



## Spatio-temporal niche plasticity of a freshwater invader as a harbinger of impact variability



Phillip J. Haubrock<sup>a,b,\*</sup>, Paride Balzani<sup>c,1</sup>, Shin-Ichiro S. Matsuzaki<sup>d</sup>, Ali Serhan Tarkan<sup>e,f</sup>,  
Melina Kourantidou<sup>g,h,i</sup>, Peter Haase<sup>a,j</sup>

<sup>a</sup> Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Clamecystrasse 12, 63571 Gelnhausen, Germany

<sup>b</sup> University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátěš 728/II, 389 25 Vodňany, Czech Republic

<sup>c</sup> Department of Biology, University of Florence, Via Madonna del Piano 6, 50019 Sesto Fiorentino, Italy

<sup>d</sup> Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, Tsukuba 305-8506, Japan

<sup>e</sup> Muğla Sıtkı Koçman University, Faculty of Fisheries, Muğla, Turkey

<sup>f</sup> University of Łódź, Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, Łódź, Poland

<sup>g</sup> Woods Hole Oceanographic Institution, Marine Policy Center, Woods Hole, MA 02543, USA

<sup>h</sup> Hellenic Center for Marine Research, Institute of Marine Biological Resources and Inland Waters, Athens 164 52, Greece

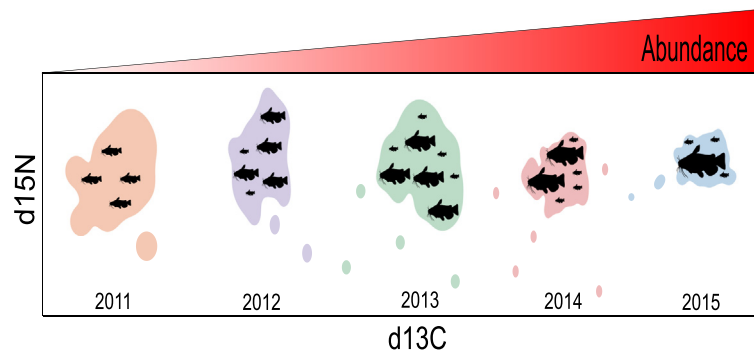
<sup>i</sup> University of Southern Denmark, Department of Sociology, Environmental and Business Economics, 6705 Esbjerg Ø, Denmark

<sup>j</sup> University of Duisburg Essen, Faculty of Biology, Universitätsstraße 5, 45141 Essen, Germany

### HIGHLIGHTS

- Invasions are processes that affect the impact of the invader.
- Aquatic invader responds to spatially variable conditions.
- Aquatic invader can express spatially and temporally varying niches within one ecosystem.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Invasive alien fishes have detrimental ecological effects on aquatic ecosystems and the services they provide. Impacts from an invasion in a single ecosystem may differ across space and time due to variability in prey availability and environmental conditions. We hypothesize that such variability can be profound, even within a single ecosystem. Stable isotopes analysis (SIA) is commonly used to quantitatively describe the trophic niche of a species. However, spatial and temporal variability in occupied niches are often not incorporated into management strategies and policy options. Here, we used long-term monitoring data to investigate the invasion stage as well as SIA to analyse the trophic niche of the invasive channel catfish *Ictalurus punctatus* in Lake Kasumigaura (Japan), a long-term ecological research site (LTER), across distant sampling sites and years. We found a significant spatio-temporal variability in relative growth and isotopic niche occupation. Moreover, we defined a new index, the Isotopic Plasticity Index (IPI), which is the ratio between core and total home range of an occupied isotopic niche, to be used as a proxy for the trophic niche stretch or density. We found that this IPI varied considerably, confirming the spatio-temporal variability in trophic niches, suggesting the IPI to be an adequate new

\* Corresponding author at: Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Clamecystrasse 12, 63571 Gelnhausen, Germany.

E-mail address: [phillip.haubrock@senckenberg.de](mailto:phillip.haubrock@senckenberg.de) (P.J. Haubrock).

<sup>1</sup> These two authors contributed equally.

isotopic metric. Our results further provide evidence for the existence of variation across invaded landscapes, implying heterogeneous impacts on recipient native communities. Therefore, our work emphasizes the importance of exploring trophic plasticity in feeding ecology and growth as such information enables a better understanding of impacts and can inform the design and implementation of effective management responses.

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## 1. Introduction

Biological invasions are among the main threats for biodiversity (Pyšek et al., 2020), especially as the number of newly introduced alien species continue to increase without signs of amelioration (Seebens et al., 2017). Freshwater ecosystems have been identified as particularly vulnerable to invasions (Gallardo et al., 2016; Poulin et al., 2011; Strayer, 2010) and especially freshwater fish have been reported to be among the most commonly introduced groups of species (Gozlan, 2008) with higher establishment rates than many other taxa (Jeschke and Strayer, 2006; Seebens et al., 2020). Their introductions are usually irreversible (Cherousset and Olden, 2011), often threatening native biodiversity in ways that are not always well understood and inducing direct and indirect costs (Lovell et al., 2006; Nico and Walsh, 2011; Tsumoda et al., 2010).

Interconnected water bodies, intense anthropogenic activities (e.g. resource exploitation, recreation, pollution) and climate change, all contribute to new freshwater species introductions and ability to successfully establish resulting in degradation of ecosystem services (Carpio et al., 2019; Nunes et al., 2015; Tricarico, 2012; Früh et al., 2012, 2017). Impacts to provisioning ecosystem services that freshwater fisheries provide are a large challenge for resource managers and policy-makers, with the threat of invasive species for the ecological integrity of inland waters being particularly concerning (Leuven et al., 2017). Freshwater fishes have been found to be the most frequently introduced in Europe (García-Berthou et al., 2005). Italy's freshwater ecosystems for example have suffered the introduction of various aquatic invasive species (Nocita et al., 2017), with more than 150 aquatic species having established over the last decades which corresponds to at least 2% of the inland-water fauna (Gherardi et al., 2008). Similarly, in Turkey which is characterized by a high level of speciation and the presence of several endemic species, close to 11% of the freshwater species are introduced (Tarkan et al., 2015). Catch and fishing effort in Japan's inland fisheries have dramatically declined in recent years (Tominaga, 2006) in part owing to the introduction of piscivorous fish (Katano and Matsuzaki, 2012; Matsuzaki and Kadoya, 2015), with a drop in the annual freshwater catch from more than 120,000 metric tons in the mid-1970s to less than 40,000 in the late 2000s (Katano et al., 2015). Indeed, the introductions have been the main driver of this nationwide decline in freshwater fisheries harvests also considering that the effect of overexploitation is relatively small since total annual catch has decreased in many Japanese lakes (Matsuzaki and Kadoya, 2015). These impacts were especially prominent in lakes, which provide multiple ecosystem goods and services (Costanza et al., 2014; Hoeinghaus et al., 2009; Schallenberg et al., 2013). Losses in provisioning and cultural ecosystem services are particularly prominent, since in Japan, wild fish harvests and the production of traditional foods largely depend on lake fisheries (Holmlund and Hammer, 1999; Katano and Matsuzaki, 2012). The task for resource managers is daunting: freshwater invasions are particularly challenging and costly to manage. Part of the difficulty has lain in the lack of understanding of impacts across space and time.

A particular noteworthy example of a difficult-to-manage invasive species in Japan is the North American channel catfish *Ictalurus punctatus* (Rafinesque 1818) (Siluriformes: Ictaluridae). It is native to North America where it is extensively cultured (Appelget and Smith, 1951; Etnier and Starnes, 2001; Olenin et al., 2008), widely distributed and provides both a major sport and food fishery (Hargreaves and Tucker, 2004; Leonard et al., 2010; Welcomme, 1988). Due to this

environmental tolerance and opportunistic omnivorous diet (Haubrock et al., 2018a; Townsend and Winterbourn, 1992), *I. punctatus* has been classified as an invasive species (CABI, 2020; Haubrock et al., 2021) due to its ability to negatively affect native communities across various trophic levels (Haubrock et al., 2019; Matsuzaki et al., 2011). Juveniles and adults of *I. punctatus* differ in their feeding spectrum and behaviour, with mature individuals preying higher trophic levels and further away from the bottom and shore (Endo et al., 2015). Therefore, both life stages express considerable trophic interactions in terms of predation and competition with native and other alien species, while expressing low to no competition among them (Haubrock et al., 2020a,b; Nesler, 1995), making it an ideal study organism for aquatic invasions. Impacts therefore likely differ across space and time, which hinders the design of targeted management approaches.

Introduced in Japan in 1971, it has escaped from aquaculture facilities or was intentionally and illegally released in consecutive years (Katano et al., 2010; Matsuzaki et al., 2011). By the early 1980s, it was already observed in natural water bodies around Lake Kasumigaura. Its introduction into Lake Kasumigaura, which represents the second largest lake in Japan, supports one of the most commercially important inland fisheries at a national level. Takamura (2012) has identified it as having become, since 2001, into the most dominant species caught in Lake Kasumigaura (reference period 1993–2003). Particularly, the introduction of *I. punctatus* has led to increased predation pressure and competition (e.g. for resources, shelter, etc.), leading to considerable declines of native species such as gobies, shrimps and aquatic insects and has consequently caused damages to commercial fisheries (Arayama, 2010; Matsuzaki et al., 2011; Yamazaki et al., 2018). In recognition of its multiple adverse impacts, it is included in the Invasive Alien Species Act in Japan, since the very beginning of the Act's enforcement, along with restrictions in place on import, transport and maintenance of channel catfish to limit further dispersal and spread (CABI, 2020). Despite these restrictions, management options for the populations already established remain limited in their scope considering the lack of knowledge on the heterogeneity of impacts within the lake.

The various studies describing the species' impacts neither capture its ability to utilize differing resources within new environments as expressed in terms of phenotypic or behavioural flexibility (e.g. trophic plasticity) nor help understand the various dimensions of its capacity and adaptive functional behaviour as an invader. This is a ubiquitous problem many resource managers and stakeholders are facing, as it directly limits the understanding of an invader's resource utilization and thus, feeding impact. It is for instance known that certain attributes of introduced species (e.g. potential to spread or impact) may vary across different invasion stages (Dunham et al., 2002; Dunham and Masser, 2012; Václavík and Meentemeyer, 2012; Lockwood et al., 2007). It is further theorized that trophic and phenotypic plasticity, particularly of invasive fish species, is high (Mittan and Zamudio, 2019; Selechnik et al., 2019) and can aid the establishment of a potential invader (Simon and Townsend, 2003; Cathcart et al., 2019). Accordingly, regional and temporally confined sampling efforts of a highly adaptable species like *I. punctatus* may fail to provide a comprehensive picture of its trophic ecology and therefore are likely to not mirror impacts on the recipient native biota adequately. This would mean that targeted management options to mitigate the impact of such invasive species need to be adapted to the respective local conditions, requiring a more localized sampling approach.

Trophic plasticity (i.e. a species' ability to express high trophic variability) in particular is one important feature of many invasive species (Almeida et al., 2012; Jackson et al., 2017; Pettitt-Wade et al., 2015) and understanding the underlying mechanisms can help elucidate the factors facilitating their establishment and spread. A useful tool to study trophic niche plasticity is Stable Isotopes Analysis (SIA) which can be used to define population, species, or community isotopic niches (Layman et al., 2007; Newsome et al., 2007; Jackson et al., 2011; Bissattini et al., 2021), thus allowing comparisons of ichthyofaunal elements of the environment (Layman et al., 2012). Indeed, isotopic niches reflect the consumed diet of a species averaged on a certain period (e.g. months for muscle tissue; Davis and Pineda-Munoz, 2016) and therefore, adequately reflect its predation impact, to some degree also a species invasiveness (Shea and Chesson, 2002; Berg and Eilers, 2010), with a generalist species expressing a wider niche than a specialist species (Balzani et al., 2020). Understanding localized differences in expressed niches can elucidate critical unknowns associated with impacts; aid resource managers in identifying risks, spur additional interest and investments in mitigating the invasion and may help identify effective pathways for management.

We therefore hypothesize that the trophic niche of an established aquatic invader is not necessarily constant within a large ecosystem, such as a lake, but can vary considerably across different sites within the same ecosystem in accordance with e.g. spatially differing prey occurrences or habitat characteristics. To test this hypothesis, we used stable isotopes to investigate localized variability in the occupied isotopic niche space of the invasive species *I. punctatus*. Acknowledging that isotopic studies exploring changes in aquatic species or entire aquatic communities spanning multiple years are generally scarce (Vander Zanden et al., 2010), we have included a higher spatial and temporal frequency than previous studies (Pettitt-Wade, 2016) in the design of this study. Using *I. punctatus* as case study, we combined long-term population and environmental monitoring data (sampled between 2005 and 2020) with a separate collection of localized samplings taken from geographically distinct sites within Lake Kasumigaura (between 2011 and 2015) for the analysis of stable isotopes. Using these two datasets, we (1) investigate the invasion stage of *I. punctatus* in Lake Kasumigaura (1a) to confirm that this invader is established, having reached a plateau phase in its population growth and (1b) to explore whether changes in environmental variables affected population dynamics. Further, we (2) describe its growth with regard to localized expressions of phenotypic plasticity. Then, (3) we aim to infer potential differences in its feeding ecology, i.e. niche occupation at its ability to express trophic plasticity after its establishment. The methodology presented here, along with the findings, advance the understanding of the trophic ecology of invasive fish species and of associated ecological impacts at larger scales and may therefore help inform the design of appropriate management policies, including spatial dimensions.

## 2. Methods

### 2.1. Sampling site

Lake Kasumigaura (Fig. 1) is a core site of the Japan Long-Term Ecological Research Network (JaLTER) that has been monitored since 1976 as part of the International Long-Term Ecological Research Network (ILTER) (Mirtl et al., 2018). Further, it is a trend-monitoring station of the United Nations Global Environment Monitoring System Water Trend Monitoring Project (GEMS/Water). It is situated approximately 60 km northeast of Tokyo and is the second largest lake in Japan (220 km<sup>2</sup>). It is a shallow and hypereutrophic lake (mean depth of approximately 4 m and a maximum depth of 7.4 m), that has a total volume of 622 million m<sup>3</sup> and a catchment area of 2157 km<sup>2</sup>

(Takamura, 2012). The fisheries it supports have played a central role in Japanese inland fisheries, producing pond smelt (*Hypomesus nipponensis*), ice fish (*Salangichthys microdon*), freshwater prawn (*Macrobrachium nipponense*) and gobiid fish (*Tridentiger brevispinis*) (Matsuzaki et al., 2018).

### 2.2. Sampling process and analysis

Using long-term monitoring data of Lake Kasumigaura, we infer the invasion stage of *I. punctatus*. Specifically, we extracted information on the annual catchments, in terms of biomass and number of caught individuals from the Lake Kasumigaura JaLTER database (<http://db.cger.nies.go.jp/gem/moni-e/inter/GEMS/database/kasumi/contents/datalist.html>). These were collected at the Futto sampling site (representative of southern Lake Kasumigaura; Fig. 1) from 2005 until March 2020, as Tominaga et al. (2013) showed that the trends of channel catfish population between Futto and Yakimaki (representative of northern Lake Kasumigaura) were similar, therefore arguably representing *I. punctatus*' invasion stage. Sampling was conducted with stationary nets (ca. 20 m width, ca. 80 m length; with three traps of ca. 6 m length, 70 cm diameter, and 3–7 mm mesh size) set for 24 h every 2–3 months and 5–6 times per year. For the purposes of describing potential trends, we tested different regression models (logarithmic vs. exponential vs. linear) to identify the model with the best fit using the Akaike Information Criterion (AIC). Additionally, we extracted data on abiotic (water temperature) and biotic (phyto- and zooplankton availability) variables from the Lake Kasumigaura JaLTER database and used Spearman correlations to check for covariance between these variables and the observed trends in abundance and biomass of *I. punctatus* in Lake Kasumigaura over time.

In addition to data from the ongoing long-term monitoring efforts described earlier, we also collected channel catfish from five sites in Lake Kasumigaura (Supplement 1, Fig. 1), with Asou situated in close proximity to the outlet of Lake Kasumigaura, Futto and Futto-ohashi close to the inlet, and last Osukazu and Yakimaki both in considerable distance to both inlet and outlet (Fig. 1). Sampling was conducted using the same stationary nets as described above in cooperation with local professional fishers from 2011 to 2015 throughout the year. Channel catfish were immediately euthanized via pithing and preserved in a cool box until they were processed in the laboratory, where standard length (SL,  $\pm 1.0$  mm; tip of the snout to the posterior end of the last vertebra) and wet weight (W,  $\pm 1.0$  g) were measured.

### 2.3. Growth analysis

Life stages were attributed for individuals sampled between 2011 and 2015 using standard length (SL; <30 cm: juvenile,  $\geq 30$  cm: adult) following (Haubrock et al., 2018b). The weight-length (WL) relationship was determined using the slopes ( $b$ ) of the linear regression model between log-transformed length and weight measures. Growth was defined as hyperallometric, that is, fish growing faster in weight than in length, if  $b > 3$ , hypoallometric, meaning that fish grow faster in length than in weight, if  $b < 3$ , or isometric, which is the case when  $b = 3$  (Karachle and Stergiou, 2012). Fitting of WL relationships was performed in R (ver. 4.0.0, R Core Team) using the libraries 'FSA' (ver. 0.8.32) and 'nlstools' (ver. 1.0–2; Ogle et al., 2000). To assess site-specific differences, the coefficients of WL relationship were compared among sites for all individuals. A multiple comparisons procedure was used to test differences in the slopes of linear regressions among the different sites (Zar, 2013). Fish body condition was evaluated by Fulton's condition coefficient (Le Cren, 1951) calculated as Fulton's condition (KF) =  $100,000 \times W / TL^3$ , where: W = total body weight [g], TL = total length [mm]. To avoid seasonal differences during different years, same seasons of the year for each sampling location were included in KF calculations.

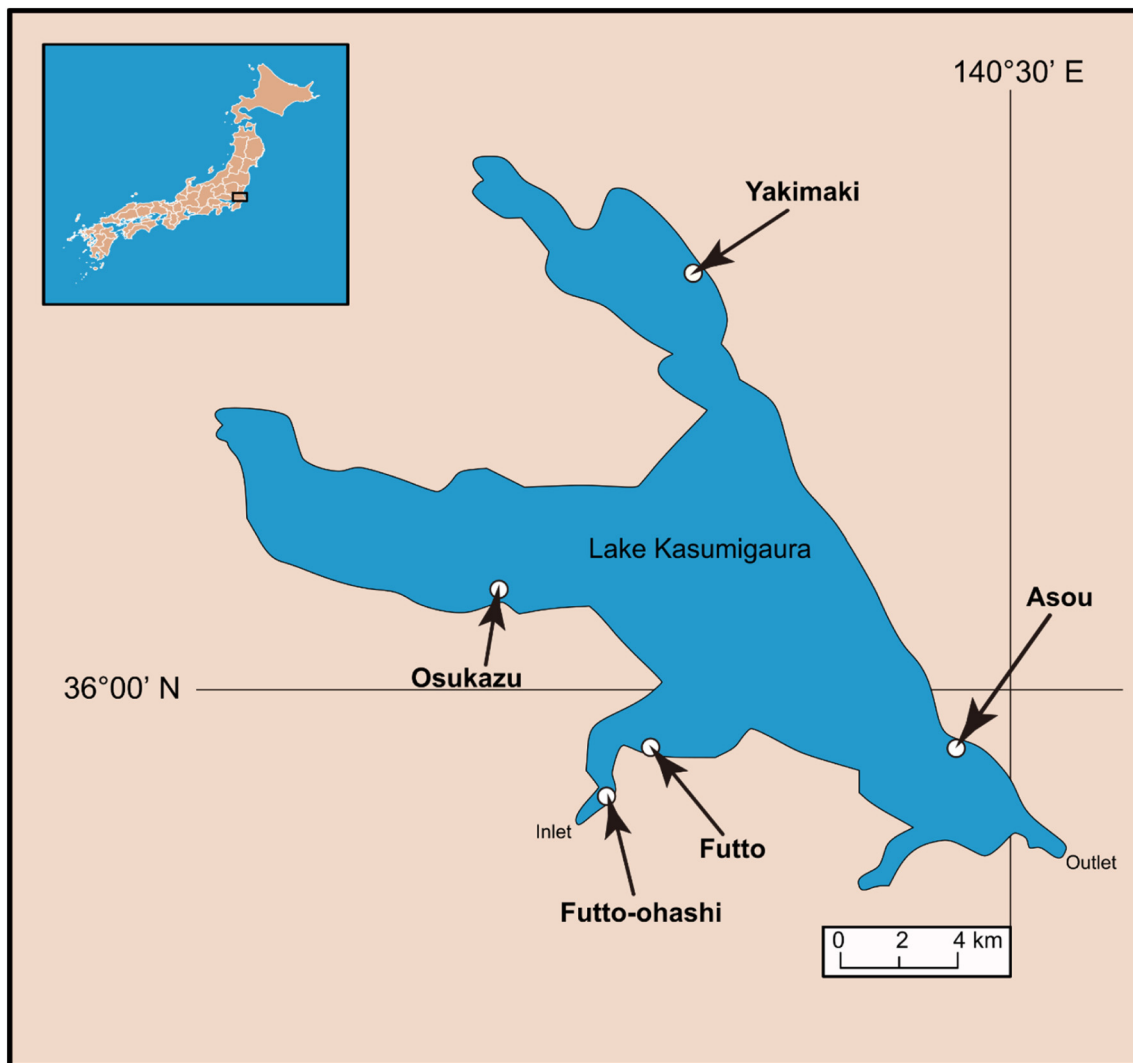


Fig. 1. The 5 sampling sites Futto, Futto-ohashi, Asou, Osukazu and Yakimaki at Lake Kasumigaura (Japan).

#### 2.4. Stable isotope analysis (SIA)

For SIA, a sample of dorsal muscle tissue was taken from each individual sampled between 2011 and 2015. White muscle tissue has lower variability in nitrogen isotopic signature compared to other tissues and does not require acidification to remove inorganic carbonates (Pinnegar and Polunin, 1999). Fish muscle samples were dried at a constant temperature (55 °C) for 48 h and ground to fine powder using an agate pestle and mortar. Because lipids are depleted in  $^{13}\text{C}$  compared with the whole organism (Post et al., 2007), lipids were extracted from all animal tissues using a 2:1 chloroform: methanol solution. SIA was performed with a continuous flow interface (ConFlo IV, Thermo Fisher Scientific, Germany) and an isotopic ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Germany). All stable isotope values are reported in the  $\delta$  notation:  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = [((R_{\text{sample}} / R_{\text{standard}}) - 1) \times 1000]$ , where R is  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratios, and the standards are atmospheric nitrogen and Pee Dee Belemnite. The standard errors of the replicates of all our analyses were 0.03‰ for  $\delta^{13}\text{C}$  and 0.11‰ for  $\delta^{15}\text{N}$ .

As isotope data and therefore the trophic niche are affected by various factors such as diet and can vary in different periods of the year (e.g. due to annual reproductive cycles and prey availability), we used data only from the active period (i.e. period of active feeding) of *I. punctatus*. This period, ranging from April to October, was inferred

from the minimum required water temperature of ~12–14 °C occurring in March (Appelget and Smith, 1951; Gerhardt and Hubert, 1991; Haubrock et al., 2021) and the belated time mediated information of stable isotopes (half-life of 1–2 months for fish muscle tissue; Vander Zanden et al., 2015) using daily water temperature measurements from the JaLTER database. The isotopic signatures strongly depend on the community's baseline (McMahon and McCarthy, 2016), which is commonly used to standardize a species trophic position (Post, 2002). Here, we did not standardize the isotopic signatures sampled across sites and year, because the trophic niche we investigated circumscribed five sites across multiple years, as we aimed to identify the entire trophic niche (as a representation of consumed prey and thus, physical impact) occupied by *I. punctatus* at any certain point in time or space. So, even if the raw isotopic signatures could be affected by the absence of such a standardization, we assumed the isotopic niche to be relatively unaffected by this bias. To quantify changes in intra-specific niche width, Layman's metrics (Layman et al., 2007) were calculated for all sites and years using the R package "SIBER" (vers. 2.1.5; Stable Isotope Bayesian Ellipses in R) (Jackson et al., 2011).  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ranges (NR and CR), the mean distance to the centroid (CD), as well as the total area encompassing all individual measures (TA) are indices of the species' trophic niche diversity (Layman et al., 2007). The mean nearest neighbour distance (MNND) and the standard deviation of the nearest neighbour distance (SDNND) relate to the isotopic distance among

individuals and indicate the degree of trophic redundancy (i.e. the inter-individual competition).

## 2.5. Statistical analysis

To identify life-history shifts in resource utilization between mature and immature individuals across the five sites sampled between April and October 2011–2015, we used the same life-stage classifications as before and tested for correlations (Spearman correlation) between stable isotope signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and standard length. Further, a permutational univariate analysis of variance (PERANOVA) was used to test the significance of differences of standard length, weight, maturity, Fulton's condition,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (as fixed factors) of *I. punctatus* among the five sampling sites. This analysis was based on a three-way (fully crossed) designed, which included the fixed factors. Differences in standard length and weight were based on a one-factor design (with years) whereas, differences in Laymans' metrics, Fulton's condition,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were based on a two-way factorial design (with sampling years, sites, SL and maturity stage noting that the latter factors were used in lieu of years for testing ontogenetic differences). For each case, following normalisation of the data, a Euclidean dissimilarity measure produced a distance matrix that was subjected to 9999 permutations of the raw data was found to have statistically significant effects for the main and interaction effects with a posteriori pairwise comparisons evaluated at  $\alpha = 0.05$ . Statistical analyses were conducted in PERMANOVA. v1.0.1 for PRIMER v6 (Anderson et al., 2008). Briefly, the use of PERMANOVA compared to traditional parametric analysis of variance, is that the stringent assumptions of normality and homoscedasticity, which prove very often unrealistic when dealing with ecological data sets, are 'relaxed' considerably (Anderson and Robinson, 2001).

Additionally, we conducted a spatial analysis of each site's populations using the isotopic coordinates in a bivariate normal kernel utilization density estimator (estKIN) to calculate 'estimated home ranges', i.e. the "kernel isotope niche" (R package "rKIN"; ver. 0.1) (Eckrich et al., 2020). To this end, we determined the kernel utilization density (KUD) of both, core (40% data) and total homing range (95% data) occupied by *I. punctatus* at each sampling site and for the overall Lake's population. We did not consider differences in life stages due to limitations imposed on the analysis by the structure of the data, but rather using the KUD as a means to describe the populations' trophic niche. We therefore assumed that the expressed trophic niche represents the site-specific populations' resource utilization. Further, as a means of estimating

each populations' plasticity, we proposed a new metric called isotopic plasticity index (IPI), defined as the ratio between total homing and core range, as a further 'stretched out' isotopic niche ratio indicates a greater ability to utilize more diverse resources. Further, we applied a linear model to exclude the possibility of sample size affecting the KUD niche areas. We used the 'step' function to build the linear model with the best fit (based on AIC) for each of these metrics (i.e. Layman and KUD).

## 3. Results

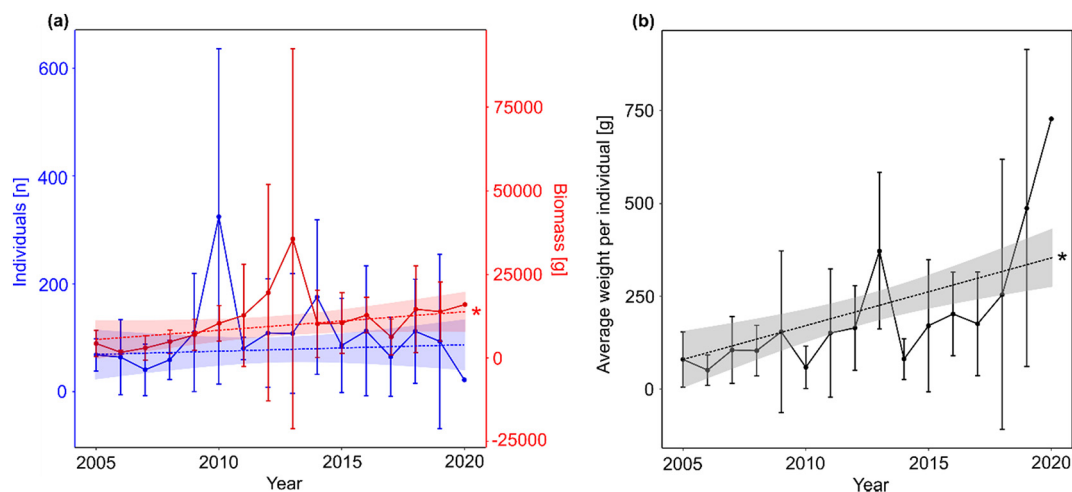
While the long term monitoring data of *I. punctatus* conducted between 2005 and 2020 shows that the number of individuals did not change significantly over time (adj.  $R^2$ : 0.03;  $p = 0.1$ ), the overall biomass captured during that period increased significantly (adj.  $R^2$ : 0.51;  $p < 0.05$ ; Fig. 2a). In addition, the average weight per individual caught increased significantly between 2005 and 2020 (adj.  $R^2$ : 0.54;  $p < 0.05$ ).

Temperature ( $t = -4.0$ ,  $df = 75$ ,  $p < 0.001$ ), and zooplankton ( $t = 10.3$ ,  $df = 75$ ,  $p < 0.001$ ) but not phytoplankton ( $t = -1.1$ ,  $df = 75$ ,  $p = 0.27$ ) changed significantly over the studied period. However, while zooplankton and temperature were significantly correlated ( $t = -2.9$ ,  $df = 75$ ,  $p < 0.001$ ), only the abundance of zooplankton correlated significantly with changes in fish biomass (adj.  $R^2 = 0.48$ ;  $p < 0.001$ ) and average weight per individual (adj.  $R^2 = 0.48$ ;  $p < 0.001$ ) of *I. punctatus*. (Supplement 1).

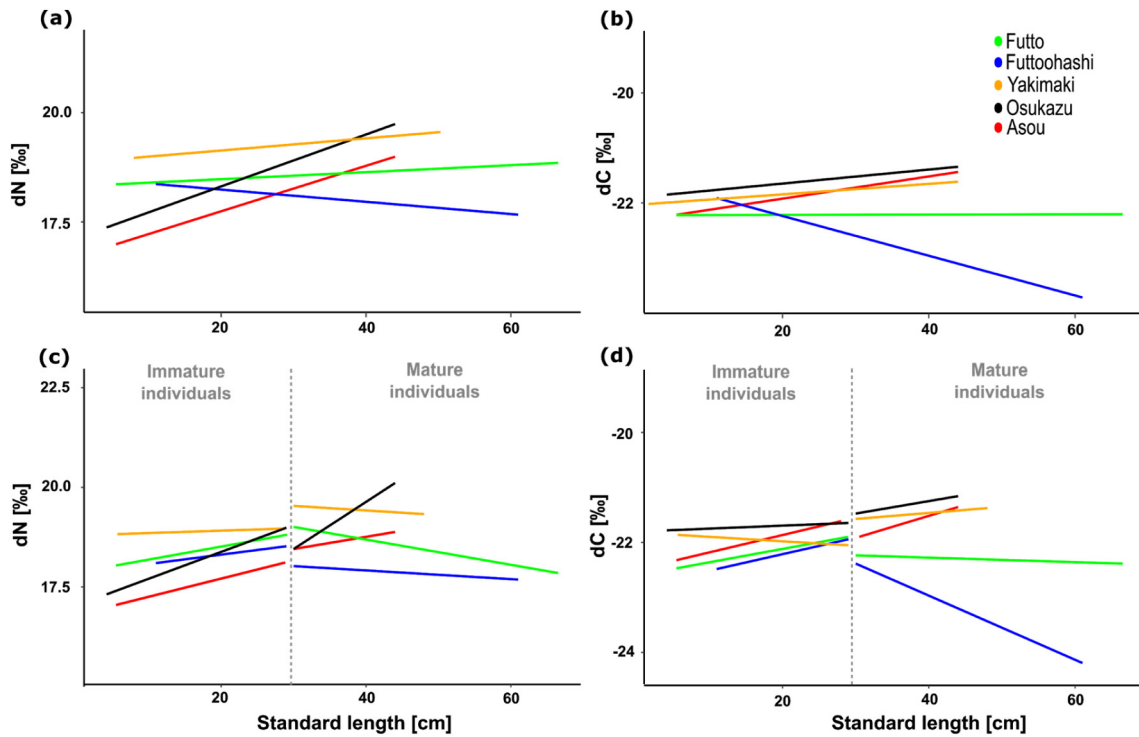
### 3.1. Site-specific sampling

In addition to data collected from the annual monitoring efforts, 791 individuals of *I. punctatus* were collected for the site-specific growth analysis. All sites displayed considerable variability in the average fish size ( $F_{\text{pseudo}} = 10.2$ ,  $P < 0.0001$ ) and weight ( $F_{\text{pseudo}} = 8.55$ ,  $P < 0.0001$ ), with the largest fish caught in Futto-ohashi (mean  $\pm$  standard deviation:  $26.9 \pm 12.9$  cm;  $0.59 \pm 0.85$  kg), followed by Asou ( $25.0 \pm 0.3$  cm;  $0.29 \pm 0.29$  kg), Futto ( $24.2 \pm 12.3$  cm;  $0.42 \pm 0.65$  kg), Osukazu ( $18.9 \pm 0.3$  cm;  $0.18 \pm 0.26$  kg), and lastly Yakimaki ( $18.3 \pm 18.3$  cm;  $0.18 \pm 0.31$  kg) which had the smallest population on average.

Weight-length relationships of channel catfish could not be fitted for Osukozu and Futto-ohashi due to a lack of individuals and narrow size ranges. Estimated values of  $b$  (as 95% CI) were  $> 3$  for Futto and just below 3 for Yakimaki (negative allometry), but spanned 3.0 in Asou



**Fig. 2.** *Ictalurus punctatus* catchments from Lake Kasumigaura from 2005 to 2020 showing (a): CPUE (Catch per Unit of Effort) in g/day/net (red) and "relative density" in individuals (n)/day/net individual biomass (blue); as well as (b): "average weight per individuals" in g/ind/day/net; dots indicate mean values with their respective standard deviation; dashed lines indicate linear trends with their respective 95% confidence interval; significance is indicated by an asterisk; catchments were conducted with stationary nets set for 24 h every 2–3 months/5.6 times per year on average. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** Relationships between isotopes and standard length (SL) of *I. punctatus* caught at Lake Kasumigaura; a)  $\delta^{15}\text{N}$  vs. SL; b)  $\delta^{13}\text{C}$  vs. SL; c)  $\delta^{15}\text{N}$  vs. mature specimens above and immature specimens below 30 cm SL; d)  $\delta^{13}\text{C}$  vs. specimens above and below 30 cm SL. Please note the different trajectories (positive negative) by mature and immature specimens.

(isometric; Supplement 3). Values of *b* were significantly higher in Futto than in Yakimaki ( $F_{\text{pseudo}} = 8.34, p < 0.0001$ ) and Asou ( $F_{\text{pseudo}} = 2.94, p < 0.0001$ ), but there was no significant difference in *b* values between Yakimaki and Asou ( $F_{\text{pseudo}} = -0.262, p > 0.05$ ). There was a significant variation in Fulton's condition (KF) in *I. punctatus* between the sampling locations, years and for the interaction term location  $\times$  year (Supplement 4). Specifically, mean FK in Futto-ohashi in 2012 (2.1492) and in 2014 (1.6786) was highest and followed by Yakimaki in 2011 (1.6503) and 2012 (1.6138), Osokozu in 2011 (1.6069), Futto in 2013 (1.5968) and in 2014 (1.5325) and Asou in 2012 (1.4242).

### 3.2. Stable isotope analysis

From the additionally sampled individuals, 328 fish were randomly selected and used for SIA.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  showed different patterns of relationships with standard length at the different sites (Fig. 3a, b). Considering the two size classes separately (Fig. 3c, d), juveniles expressed a positive increase in  $\delta^{15}\text{N}$  with increasing standard length at all sites. This trend was the same also in adults from Asou and Osukazu, while in Futto-ohashi, Futto and Yakimaki, adults exhibited a decline in  $\delta^{15}\text{N}$  with increasing standard length. Similar trends were observed for the relationship between  $\delta^{13}\text{C}$  and standard length except for specimens caught at site Yakimaki, where the trend observed was found to be opposite (i.e. a decrease in juveniles and an increase in adults) (Fig. 3). The applied PERANOVA confirmed these results, as indicated by the significance of size and site separately, as well as differences in the level of significance between the trajectories of  $\delta^{15}\text{N}$  among sites (Table 1).

Isotopic signatures varied differently across years and sites (as indicated by the significant interaction terms), but without a consistent pattern. In particular, the factor 'year' explained most of the respective isotope's variability for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Supplement 5). They also varied between juveniles and adults across the different sites, with  $\delta^{15}\text{N}$  in Asou and Osukazu significantly different (Table 1; Supplement 6). The presence of a significant interaction between factors 'Site' and 'Year' indicates that the effect of the individual predictors on the

response variable differed at different values of the other predictor variable, underlining the expressed variability of both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

Layman's metrics varied significantly across sites (Table 2), with the exception of MNND for which there were significant differences only between years ( $F_{4,16}^{\#} = 4.80, P = 0.0314$ ). For the remainder of the metrics, nitrogen range ( $F_{4,16}^{\#} = 5.44, P = 0.0228$ ), carbon range ( $F_{4,16}^{\#} = 4.85, P = 0.0329$ ), TA ( $F_{4,16}^{\#} = 4.66, P = 0.0320$ ), distance to centroid ( $F_{4,16}^{\#} = 7.89, P = 0.0097$ ) and SDNND ( $F_{4,16}^{\#} = 7.30, P = 0.0085$ )

**Table 1**

PERANOVA results on the differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of *I. punctatus* by site and size (J = juvenile; A = adult).

Source of variation	df	MS	$F^{\#}$	$t^{\#}$	$P^{\#}$
$\delta^{13}\text{C}$					
Site	4	8.88	9.67		<b><math>p &lt; 0.05</math></b>
Size of individuals	1	0.14	0.15		$P > 0.05$
Site $\times$ Size	4	2.27	2.48		<b><math>p &lt; 0.05</math></b>
Asou (J vs A)				0.81	$P > 0.05$
Futto (J vs A)				1.03	$P > 0.05$
Futto-ohashi (J vs A)				1.64	$P > 0.05$
Osukazu (J vs A)				1.38	$P > 0.05$
Yakimaki (J vs A)				1.39	$P > 0.05$
Res	467	0.92			
Total	476				
$\delta^{15}\text{N}$					
Site	4	4.95	2.53		<b><math>p &lt; 0.05</math></b>
Size of individuals	1	10.28	5.26		<b><math>p &lt; 0.05</math></b>
Site $\times$ Size of individuals	4	10.88	1.39		$P > 0.05$
Asou (J vs A)				4.10	<b><math>p &lt; 0.05</math></b>
Futto (J vs A)				1.28	$P > 0.05$
Futto-ohashi (J vs A)				0.55	$P > 0.05$
Osukazu (J vs A)				2.24	<b><math>p &lt; 0.05</math></b>
Yakimaki (J vs A)				0.78	$P > 0.05$
Res	467	1.96			
Total	476				

*A posteriori* pairwise comparisons are given for the statistically effect of interest ( $\alpha = 0.05$ , in bold type).  $F^{\#}$  = permutational F value;  $t^{\#}$  = permutational t-test value;  $P^{\#}$  = permutational probability value; MS = mean square

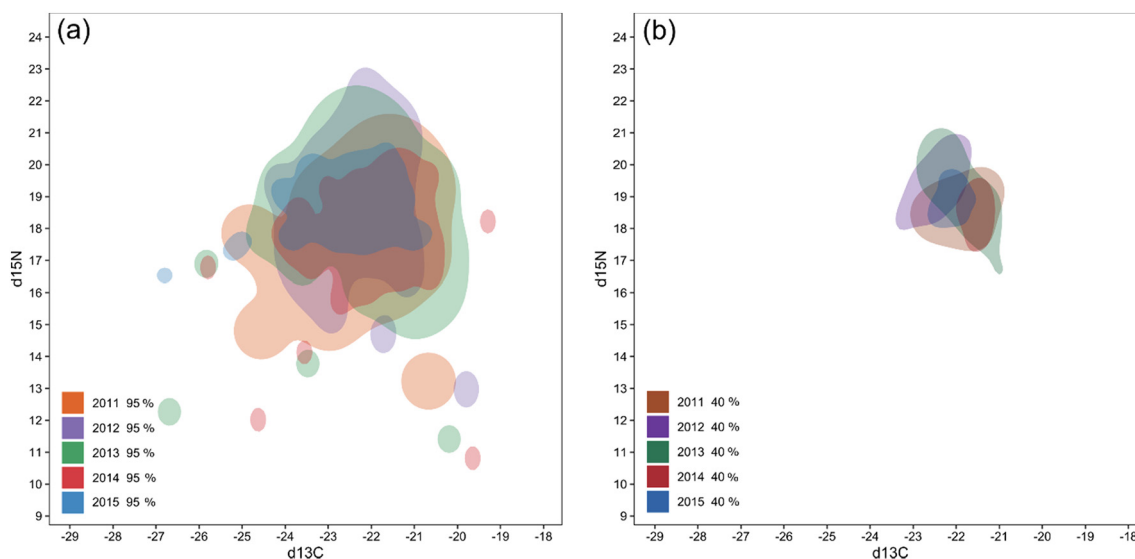
**Table 2**

Estimated Layman's metrics and stable isotope results for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of all populations of *Ictalurus punctatus* estimated per site and year. NR =  $\delta^{15}\text{N}$  range, CR =  $\delta^{13}\text{C}$  range, TA = convex hull area, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDNND = standard deviation of the nearest neighbour distance, KUD = kernel utilization density considering 40% and 95% core data, and Isotopic Plasticity Index (IPI).

Site	Year	NR	CR	TA	CD	MNND	SDNND	KUD [40%]	KUD [95%]	IPI	n
Asou	2012	1.98	1.91	2.39	0.97	1.03	0.20	2.66	14.19	5.3	5
	2014	2.23	2.49	2.91	0.66	0.24	0.35	0.72	4.11	5.7	23
	Overall (2012–2014)	3.52	2.78	6.36	0.88	0.31	0.35	1.01	8.29	8.2	28
Futto	2011	4.76	2.74	6.04	1.40	0.95	0.65	3.49	26.43	7.6	8
	2012	6.94	4.39	13.53	1.26	0.47	0.73	2.47	16.65	6.7	28
	2013	9.96	4.36	23.84	1.52	0.43	0.68	3.56	23.65	6.6	51
	2014	8.73	4.15	20.93	1.26	0.35	0.81	2.01	12.84	6.4	46
	2015	2.26	3.27	5.28	0.77	0.15	0.12	1.43	9.30	6.5	73
	Overall (2011–2015)	10.56	7.15	36.30	1.31	0.14	0.19	2.58	19.95	7.7	206
Futto ohashi	2012	2.51	1.03	0.78	1.09	1.24	0.80	2.30	10.15	4.4	5
	2013	8.45	5.50	13.13	3.02	2.22	1.59	14.26	85.04	6.0	6
	2014	7.73	5.34	17.42	1.42	0.79	1.22	3.10	21.94	7.1	18
	2015	2.62	4.18	5.16	1.15	0.37	0.30	1.84	11.53	6.3	15
	Overall (2012–2015)	8.71	8.39	35.60	1.63	0.44	0.58	4.25	30.67	7.2	44
Osukazu	2011	1.31	0.87	0.63	0.56	0.49	0.28	0.52	2.64	5.1	5
	2012	2.91	0.81	0.85	0.66	0.42	0.40	4.30	27.23	6.3	8
	2013	1.28	1.28	0.48	0.75	0.97	0.31	2.50	15.34	6.1	5
	2014	2.70	1.23	2.71	0.72	0.27	0.19	0.67	4.69	7.0	20
	Overall (2011–2014)	6.06	3.38	14.42	1.35	0.23	0.22	2.76	16.95	6.1	48
Yakimaki	2011	4.26	1.78	4.82	1.54	0.71	0.27	1.31	9.00	6.9	8
	2012	1.31	1.19	0.59	0.75	1.06	0.15	2.08	12.64	6.1	7
	2013	3.17	2.99	4.74	1.15	0.57	0.51	1.01	6.63	6.6	9
	2014	2.91	1.46	1.60	1.28	0.63	0.37	3.24	15.50	4.8	5
	2015	1.85	2.04	1.88	0.68	0.33	0.17	0.98	4.94	5.0	11
Overall (2011–2015)	6.65	2.99	12.33	1.43	0.31	0.18	3.97	19.35	4.9	50	
Lake Kasumigaura	2011	7.19	4.18	20.50	1.54	0.55	0.56	4.31	29.65	6.9	35
	2012	9.41	4.39	20.50	1.42	0.29	0.37	3.33	21.38	6.4	77
	2013	9.96	7.48	48.19	1.69	0.29	0.61	4.73	29.04	6.1	117
	2014	9.00	6.50	43.35	1.16	0.23	0.54	1.59	14.72	9.3	135
	2015	3.91	5.98	13.11	0.92	0.16	0.21	1.51	10.16	6.7	114
	Overall (2011–2015)	11.57	8.38	63.23	1.38	0.13	0.22	2.99	21.76	7.3	481

there were significant differences across sites. Pairwise comparisons revealed significant differences between Futto and Osukazu in nitrogen range ( $t^\# = 4.70$ ,  $P^\# = 0.0101$ ), CR ( $t^\# = 7.96$ ,  $P^\# = 0.0059$ ), TA ( $t^\# = 3.88$ ,  $P^\# = 0.0097$ ), distance to centroid ( $t^\# = 9.77$ ,  $P^\# = 0.0067$ ) and SDNND ( $t^\# = 6.35$ ,  $P^\# = 0.0118$ ). All other pairwise comparisons between sites showed no significant differences with the exception of the ones between Asous and Osukazu in carbon range ( $t^\# = 14.75$ ,  $P^\# = 0.0326$ ) and Asou and Futto-ohashi in SDNND ( $t^\# = 5.44$ ,  $P^\# = 0.0365$ ).

The isotopic homing range (KUD), proxying the occupied trophic niche, did not show any clear relationship with site nor year ( $P > 0.05$ ). Significant relationships were found for the 40% core area (site:  $F_{4,16}^\# = 0.52$ ,  $P = 0.0239$ ; year:  $F_{4,16}^\# = 1.14$ ,  $P = 0.4090$ ) but not for the 95% area (site:  $F_{4,16}^\# = 0.66$ ,  $P = 0.6358$ ; year:  $F_{4,16}^\# = 0.81$ ,  $P = 0.55$ ). Indeed, there was a certain similarity in the usage of resources (i.e. resources with a similar isotopic composition), as the core area (40% KUD) from all sampling years were overlapping (Fig. 4). However, a considerable degree of variability across years was present (as



**Fig. 4.** Displacement and variability of isotopic niche area (a: 95%; b: 40%) occupied by specimens caught from Lake Kasumigaura without reference to specific sampling sites over the studied period.

highlighted by the 95% KUD area; Supplement 7). In regards to specific sites, the widest occupied area was identified for Futto-ohashi, followed by Yakimaki and Futto. Within the same site, the 95% homing area varied considerably over the studied period ( $p < 0.05$ ; Supplement 8) but neither the 95% nor 40% KUD showed a significant relationship with the sample size ( $R^2 < 0.01$ ;  $p > 0.05$ ) indicating that the occupied niche was not affected by the sampling effort. Furthermore, when presented separately for years, the 95% KUD showed considerable variability, while the 40% KUD showed a high degree of overlap. The IPI, i.e. the ratio between home and core range of *I. punctatus* at each site and for each year, provided evidence for the fact that the population's trophic niche differed across sites. At Asou, the expressed niche was small (as indicated by the 95% homing area) and less dense in respect to the core home range, followed by the population at Futto and Futto-ohashi, also indicating that the population at Yakimaki expressed the trophically widest and densest niche in respect to the core home range (Table 2).

#### 4. Discussion

Typically, when the abundance of an alien species population does not increase further, this is an indication that it has likely reached its plateau phase (i.e. carrying capacity) (Arim et al., 2005). At this stage, we found that individuals increase in their size or weight, but numbers remain constant unless environmental conditions change. The population of the channel catfish in Lake Kasumigaura seems to have reached this plateau and can be considered established. Population growth is bolstered by the presence of dense zooplankton communities (Mischke et al., 2009), which are abundant in Lake Kasumigaura. We found no direct link between temperature and the channel catfish population but we identified a significant relationship between temperature and zooplankton.

In most cases, at the time when an alien species is reported for the first time, there is little evidence regarding differentiation across sites within a single ecosystem, in spite of the species' migratory capacity or possibly considerable geographic dispersion among introduced/detected individuals. In the case of *I. punctatus* in Lake Kasumigaura, individuals that were introduced likely originated from a single source population (Mukai et al., 2016). As such, other factors (habitat structure, food source, and habitat range) could have affected the differences among sites, eventually leading to differences in physiological conditions. Throughout time, this may have led to variations in mean size or weight. Indeed, site-specific introductions of different aquaculture lineages (Argue et al., 2003; Dunham et al., 1994) with limited exchange, varying availability of prey or variation in environmental conditions could have shaped different "populations" with unique characteristics (Carson, 1990; Saccheri et al., 2001). Such potential differences could be revealed through the analysis of more rudimentary growth patterns (Copp and Fox, 2007; Novomeská et al., 2013). Despite the overall growth being allometric and similar across all sites, the Asou population was significantly different from the rest, possibly owing to different water temperatures or food availability. Indeed, earlier findings support linkages between plankton abundance and *I. punctatus* growth (Havens et al., 2001) and hence, it is possible that the community composition and thus prey availability near the outlet differed. Furthermore, it is possible that the different sites within the lake have been colonized at different periods. Indeed, by the early 1980s, it was already observed in various natural water bodies around Lake Kasumigaura (Hanzawa, 2004). Thus, differing habitat and food structure, composition, and conditions across these sites might have shaped the expression of differences in trophic niches, resulting in variable trophic 'starting points' when reaching Lake Kasumigaura. Nevertheless, the observed pattern may simply reflect different succession stages, which may have vanished over time under the assumption that the lake was biologically homogenous.

Nitrogen signature ( $\delta^{15}\text{N}$ ) generally increases with fish size, indicating that larger individuals consume prey from higher trophic levels. In Lake Kasumigaura, populations from all sites showed a generally positive relationship between  $\delta^{15}\text{N}$  and size, except for Futto-ohashi. This observation may have originated from a lower number of juveniles. However, considering separately the two size classes, revealed a more complex pattern. A positive relationship was consistently found in all populations for juveniles, while a greater variability was found for adults, with some populations (Futto-ohashi, the close site Futto and, to a lesser extent, Yakimaki) exhibiting a negative correlation between size and  $\delta^{15}\text{N}$ . This was supported by significant differences in  $\delta^{15}\text{N}$  of juveniles and adults found by the applied PERMANOVA in two sampling sites (Supplement 4). The geographical position of the sampling sites could partially explain this trend, as Futto-ohashi is positioned downstream of the outlet of the tributary Onogawa River and not directly within Lake Kasumigaura. Similarly, Futto is close to the riverine incoming water. Previous studies showed that *I. punctatus* juveniles in the Arno River (Italy) occupy a slightly higher trophic position than adults (Haubrock et al., 2019, 2020a). This observation was explained by the finding that juveniles were mostly feeding on isotopically enriched detritus. Indeed, detritus is a complex substrate constituted by dead organic matter and the microbial community consuming it, thus acting as metazoan consumers (Steffan et al., 2015; Steffan and Dharampal, 2019). This in turn leads to the fact that detritivorous animals consume both the components, thus elevating their isotopic signature and therefore their trophic position (Steffan et al., 2017).

One of the main results of this study is that the existence of distinct populations of *I. punctatus* were reflected not only through variable niches across Lake Kasumigaura, but also through a significant change in isotopic ranges over time in response to the different sites. This variability was not identifiable when pooling together isotopic data from all sites, emphasizing the need to treat results of such analyses with care when sampling (or pooling data from) different sites or over long periods in large ecosystems like Lake Kasumigaura. The temporal variability in the trophic niche for the period between 2011 and 2015, observed in the same site, is likely due to variations in the isotopic composition of prey, prey availability and/or environmental conditions and thus nutrient availability. This was reflected by the stable isotope composition of primary producers and subsequently by all the consumers in the food web. Indeed, the influence of source isotope variations across sites was recently shown in the heterogeneity of sedimentary characteristics and Chironomid's stable isotopes within Lake Kasumigaura (Tsuchiya et al., 2020). This complex spatial-temporal variability points at a confounding effect of these two variables on each other, so that studies on spatial differences need to control for temporal variability, and vice versa (Vander Zanden and Rasmussen, 2001; Post, 2002). While this was not possible in our analysis due to suitable data, our study provides evidence that occasional point-like variations likely do not mediate within a few years (five in this study), so that spatial and temporal variabilities are not negligible. Additionally, it should be acknowledged that seasonal variability is also possible. However, pooling the isotopic data from only the inferred period of active feeding should have strongly reduced the effects of such variability in our study.

It can further be assumed that aside from the influence of source isotope variations across sites, spatial differences in the trophic niche depend on the dispersal capacities and feeding strategies; such differences are likely smaller in species that have distinct feeding grounds and are less likely to migrate or express a great capacity for movements. Generally known to prefer reed zones (Endo et al., 2015), *I. punctatus* shows site-fidelity and limited migration/feeding dispersal, mostly related to finding suitable prey and spawning habitats (Pellett et al., 1998; Tatarenkov et al., 2006), returning to deeper pools following potential prey in the fall or to sustain during the cold winter months. Almost all studies investigating the movement of *I. punctatus* have focused on rivers and streams (Dames et al., 1989; Pellett et al., 1998). (Cooke and McKinley, 1999). Relying on radio tracking to investigate the



displacement of *I. punctatus* along a channel, they identified a highly active but localized movement. However, the range upon which they dispersed was difficult to identify and generally attributed migration (<3 km) to dependence on prey availability. Lake Kasumigaura is a relatively large eutrophic lake, hence, a nutrient rich environment. As such, food sources for juveniles must be presumed as abundant, limiting their spread across the river through deeper zones or along the shore. Additionally, given the species' preference for the reed zone, any potential active migration likely occurs along the shoreline, underlining the low possibility of specimens moving from one site to another given the general considerable distance among them (e.g. Asou – Yakimaki: ~18 km; Asou – Osukazu: ~17 km; Futto – Futto-ohashi: 2 km). Further, the differences in niche space identified across different sites reflect the distance and thus suggest potential ecological differences. Taken together, all these factors suggest that an exchange between sites is not occurring at a considerable rate. However, to develop a more comprehensive picture, further research, specifically genetic studies on these populations and trophic comparisons between native and introduced populations are needed.

Trophic plasticity in fish species has been discussed based on consumed prey across a streams' longitudinal distribution (e.g. Uieda and Pinto, 2011), and using stable isotopes across seasons (Pool et al., 2017). Furthermore, the expression of phenotypic and trophic plasticity in introduced species has often been discussed as a corollary hypothesis underlying the success of invasions (Simon and Townsend, 2003; Cathcart et al., 2019; Balzani et al., 2021). Here, we showed that trophic plasticity is not only aiding the success of an introduced species establishment, but also emphasize, that spatial variability in trophic plasticity can help a species maintain its presence, therefore exceeding the phase of an invaders' establishment (Lockwood et al., 2007). To this extent, the trophic plasticity we identified reflects an adaptation to persist in spatially variable, heterogeneous ecosystems (Cathcart et al., 2019). This aspect was prevalent by the strong overlap of the different sites' 40% KUD, compared to the very versatile 95%, underlining the ability of *I. punctatus* to adapt or shift to a wider range of resources (i.e. expressing a wider trophic niche), while using a similar set of resources, which is reflected in the 40% KUD. Another major finding was the identification of differing IPI ratios (95% home range/40% core region) across sites and years. While we had to neglect possible differences between mature and immature individuals due to the nature of the data and analyses, which ultimately led to an overall larger isotopic niche expressed at each site and thus, larger overlap, we note that demographic differences at each site may have played a role, which we cannot quantify at this stage. However, based on the observed differences, we infer that those sites that are characterized by a wider IPI have a generally greater availability of food sources or greater variability in baseline isotope signatures, while those that are condensed have fewer sources or less isotope variability in the available baseline organisms with all individuals consuming the same or similar preys. As such, we believe that the IPI is a promising addition to the currently established metrics used to describe a species' and potentially communities' trophic ecology. The observations made with the IPI may further reflect a form of intraspecific redundancy, as a dense niche might indicate more competition, which would eventually be reflected in different growth slopes as indicated by the linear model for Asou. At this site, the low  $\delta^{15}\text{N}$  range, coupled with the small niche suggests the possibility of a reliance on fewer food sources in contrast to Futto and Futto-ohashi. However, considering the growth curve of individuals from this site, a high abundance and nutritional value of the local prey can be assumed, given that heavier juveniles were found at this site. Indeed, we infer that the juvenile growth is bolstered at Asou. As juvenile individuals commonly constitute the majority of this species' population, the high abundance and biomass in Asou is likely an imminent threat for smaller prey and resources utilized by native species, potentially disrupting the trophic web. As such, we argue that the IPI is an adequate and new measure to investigate isotopic niche variability. Nevertheless, it should be

noted that differences in locally occurring competition with native species might lead to niche variation, which allows species to coexist through space and time (Balzani et al., 2016), albeit *I. punctatus* being the only piscivorous predator in Lake Kasumigaura. Consequently, given the lack of knowledge of variation in stable isotopes at the source, particularly given that Lake Kasumigaura is a shallow lake, which is vulnerable to eutrophication, extreme fluctuations in environmental conditions and nutrient input, the indication of functional redundancy must be considered with care.

We have also shown that the associated impacts differed across years. Considering the various impacts this invasion can have on native fish, amphibian, and macroinvertebrate species (Bucciarelli et al., 2014), it is likely that the Lake Kasumigaura fishery is affected more at Futto and Futto-ohashi, as the wider range of  $\delta^{15}\text{N}$  indicates a stronger feeding activity on high trophic levels such as fish species. The wider niche indicates a broader range of consumed prey and thus, a higher possibility to compete with native species. Our proposed IPI, an index of isotopic niche plasticity, confirmed these inferences for Futto and Futto-ohashi, thus proving to be a reliable proxy for understanding the potential of individual plasticity to impact a diverse range of taxa.

The different isotopic niches occupied at different sites over time generally relate to different food availability, elevated levels of competition, or environmental conditions (e.g. temperature gradients, microclimatic differences, different vegetation types). This ultimately leads to differing impacts of *I. punctatus* on native communities across different sites, highlighting the spatial variability of trophic interactions, which needs to be considered when investigating the impacts of alien fish species and designing management actions that should likely be spatially differentiated. The results can help highlight areas that require more intense management efforts due to e.g. intense local foraging, predation etc., therefore aiding resource managers to prioritize and/or focus resources accordingly (e.g. through incentivizing higher harvesting rates in places where impacts are expected to be higher). Similarly, our work can help point at those high-impact size classes that control efforts may need to target first, therefore aiding again resource managers design and prioritize management actions. Using the evidence provided in this paper, future research efforts directed at informing management may focus on understanding how niche metrics change with decreasing populations of *I. punctatus* to assess the effects of control efforts on the magnitude of the impacts from the invasion. Additionally, understanding the drivers of differences behind niche expression provides recourse managers with an important tool to better understand impacts and control for them by directly addressing the drivers of impact variability across space and time.

### CRediT authorship contribution statement

**Phillip J. Haubrock:** Conceptualization, Methodology, Writing – original draft, Visualization. **Paride Balzani:** Methodology, Visualization, Investigation, Writing – original draft. **Shin-Ichiro S. Matsuzaki:** Data curation, Writing – review & editing. **Ali Serhan Tarkan:** Methodology, Writing – review & editing. **Melina Kourantidou:** Conceptualization, Writing – review & editing. **Peter Haase:** Conceptualization, Supervision, Writing – review & editing.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability statement

Underlying data can be accessed from the referenced repositories.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.145947>.

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