Honghu Lake in 2016.

Table 1. Life-history traits of *Odontobutis sinensis* collected from Honghu Lake in 2016, in comparison with two historical populations in the middle Yangtze River, China.

Population	Year of Collection	Age Structure (Number Percentage, %)				Absolute Fecundity (Eggs)	Relative Fecundity (Eggs·g^{-1})
		1	2	3	4	Range (Mean ± SD)	Range (Mean ± SD)
Liangzi Lake [1]	1957	30.8	25.6	43.6		245–2505	21.8–43.3
Bao'an Lake	1993–1994	14.2	43.7	30.9	11.3	540–1943 (1154 ± 317)	33.3–63.3 (45.4 ± 7.5)
Honghu Lake	2016	54.5	43.4	2.1		481–1869 (1053 ± 366)	28.7–117.4 (58.0 ± 20.5)

[1] The absolute and relative fecundities in Liangzi Lake presented as a range. They could not be calculated for their average value.

The mean SL at age 1 in Honghu Lake was 89.7 mm, which was larger than that of the Liangzi Lake population (75.6 mm) and the Bao'an Lake population (65.2 mm). SL at age 2 in the Honghu Lake was smaller than in Liangzi Lake and similar to Bao'an Lake (Figure 3). A significant ANCOVA model was developed which predicted SL strongly as a function of $\log_{10}$(age) and time period ($F = 18.1$, $R^2 = 0.90$, $p = 0.002$). Even though sample sizes were small because of a low number of age classes, there were also differences observed in growth rates (calculated as the slope of the SL-$\log_{10}$(age) regression) across time periods. Growth was significantly different between the Liangzi Lake and Honghu Lake populations (Tukey's $p < 0.10$), while other post hoc comparisons approached significance (Honghu Lake vs. Bao'an Lake, $p = 0.37$; Bao'an Lake vs. Liangzi Lake, $p = 0.17$).

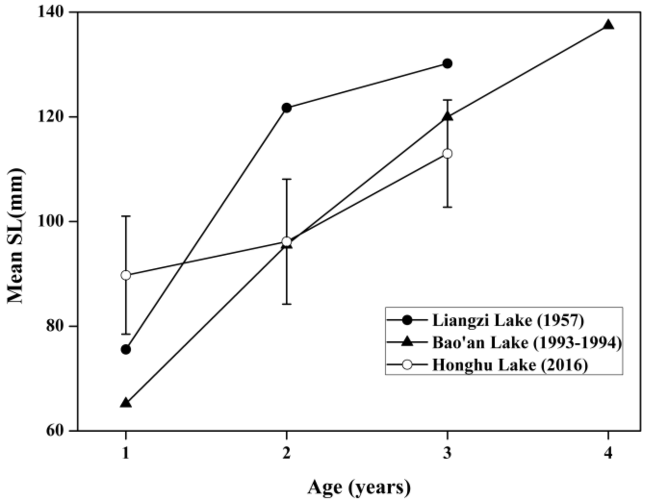

Figure 3. Estimated mean standard length (SL)-at-age of the studied modern-day population (Honghu Lake) and two historical populations (Bao'an Lake and Liangzi Lake) of *Odontobutis sinensis* in the middle Yangtze River, China.

Fecundity was determined for 36 females from Honghu Lake, which ranged from 68.5 to 123.6 mm SL and included the three age classes. AF increased significantly with BW and was fitted to the linear function AF = 24.5BW + 573.1 ($R^2 = 0.32$, $n = 36$, $p < 0.05$) (Figure 2d). AF ranged from 481 to 1869 eggs, with a mean (± SD) of 1053 ± 366. For age 1 fish, fecundity ranged from 481 to 1488 eggs with a mean of 955 ± 316 ($n = 14$). For age 2 fish fecundity ranged 569 to 1869 eggs with a mean of 1112 ± 397 ($n = 21$). Finally, one age 3 fish had a fecundity = 1190 eggs (Figure 2d). RF ranged from 28.7 to 117.4 eggs·g^{-1} with a mean of 58.0 ± 20.5 eggs·g^{-1}. This value was higher than that reported for the Bao'an Lake population (45.4 ± 7.5 eggs·g^{-1}) and consequently also higher than the Liangzi Lake population (21.8–43.3 eggs·g^{-1}) (Table 1).

A PCA was built that explained 100% of the variation in the four life-history traits examined (Figure 4). PC1 and PC2 explained 84% and 16% of the variance, respectively. PC1 was positively driven by SL at age 1 and percent of age 1 individuals and negatively driven by growth rate. In contrast, PC2 was negatively driven by RF. Thus the contemporary samples from Honghu Lake were characterized by larger size at age 1, a higher percent of age-1 individuals and a slower growth rate compared to the two historical populations.

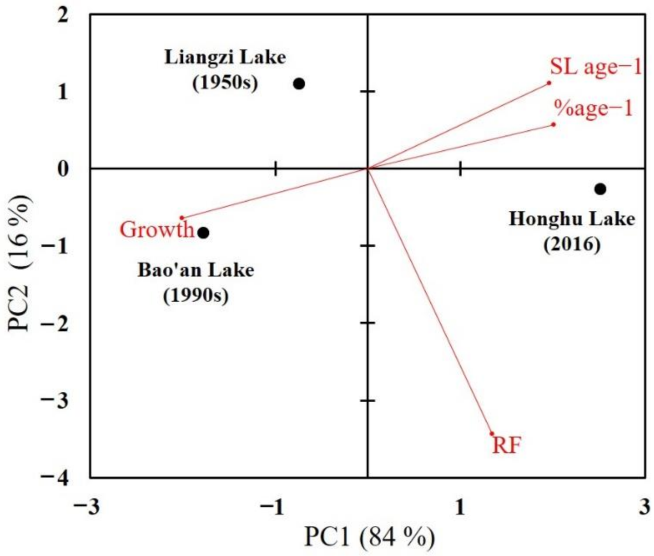

Figure 4. Temporal changes in the life-histories of *Odontobutis sinensis* in the middle Yangtze River as revealed through PCA. Increasing PC1 values correspond with increasing size at age-1, percent of fish mature at age-1, and decreased growth. PC2 values denote changes to the relative fecundity of fish (Table 1). Thus modern fish in Honghu Lake are larger, faster-growing, have increased fecundities, and have a high percent of sexually mature individuals.

4. Discussion

Overall, the results of this study show how the life-history of the sleeper became increasingly opportunistic in connection with population decline over multiple decades in the Yangtze Lakes, China. The sleeper is a nesting species in which the males guard fertilized eggs [32] and is a typical equilibrium species in the frame of the triangular life-history theory [11]. Below, we discuss potential factors inducing this pattern of life-history changes and the implications for conservation and management.

The three study populations covered 59 years and spanned different population statuses due to overharvesting and long-term environmental changes. During the 1950s, when Liangzi Lake was sampled, the fishing intensity was low in the Yangtze lakes in China [32]. For example, fisheries resources in the Yangtze lakes were commonly referred to as “underexploited” during this period [35]. Although there were impacts from fishing during this period, the intensity of fishing now bears little resemblance to that typically observed during the 1950s. The sleeper was a common by-catch species in shrimp traps during this period. Beginning in the 1980s, fishing intensity in inland waters in China increased sharply, resulting in widespread declines in fishable resources, especially in floodplain lakes along the Yangtze River [29]. The Bao’an Lake sleeper population (1993–1994) represented a period when the resources had already experienced sustained high fishing intensity. During this time, the sleeper occurred in ichthyological surveys throughout most lakes [34,44] but was no longer a common species in commercial harvest efforts [45]. The modern population in Honghu Lake represents an endpoint wherein the population has experienced a sustained period of intense over-exploitation and the abundance has functionally collapsed. Currently, the sleeper is rarely captured in ichthyological surveys or commercial traps. Indeed, the only reason this study was possible is that Honghu Lake was designated as a natural reserve of Hubei Province in 2000, and then as a national natural reserve in 2014. As part of these conservation efforts, the fishing intensity has declined compared to other lakes, resulting in some recovery of local abundance. Thus, overfishing over multiple decades in the Yangtze lakes, which have induced a dramatic decline in fish resources, should be a major factor inducing these opportunistic-tending life-history traits of the sleeper.

Among the three compared populations, small fish and age-1 and -2 individuals only dominated the population in Honghu Lake. In contrast, both historical populations had substantially higher proportions of larger and older fish. Intense fishing generated an erosion in size- and age-structure, as is commonly observed in other intense freshwater fisheries [46]. The sleeper is a demersal species, commonly associated with complex structures in benthic habitats, and is likely relatively non-motile outside of the spawning season. Adults become active and more motile in conjunction with spawning, usually from late March to May [32]. During these months shrimp traps commonly capture sleepers, whereas, during other periods, fishermen rarely capture them [33,41]. The collected individuals in Honghu Lake were all adults with well-developed gonads. The samplings from the Liangzi and the Bao'an Lake populations was also carried out during the spawning season; thus available samples from all three periods reflect similarly gravid individuals. Differences in age composition across periods therefore do not reflect differences in sampling bias, but rather the deleterious effects of harvest on the size- and age-structures of spawning stocks. Furthermore, a lower percentage of age-1 individuals overall in both historical populations suggests a higher proportion of age-1 individuals were immature in the two historical populations compared to the Honghu Lake population. If more fish had been sexually mature, they should have been captured in trap nets coincident with spawning. Therefore, it is likely that a higher proportion of fish are becoming sexually mature during their first year now while this pattern was rare in historical samples. However, the proportion of age-3 fish was even higher than age-2 fish in the Liangzi Lake population of 1957. One potential reason might be a particularly successful year class in 1954 (producing age-3 fish in 1957). High flooding was recorded in 1954 [47], which might have induced low fishing intensity on spawning stocks and high recruitment success of this species, though this could not be verified.

These fisheries may also be changing because of other global environmental change factors. Global climate change is already affecting the life-history traits of diverse species [22,48], and water temperatures in the middle Yangtze Lakes are projected to increase by 0.26–0.28 °C per decade [49]. Meanwhile, eutrophication is also known to effect the life-history traits of fishes [21,50]. The Yangtze lakes have been heavily eutrophicated over the past half-century [51], and the influence on the life-history traits of fishes should be investigated. Whether life-history changes reflect population- or ecosystem-level processes remains unknown. However, a rise in opportunistic life-histories within intensely exploited ecosystems has implications for conservation management.

Opportunistic-tending life-history traits, such as younger age at first maturation, increased fecundity, and a larger size at a young age, have been observed in many fish populations experiencing population decline [19,52]. Changes in life-history traits may reflect phenotypic plasticity to environmental variability, or potentially rapid fisheries-induced evolution [53,54]. For example, heavy exploitation induces abundance declines, which in turn reduces intraspecific competition and the availability of food resources. Consequently, larger size at a young age is common and may be a compensatory response to exploitation, along with increased reproduction investment [55]. Yet it is also increasingly clear that compensatory responses occur at much lower levels, and exploitation beyond these values can lead to biomass decline [56,57] and potentially evolutionary impacts [58]. Opportunistic life-histories are thought to be an adaptation for maximizing colonizing ability in environments that vary unpredictable across both space and time. Indeed, the occurrence of opportunistic strategists is positively related to measures of environmental variability and negatively related to seasonality of habitats [59]. That opportunistic life-histories that increased as a response to population decline may fundamentally destabilize ecosystems, thereby promoting the rise of life-histories better adapted to more stochastic and random ecological environments.

Species and fisheries are declining worldwide and require immediate science-based management [60–62]. High-quality long-term data are lacking for most species and ecosystems, even though critical management decisions still must be made regardless of high levels of uncertainty. Our study was carried out using specimens from the commercial catch, which can be biased in terms of the accuracy of reported catch or representativeness of a sampling location, and there may be high variation in capture efficiencies. However, it can also give managers access to a very large dataset which may be highly informative. Indeed, in our study, the focal species has declined dramatically across the middle Yangtze Basin due to high intensity human activities over the last several decades. Therefore, while challenging, we are still using the best available data for this species and system. Study populations are geographically close, were historically connected to the main Yangtze River, and have similar/connected management histories. For these reasons, we assume these populations are comparable and reflect general changes in the life-history traits of the species in the larger ecosystem context. Similar assumptions have been made in a variety of other long-term-ecological-research studies where high-quality historical data were lacking [63–65]. We suggested further confirmation of the patterns of these observed changes in the life-history traits of the sleeper by analyzing the Honghu Lake population over more years, if possible. We also suggested focusing on the long-term changes in life-history traits of other species of different life-history strategies, using the historical data available to generate potential general patterns.

5. Conclusions

Many freshwater fish populations in the Yangtze River and its affiliated floodplain lakes have been over-exploited and have declined over the last half-century [28]. Results from this study, combined with others, demonstrate that opportunistic life-history traits commonly arise in those populations in this system, e.g., with *C. mystus* [19] and *S. kneri* [36]. Opportunistic life-histories are problematic from a management standpoint for several reasons. (1) Populations will be dominated by small, reproductively mature fish, which are often undesirable for fisheries; (2) simply reducing or eliminating fishing may be insufficient to stimulate a recovery in size-structure. For example, given strong density-dependent effects, populations may become locked into high-density, high-competition scenarios wherein fish remain small in spite of reduced fishing effort. Under these conditions, the protection of large individuals might be prioritized via special fishing regulations (e.g., slot limits, maximum size limits) aimed at recovering age class diversity and size-structure. (3) Increases in fecundity in declined populations suggest natural mortality may have also increased. Thus, issues related to habitat quality may also need to be addressed to enhance survivorship and natural production [60,66]. For example, seasonal floods are likely important to enhancing survivorship in these populations, but have been removed or greatly dampened as an environmental driver in these ecosystems. Beginning in 2020, strategic fishing bans are planned for the whole Yangtze River for 10 years and will include most floodplain lakes [67]. Adaptive management experiments will provide critical opportunities to assess how life-history traits of diverse exploited populations change with various conservation management approaches.

Author Contributions: Conceptualization, F.C. and S.X.; methodology, M.X., J.Q. and L.Z.; software, M.X. and A.L.R.; validation, M.X., L.Z. and A.L.R.; formal analysis, M.X. and A.L.R.; investigation, M.X., J.Q. and L.Z.; resources, M.X.; data curation, A.L.R. and J.Q.; writing—original draft preparation, M.X.; writing—review and editing, F.C., Y.C. and S.X.; visualization, M.X. and A.L.R.; supervision, F.C. and S.X.; project administration, A.L.R., F.C. and S.X.; funding acquisition, A.L.R., F.C. and S.X. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA23040402), the Key Project in Frontier Science of Chinese Academy of Sciences (QYZDB-SSW-SMC041), and the National Natural Science Foundation of China (31570420 and 31870398). A.L.R. was supported by the Peter B. Moyle & California Trout Endowment for Coldwater Fish Conservation and the California Agricultural Experimental Station of the University of California Davis, grant number CA-D-WFB-2467-H.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data from this research are available from the corresponding authors upon reasonable request.

Conflicts of Interest: The authors declare no conflict of interest.

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