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Diets and Stable Isotope Signatures of Native and Nonnative Leucisid Fishes Advances Our Understanding of the Yellowstone Lake Food Web

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Abstract: (1) Many forage fishes, such as Leucisids (minnows) have depauperate studies on diet composition or stable isotope signatures, as these fishes are often only viewed as food for higher trophic levels. The need exists to understand and document the diet and stable isotope signatures of Leucisids (redside shiner, longnose dace, lake chub) in relation to the community ecology and food-web dynamics in Yellowstone Lake, especially given an invasive piscivore introduction and potential future effects of climate change on the Yellowstone Lake ecosystem. (2) Diet data collected during summer of 2020 were analyzed by species using proportion by number, frequency of occurrence, and mean proportion by weight, and diet overlap was compared using Schoener's index (D). Stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values were estimated by collecting tissue during the summer of 2020 by species, and isotopic overlap was compared using 40% Bayesian ellipses. (3) Nonnative redside shiners and lake chub had similar diets, and native longnose dace diet differed from the nonnative Leucisids. Diet overlap was also higher between the nonnative Leucisids, and insignificant when comparing native and nonnative Leucisids. No evidence existed to suggest a difference in $\delta^{15}N$ signatures among the species. Longnose dace had a mean $\delta^{13}C$ signature of -15.65, indicating an decreased reliance on pelagic prey compared to nonnative Leucisids. Nonnative redside shiners and lake chub shared 95% of isotopic niche space, but stable isotope overlap was <25% for comparisons between native longnose dace and the nonnative Leucisids. (4) This study established the diet composition and stable isotope signatures of Leusicids residing in Yellowstone Lake, thus expanding our knowledge of Leucisid feeding patterns and ecology in relation to the native and nonnative species in the ecosystem. We also expand upon our knowledge of Leucisids in North America. Additionally, quantifying minnow diets can provide a baseline for understanding food web response to invasive suppression management actions.

Keywords: minnows; community ecology; forage fishes; introduced fishes

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1. Introduction

Fish diets can integrate many ecological characteristics of a species, including behavior, habitat use, energy intake, and interactions within populations or communities [1]. Research on fish diets can compare consequences of environmental change [2–5] or species introductions [6–9]. Diet data can provide insight into prey resources used, thereby guiding management of species [10,11], or define the energetic demand of species to benefit production for aquaculture or commercial fishing applications [12,13]. Descriptions of fish diet can also clarify trophic interactions in aquatic food webs [6,7,14–16]. In addition to diet analysis, stable isotope analysis can be used to evaluate stages of ontogeny, habitat use [1], or compare trophic positioning of species.

A longer-term representation of diet, as well as trophic status, can be assessed using stable nitrogen and carbon isotope ratios because they are accumulated over extended periods (months or years) in muscle tissue [17,18]. Stomach diet content analyses provide short-term estimates of trophic position and diet overlap among animals within food webs [1]; however, diet estimates can be biased by digestion rates and the method of fish capture [19]. Seasonal and diel prey availability and feeding patterns can influence stomach content, further demonstrating stomach content as a short-term indicator of diet. Using stable isotopes and diet composition jointly can enhance estimation of feeding patterns and can aid in our understanding of fishes in their environment.

Diet composition and stable isotope signatures have been studied for the larger fishes of Yellowstone Lake, such as invasive lake trout (*Salvelinus namaycush*) [6,7], native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) [6,20–22], and introduced longnose sucker (*Catostomus catostomus*) [23,24], but no peer-reviewed research exists on the diet composition and stable isotope signatures of the smaller fishes of Yellowstone Lake (i.e., redside shiner *Richardsonius balteatus*, lake chub *Couesius plumbeus*, and longnose dace *Rhinichthys cataractae*, hereafter referred to as minnows). Quantifying diet composition and estimating stable isotope signatures of all fish species in Yellowstone Lake is valuable to establish an ecological baseline during lake trout invasion as changes in large fish abundance, cascading trophic interactions [16,25,26], and influences of climate change are likely in the future [27]. Knowledge on diet composition and stable isotope signatures during a period of lake trout decline and Yellowstone cutthroat trout recovery is also useful for comparison to future, post-restoration periods on Yellowstone Lake, to compare to other systems, or to use in community-based research. For this study, we had the following questions: (1) what is diet composition for nonnative redside shiner and lake chub, and native longnose dace in Yellowstone Lake, (2) what degree of diet overlap exist among the native and nonnative minnows, (3) what are the isotopic trophic position(s) of nonnative redside shiner and lake chub, and native longnose dace in Yellowstone Lake, (4) what degree of stable isotope overlap exist among the native and nonnative minnows?

2. Materials and Methods

2.1. Study Area

Yellowstone Lake is in Yellowstone National Park in northwestern Wyoming, USA (Figure 1), and is the largest high elevation lake above 2000 m in North America (at 2357 m). The lake has a surface area of 34,020 ha [28] and a maximum depth of 133 m [29]. In addition to the native longnose dace and Yellowstone cutthroat trout, three non-native fishes, redside shiner (introduced in the 1950s) [30], lake chub (introduced in the 1950s) [30], and longnose sucker (introduced in the 1930s) [23], and one invasive fish, lake trout (introduced in the late 1980s) [26], comprise the fish assemblage in Yellowstone Lake [31]. We make the distinction between non-native and invasive with invasive species being non-native and causing measurable change to ecosystem function or abundance of native species. Larger fishes (Yellowstone cutthroat trout, lake trout, and longnose sucker) can move easily between different zones (e.g., pelagic, littoral, benthic) of the lake; the minnow species inhabit only vegetated bays and other littoral areas [32].

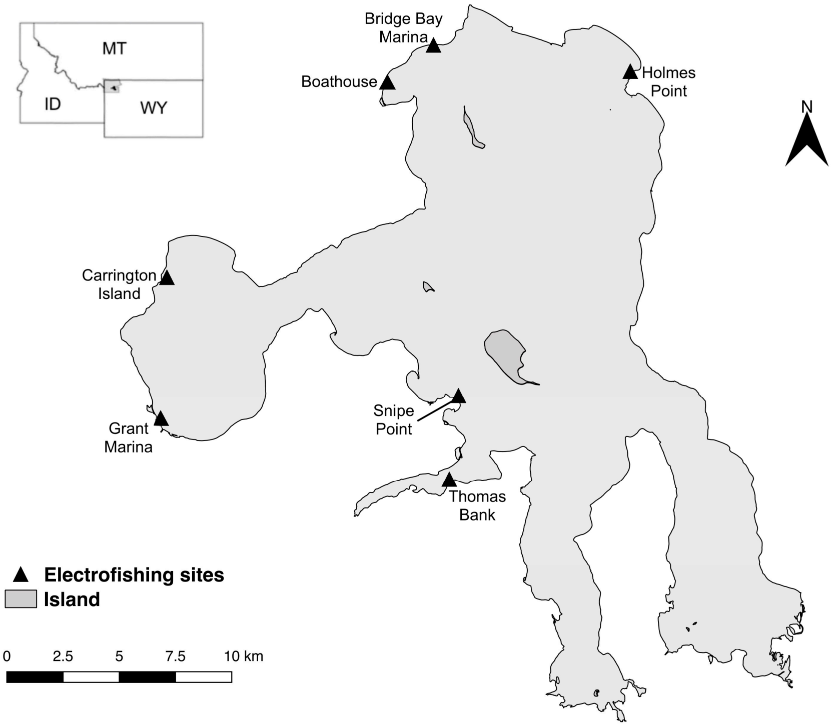

Figure 1. Map of Yellowstone Lake, Wyoming with 2020 electrofishing sites.

2.2. Field Sampling

We sampled longnose dace, redside shiner, and lake chub using a backpack electrofisher at seven sites around Yellowstone Lake during part of the ice-free season (26 May–27 July) of 2020 (Figure 1). Sites were selected based on habitat type, depth <2 m, rocky or vegetated habitat type, accessible by boat or hiking, and feasibility to electrofish. Sampled fish were placed in a container and euthanized with an overdose of MS-222. Fish were measured for total length to the nearest mm and weighed to the nearest tenth of a gram.

Tissue samples (~10 mg of dorsal muscle tissue) were collected for stable isotope analysis with a sterile blade. Methods for tissue collection, storage, and preparation were identical to [6]. We stored tissue samples in a vial and placed vials in a freezer for long-term storage.

2.3. Laboratory Processing

Stomach contents were analyzed by separating prey items by taxon (i.e., zooplankton to class or genus, macroinvertebrates to order or genus; food mastication by minnow pharyngeal teeth makes identifying to lower taxonomic resolutions impossible), counting all prey items by taxon, and then subsampling 10 items in each taxon to measure for length–weight relationships. Measuring blotted wet weight was not feasible due to size constraints of diets, inhibiting accurate measurement. We measured body length and head width using a digital microscope at 120× magnification (Leica Application Suite v4.1, Leica Camera AG, Wetzlar, Germany). Weights for non-zooplankton invertebrates (Amphipoda, Ostracoda, Apatania, Tricoptera, Chironomidae Non-tanypodinae, Tanypodinae, Ephemerella, Baetidae) were calculated using length–mass relationships for invertebrates [33] and for zooplankton [34].

Tissue samples of fish muscle were freeze-dried for 18–36 h using a Labconco Freezone 1 (Labconco Corporation, Kansas City, MO, USA) and ground to a fine powder with a mortar and pestle. Approximately 1 mg of the ground sample was placed in a tin capsule and analyzed at the University of Wyoming Stable Isotope Facility using a Thermo Finnigan Delta Plus XP, Costech 4010 and Carlo Erba 1110 Elemental Analyzer, Costech Zero Blank

Autosampler, and Finnigan Conflo III Interface. Stable isotope ratios were calculated using standard procedures outlined in [18,35].

2.4. Analysis

Diets were analyzed using frequency of occurrence (O_i), proportion by number (N_i), and mean proportion by weight (MW_i). Three measures of diet were used because each index emphasizes different information about the diet of fishes [36,37]. Frequency of occurrence was calculated using:

$$O_i = \frac{J_i}{P}, \tag{1}$$

where i is the food or prey item, J is the number of fish, and P is the number of fish with food in their stomachs and provided information on how often a prey item was eaten but did not signify the relative importance of the prey item to the overall diet [1]. Proportion by number was calculated using:

$$N_i = \frac{N_i}{\sum_{i=1}^{Q} N_i}, \tag{2}$$

where N is the number in food category i and Q is the number of food types. This method emphasized small prey in the diet, which may not be completely representative of prey preference [1]. Finally, mean proportion by weight was calculated using:

$$MW_i = \frac{1}{P}\sum_{i=1}^{P}\left(\frac{W_{ij}}{\sum_{i=1}^{Q} W_{ij}}\right), \tag{3}$$

where W_{ij} is the weight of prey type i in fish j and all other symbols are as defined above. This method emphasized the relative importance of larger prey [1].

Diet overlap among redside shiner, lake chub, and longnose dace was calculated using Schoener's index of niche overlap (D):

$$D = 1 - 0.5\left(\sum_{i=1}^{n}\left|p_{ij} - p_{ik}\right|\right), \tag{4}$$

where p_{ij} is the proportional contribution by weight of prey type i to the diet for species j and p_{ik} is the proportional contribution of prey type i to the diet for species k [38]. We estimated D (niche overlap) among redside shiner, lake chub, and longnose dace for mean proportion by weight (MW_i). Values of $D > 0.60$ indicated a high degree of diet overlap [39].

We used a Bayesian framework to compare $\delta^{15}N$ and $\delta^{13}C$ by species to determine whether trophic position varied among species. The SIBER package in R (Jackson, Inger, Parnell & Bearhop, 2011; version 2.1.4) was used to create 40% Bayesian standard ellipse areas (SEA_B), as SEA_B represents a standard amount of the data regardless of sample size [40,41], and to calculate percent of ellipse overlap. In addition to the Shoener's index of diet overlap, isotopic ellipse overlap can represent potential niche overlap among species in Yellowstone Lake.

3. Results

Of the 44 redside shiners (total length TL; 44–90 mm), 22 lake chub (TL; 33–129 mm), and 50 longnose dace (TL; 40–86 mm) diets, we identified 12 prey taxa, including Amphipoda, Ostracoda, *Apatania*, Trichoptera, Chironomidae Non-tanypodinae, Chironomidae Tanypodinae, *Ephemerella*, Baetidae, Copepoda, *Daphnia*, and Rotifera. Fishes were collected across seven different sampling sites with varying frequencies at each site depending on species (Table S1). Frequency of occurrence (O_i), proportion by number (N_i), and mean proportion by weight (MW_i) of diet items were similar for nonnative minnows, but not when comparing native and nonnative minnows (Table 1). For frequency of occurrence, Chironomidae Non-tanypodinae, and Amphipoda combined were >0.58 of the diet composition for all species (Table 1). Longnose dace had the highest frequency of occurrence for Amphipoda with 50% of the individuals having at least one amphipod in the diet. Chironomidae Non-tanypodinae were $\geq$0.47 of the diet composition for all species using proportion by number (Table 1). Redside shiner had the highest proportion by number for Chironomidae Non-tanypodinae of 0.75, and proportion by number was 0.01 for Amphipoda. *Daphnia* and Chironomidae Non-tanypodinae proportion by number was $\geq$0.45 for lake chub and 0.01 (a very low proportion by number) for Amphipoda (Table 1). Longnose dace had a proportion by number in Chironomidae Non-tanypodinae of 0.57, and proportion by number for Amphipoda was 0.10 (Table 1). For mean proportion by weight, Chironomidae Non-tanypodinae comprised 0.59 of diet for redside shiner and lake chub. Amphipoda comprised 0.49 of diet by mean proportion by weight for longnose dace (Table 1). The two nonnative species, redside shiner and lake chub, had the greatest diet overlap (Table 2), which can be attributed to their high reliance on Chironomidae Non-tanypodinae and Daphnia (Table 1). However, no overlap was observed between the native and nonnative minnows (Table 2) because of the high reliance on Amphipoda by longnose dace (Table 1).

Table 1. Diet contents for redside shiner, longnose dace, and lake chub collected in the littoral zone of Yellowstone Lake, Yellowstone National Park, USA during the ice-free season of 2020 by frequency of occurrence, proportion by number, and mean proportion by weight. Chironomidae include non-tanypodinae and tanypodinae diet items.

		Frequency of Occurrence										
Species	**Sample Size**	**Amphipoda**	**Ostracoda**	***Apatania***	**Tricoptera**	**Non-Tanypodinae**	**Tanypodinae**	***Ephemerella***	**Baetidae**	**Copepoda**	***Daphnia***	**Rotifera**
Redside shiner	44	0.07	0.02	0.00	0.02	0.66	0.09	0.14	0.02	0.11	0.36	0.02
Longnose dace	50	0.50	0.04	0.00	0.06	0.58	0.10	0.16	0.00	0.04	0.02	0.08
Lake chub	22	0.14	0.00	0.05	0.09	0.45	0.09	0.05	0.00	0.14	0.59	0.00
		Proportion by number										
Redside shiner	44	0.01	0.01	0.00	0.00	0.75	0.02	0.01	0.00	0.04	0.16	0.00
Longnose dace	50	0.10	0.01	0.00	0.00	0.57	0.25	0.01	0.00	0.02	0.00	0.03
Lake chub	22	0.01	0.00	0.00	0.03	0.47	0.01	0.00	0.00	0.02	0.45	0.00
		Mean proportion by weight										
Redside shiner	44	0.06	0.03	0.00	0.03	0.59	0.08	0.09	0.00	0.03	0.09	0.00
Longnose dace	50	0.49	0.06	0.00	0.05	0.20	0.04	0.14	0.00	0.01	0.01	0.00
Lake chub	22	0.00	0.00	0.09	0.18	0.59	0.14	0.00	0.00	0.00	0.00	0.00

Table 2. Schoener's index of dietary overlap (D) for redside shiner, longnose dace, and lake chub collected in the littoral zone of Yellowstone Lake during the ice-free season of 2020. Bold values indicate a high degree of dietary overlap (>0.60 [39]).

Species Comparison	**D**
Redside shiner–longnose dace	0.47
Redside shiner–lake chub	**0.69**
Lake chub–longnose dace	0.29

We analyzed more stable isotope signatures than diets. All minnows had similar δ^{15}N signatures, but δ^{13}C signatures were not similar when comparing native and nonnative minnows. Redside shiners had a mean δ^{15}N signature of 6.40, and lake chub had a mean δ^{15}N signature of 6.28 with the most variability of the minnows. Longnose dace had a mean δ^{15}N signature of 5.88, and 95% confidence intervals overlapped for all minnow δ^{15}N signatures (Table 3). Redside shiner and lake chub had the lowest mean δ^{13}C signatures of -19.65, and longnose dace had the highest mean δ^{13}C signature of -15.65 (Table 3). Isotopic overlap was high for the 40% ellipses of nonnative minnows, redside shiners and lake chub (95%), but low for the 40% ellipses of longnose dace and redside shiners (24%), and for the 40% ellipses of longnose dace and lake chub (15%) (Figure 2).

Table 3. Mean stable isotope signatures and 95% confidence intervals (CI) for redside shiner, longnose dace, and lake chub collected in the littoral zone of Yellowstone Lake during the ice-free season of 2020.

Species	N	δ^{15}N (‰)	δ^{13}C (‰)
Redside shiner	63	6.40 (6.13–6.67)	−19.65 (−20.38–−18.92)
Longnose dace	27	5.88 (5.47–6.29)	−15.65 (−16.85–−14.45)
Lake chub	54	6.28 (4.61–7.96)	−19.65 (−20.24–−19.06)

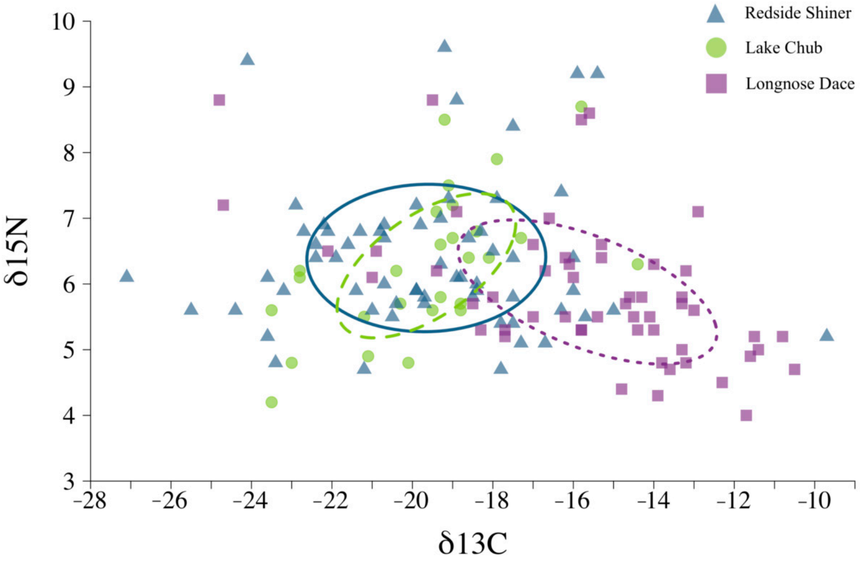

Figure 2. Stable isotope biplot of redside shiner (blue triangles), lake chub (green circles), and longnose dace (purple squares). Spheres represent 40% Bayesian standard ellipse areas for stable isotope signatures of redside shiner (blue solid), lake chub (green dash), and longnose dace (purple dot).

4. Discussion

Yellowstone Lake has a rich history of research surrounding the food web, and more specifically fish diets [6,7,20–24,32], but minnows have largely been excluded. We showed that a dichotomy exists between native and nonnative minnows in Yellowstone Lake in relation to diet and stable isotope signatures. Native longnose dace relied heavily on Amphipoda, a preferred diet item for native Yellowstone cutthroat trout [6,7,32,42], and a prevalent diet item for invasive lake trout in Yellowstone Lake [6]. Nonnative minnows, redside shiner and lake chub, consumed primarily Chironomidae and had nearly identical stable isotope signatures, showing clear partitioning from native longnose dace. As expected, all minnows occupied a slightly lower trophic level regarding δ^{15}N (δ^{15}N mean 6.14 among species) than Yellowstone cutthroat trout [6] (δ^{15}N mean 7.04 among length classes), and a much lower trophic level than lake trout [6] (δ^{15}N mean 9.14 among length classes). Diet and stable isotope data were pooled among sites and lengths within species, and further research could explore site-specific differences or ontogenetic shifts within the minnows of Yellowstone Lake. This research fills a knowledge gap in the Yellowstone Lake ecosystem and more comprehensively completes research relating to the food web.

Studies on the diets of nonnative redside shiner [43–45], lake chub in native and nonnative ranges [46–48], and native longnose dace [49–53] have been conducted in aquatic systems throughout North America. Many of these studies quantified diets using volumetric analysis, making proportional comparisons with our study difficult. However, we can directly compare diet items between studies, which is valuable because contrasts among studies can expand upon knowledge of minnow diet preferences. Common diet items for nonnative redside shiner in this study and previous studies include *Daphnia*, Amphipoda, Chironomidae, fish scales, and fish eggs [43–45]. Though we did not find evidence of fish [47] in nonnative lake chub diets in our study, lake chub did consume Trichoptera, which has been previously reported [46]. Discrepancies in common diet items may be due to sampling location for some fishes, specifically in lotic habitat [46] versus lentic habitat (this study); lentic-dwelling lake chub are expected to have different diet items and larger proportions of zooplankton than lotic-dwelling lake chub [48]. Chironomidae and Ephemeroptera were common taxon in other diet studies of longnose dace [49,51–53].

Stable isotope signatures have been previously collected for redside shiner [54,55], lake chub [56–58], and longnose dace [55,56]. Mean δ^{15}N and δ^{13}C signatures for redside shiner in this study were comparable to previous studies [54,55,59]. Lake chub signatures were also similar to published studies [56–58], though our samples had much greater variability. Longnose dace δ^{15}N signatures were comparable to other peer-reviewed research [55,56]; however, δ^{13}C signatures for longnose dace in this study were more positive than previous research [55,56], indicating more use of benthic resources, likely due to their reliance on amphipods. Diets and stable isotopes of redside shiner, lake chub, and longnose dace in Yellowstone Lake were comparable to other studies, though some differences existed in reported diet composition and stable isotope signatures, likely due to differences in lotic and lentic habitats.

Overlap between native and nonnative minnows has interesting parallels to other diet overlap comparisons in Yellowstone Lake. Diet overlap becomes higher as the species of comparison consume more of the same diet items and in similar quantities [39]. In Yellowstone Lake, the nonnative minnows had high overlap, but the native and nonnative minnows did not. This comparison is interesting given studies in Yellowstone Lake comparing native Yellowstone cutthroat trout and invasive lake trout diet overlap [6]. Diet overlap varied for native and invasive trout during different periods of invasive trout suppression [6] but, for minnows, we do not know whether diets of minnows or diet overlap has shifted through time with the introduction of lake trout into Yellowstone Lake. If lake trout are reduced even further through gillnetting efforts [60], more research on the diets and stable isotope signatures of minnows could provide insight into whether lake trout affect more than only the Yellowstone cutthroat trout diet [6].

5. Conclusions

Our research quantified the diet composition and stable isotope signatures of Leusicids residing in Yellowstone Lake, thus, growing our knowledge of minnow feeding patterns and ecology in relation to the native and nonnative species in the ecosystem. Studying the feeding habits and trophic positioning of non-native fishes is critical for determining the ecological effects of nonnative species and competition between nonnative and native species [6]. We show that the native longnose dace follows similar diet patterns as native Yellowstone cutthroat trout, and the probability of competition between native fishes and nonnative minnows for food resources is low. Here, we expanded knowledge of minnow ecology and added to the limited research existing on minnows in lacustrine habitats. Plans exist to include this research in fluxweb [61] and Ecopath [62] modelling that will be incorporated to further understand the influence of nonnative and invasive species in Yellowstone Lake.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/fishes6040051/s1, Table S1: Number and location of species collected.

Author Contributions: Conceptualization, H.C.G. and C.S.G.; methodology H.C.G. and C.S.G.; formal analysis, H.C.G.; writing—original draft preparation, H.C.G.; writing—review and editing, C.S.G. and T.M.K.; supervision, C.S.G. and T.M.K.; funding acquisition, H.C.G., C.S.G. and T.M.K. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data that support the findings of this study are available with permission from the authors.

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