

Large-bodied fish migration and residency in a flood basin of the Sacramento River, California, USA

Ted R. Sommer¹, William C. Harrell¹, Frederick Feyrer²

¹California Department of Water Resources, Sacramento, CA USA

²US Bureau of Reclamation, Sacramento, CA USA

Accepted for publication July 29, 2013

Abstract – River–floodplain complexes represent some of the most variable and diverse habitats on earth, yet they are among our planet’s most threatened ecosystems. Use of these habitats by large-bodied fishes is especially poorly understood, particularly in temperate regions. To provide insight into the factors that affect floodplain assemblages and migration, we sampled large-bodied fishes with a fyke trap for 7 years in the Yolo Bypass, the primary flood basin of the Sacramento River, California. We collected a total of 18,336 individual fish comprised of 27 species, only 41% of which were native. Year-round resident species white catfish *Ameiurus catus*, channel catfish *Ictalurus punctatus* and common carp *Cyprinus carpio* (all alien species) were the most abundant and comprised 74% of the total catch. Splittail *Pogonichthys macrolepidotus* (3.8%), white sturgeon *Acipenser transmontanus* (2.3%) and Sacramento sucker *Catostomus occidentalis* (1.1%) were the primary native species. We found that seasonal variation in water temperature and flood stage were important factors affecting the fish assemblage structure and the presence of migratory species. American shad *Alosa sapidissima*, an alien species, showed highest abundance during the early summer upstream migration, when temperatures were warmer. For native species, the abundances of white sturgeon, splittail, Sacramento pikeminnow *Ptychocheilus grandis* and Sacramento sucker were all highest during flood pulses. While our results suggest that flow alone is not sufficient to control alien species, the strong linkage between native fish migration and flow pulses highlights the importance of river–floodplain connectivity for the conservation of native fishes.

Key words: floodplain; Sacramento River; native fishes; fyke trap; migration

Introduction

River–floodplain environments are one of the most variable and diverse freshwater habitats on earth (Power et al. 1995; Puckridge et al. 1998). Variability in river stage and the resulting inundation of floodplain habitat can dramatically alter landscapes across interacting spatial and temporal scales (Bowen et al. 2003; Sommer et al. 2004a). This variability offers special challenges to fishes, many of which are affected by seasonal inundation for at least part of their life cycles. Hence, fish assemblages in flood-prone environments typically consist of species well-adapted to the physically harsh environments (Harrell 1978; Goulding 1980). This tenet holds true for the

Yolo Bypass, the primary flood basin of the Sacramento River (Figure 1), which supports an assemblage of native and alien fishes (Sommer et al. 1997, 2004b; Feyrer et al. 2006a).

The recognition that seasonal habitat represents key migration, production and nursery areas for native fishes has made floodplain conservation and restoration a major goal in many regions (Opperman et al. 2009; Bunn & Arthington 2002). Unfortunately, these habitats are among the world’s most threatened ecosystems as a result of widespread anthropogenic effects and alien species (Tockner et al. 2010). With this growing interest in floodplain restoration comes a need for better information about the mechanisms by which this habitat type supports fish communities

Correspondence: T. R. Sommer, California Department of Water Resources, PO Box 942836, Sacramento CA 94236-0001, USA. E-mail: Ted.Sommer@water.ca.gov

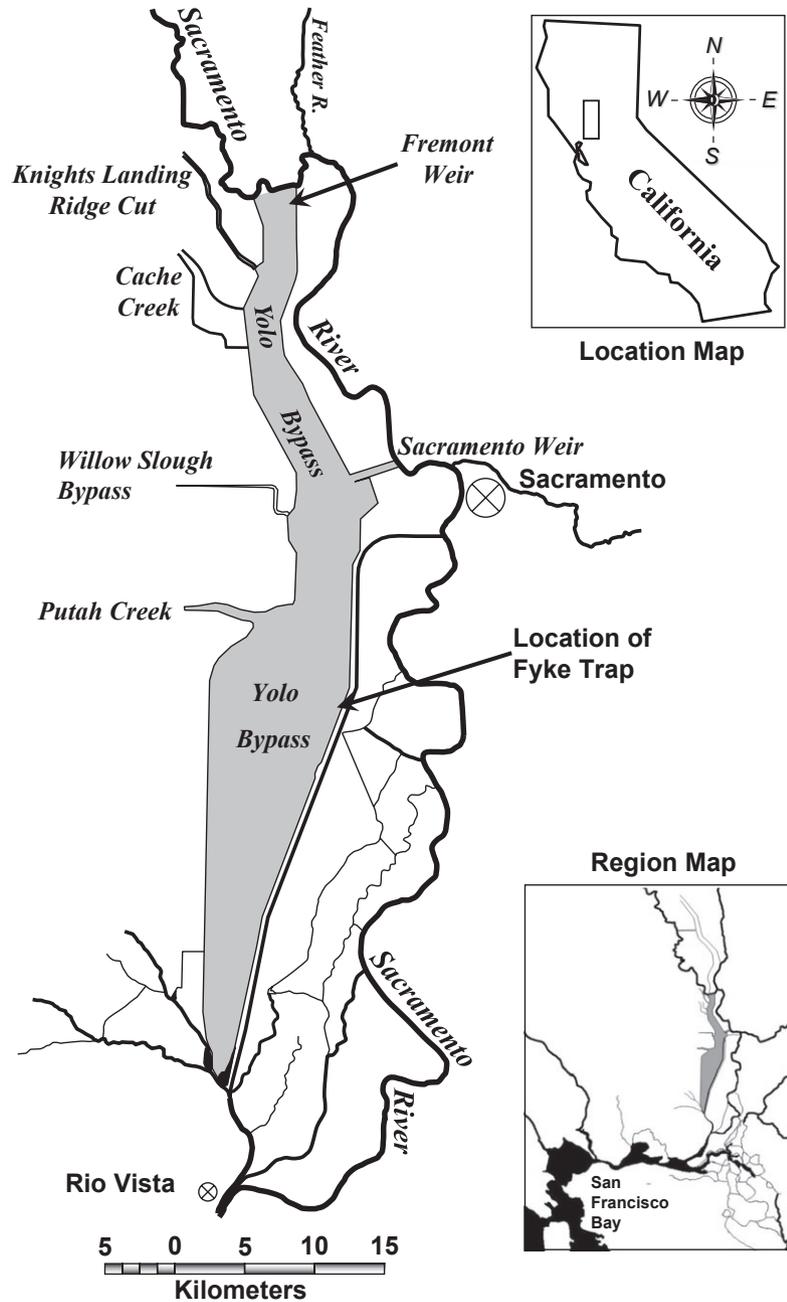


Fig. 1. Map of Yolo Bypass and surrounding area.

and migration. The current knowledge base includes research on many tropical (Welcomme 1979; Copp 1989; Agostinho & Zaliwski 1995; Henderson & Hamilton 1995; Winemiller & Jepsen 1988) and temperate ecosystems (Kurmayer et al. 1996; Kwak 1988; King et al. 2003; Gorski et al. 2010; Schomaker & Wolter 2011), as well as studies focusing on specific floodplain habitat types such as ponds, lakes (Halyk & Balon 1983; Rodriguez & Lewis 1994) and wetlands (Modde et al. 2001). There has been a significant amount of information obtained on young and small-bodied fishes (e.g., Ross & Baker 1983; Copp 1989; Crain et al. 2004; Feyrer et al.

2006a); however, relatively little is known about how large-bodied fishes (e.g., >300 mm FL) utilise floodplains, especially in temperate ecosystems (Hoggarth et al. 1999; Molls 1999). It is clear that many adult fish use floodplains for foraging and reproduction (Copp 1989; Winemiller & Jepsen 1998; Gorski et al. 2010), but specific data on fish movements are rare (however, see Kwak 1988). Our lack of understanding about native fish movements through large river floodplains is especially troublesome as migrants including sturgeon and several salmonids are among the world's most endangered fishes (Moyle 2002; Pritchard et al. 2005). Indeed, high profile collapses of

several salmonids and sturgeon have led to threatened or endangered status for these fishes in California (Moyle 2002; Service 2007). Native fish in the Sacramento River face substantial threats from multiple factors including alien species, food web changes, water diversions and habitat degradation (Brown & Moyle 2005). These problems appear to be part of a growing global degradation of coupled river–floodplain ecosystems, which may become even more challenging to manage with future climate change (Tockner et al. 2010).

In this study, we examine data from 7 years of sampling in a flood basin of the Sacramento River–floodplain complex to describe the assemblage and migration of large-bodied fishes. Specific research questions included: (i) Which fishes use the flood basin? (ii) Do native and alien fishes show different patterns of flood basin use? (iii) What environmental variables regulate use of the flood basin? Answering these questions will improve our general understanding of the fish use of large river temperate floodplains. This information is particularly relevant to restoration actions because it will help resource managers better understand and evaluate alternative actions to manage river–floodplain complexes, a globally threatened ecosystem.

Study area

California's Central Valley is drained primarily by the state's two largest rivers, Sacramento River from the north and San Joaquin River from the south. The rivers drain a watershed encompassing 40% of California's surface area (100,000 km²) and converge to form the Sacramento-San Joaquin Delta (3000 km²), a complex network of tidal freshwater channels between large, leveed agricultural islands. The Sacramento River basin conveys 85% of total flow into the Delta (Kimmerer 2002). The primary flood basin of the Sacramento River is Yolo Bypass (Fig. 1; Sommer et al. 2001a,b), a 61-km-long, 24,000 ha seasonally inundated area. The flood basin was substantially modified in the early 1930s to protect the greater Sacramento region from flooding, but as described below, retains many features of the historical system (Whipple et al. 2012).

Hydrology: The Yolo Bypass flood basin still represents a relatively broad and seasonal overflow area for the Sacramento River (Whipple et al. 2012). The main channel of the Sacramento River conveys just a fraction of peak flood flows, with the majority of flow redirected into the flood basins. Historically, this overflow occurred through natural levees between the river and flood basin. Under current conditions, Sacramento River spills over a partially reinforced levee called Fremont Weir, as well the complex down-

stream structure called Sacramento Weir (Fig. 1). Under typical flood events, water spills into Yolo Bypass at Fremont Weir when Sacramento River flows surpass approximately 2000 m³ s⁻¹ and at Sacramento Weir at flows of approximately 5000 m³ s⁻¹ (Sommer et al. 2001b). Yolo Bypass can convey flows up to 14,000 m³ s⁻¹, representing 80% of total Sacramento River basin flow during a large flood. It normally floods in winter and spring in about 70% of years. As in historical periods, the Yolo Bypass still provides a drainage basin for smaller tributaries such as Cache and Putah Creeks (Whipple et al. 2012). During periods when flow does not enter Yolo Bypass from the Sacramento River weirs, substantial short-term flooding (e.g., 1–3 weeks) can also occur from these smaller tributaries.

Another similarity with the historical flood basin is that floodwaters spill out across the landscape and then eventually drain to the Delta through southerly outlets. (Whipple et al. 2012). Except during extreme high-flow events, the mean depth of the floodplain is generally less than 2 m, creating broad expanses of shallow water habitat. A small perennial channel (capacity ~ 100 m³ s⁻¹) helps to drain the basin as floodwaters recede (Sommer et al. 2001b). During dry seasons, the perennial channel remains inundated as a result of tidal action along its southern half and from agricultural drainage along its northern half.

Habitat types: Yolo Bypass was historically dominated by vast areas of Tule (*Scirpus*) marsh, a habitat type that is still present in substantially smaller managed wetlands in the northern and central portions of the flood basin, and in larger expanses of marsh in southern Yolo Bypass (Whipple et al. 2012). Land use in Yolo Bypass is dominated by agriculture during the dry season, but approximately one-third of the area remains a mosaic of 'natural' habitat types including riparian and upland habitat, emergent marsh, open water and permanent ponds (Sommer et al. 2001b; Feyrer et al. 2006a; Whipple et al. 2012). Like the historical flood basin, the habitats grade from seasonally inundated areas in the north with few channels to perennial tidal channels in the south.

Methods

Field sampling

We sampled large-bodied fishes in Yolo Bypass with a large cylindrical fyke trap. The steel-framed trap was seven metres long, three metres in diameter and was wrapped with 5.5-cm steel mesh. The terminal chamber of the trap was lined with 20-mm square plastic mesh and included two access doors for removing captured fish. The trap was secured in place with a steel nose cable that was anchored to the

bank 100-m upstream of the trap and positioned with its 3-m diameter opening facing downstream. We positioned the trap in the perennial channel in the southwest portion of the flood basin on a firm mud substrate in open water (Fig. 1). We selected this channel because it is one of the few perennially wetted areas that can be sampled and is the primary migration corridor into the flood basin. Similar sampling was not possible in the seasonally dewatered habitat to the west or north. Water depth ranged from 3 to 4 m according to tidal stage during the dry season and up to 5 m during flood events. The trap was accessed by rolling it up the bank with a series of cables and a truck-mounted winch. Sampling was typically conducted from October to June each year from 1999 through 2006. The trap essentially fished continuously during this time period, except during the most extreme flow events when the high debris load made sampling particularly dangerous. The trap was normally serviced every 48 h. Fishes collected during each set were removed from the trap with a variety of dip nets, identified to species and then released back into the channel. Temperature was recorded continuously with an Onset logger deployed next to the trap.

Data analysis

Fish were categorised as native or alien based on Moyle (2002). Migratory or resident types were also identified based on life-history information from Moyle (2002) and the seasonality of catch in our fyke trap (e.g., capture in all seasons = resident). We summarised the catch of each species as the average number of individuals collected per trap set per week. For each weekly period, we summarised three environmental variables at the sampling site: water temperature ($^{\circ}\text{C}$); and flow ($\text{m}^3 \text{s}^{-1}$) and stage (m) both obtained from the DAYFLOW database (<http://www.iep.water.ca.gov/dayflow/index.html>). Due to the physical structure of the floodplain basin, flow and stage have a complex relationship. Stage is not related to $\log(\text{flow } \text{m}^3 \text{ s}^{-1})$ until $\log(\text{flow } \text{m}^3 \text{ s}^{-1})$ reaches about 10 and then the two variables are essentially linearly related (W Harrell, California Department of Water Resources, unpublished data). This is because tidal effects dominate the stage of the perennial channel until its channel capacity is exceeded by flood inputs.

We used both direct and indirect ordination methods as two complimentary multivariate statistical methods to analyse the fish data. First, we used canonical correspondence analysis (CCA) as an exploratory analysis to examine how the abundances of fishes related to the environmental variables (Legendre & Legendre 2000). We used CCA instead of more tradi-

tional regression approaches because it allowed us to examine the environmental associations among multiple species in a single biplot. The CCA was conducted with CANOCO software program (ter Braak & Šmilauer 1998). We included all three environmental variables in the analysis and constrained the final model to only include those significant at $P < 0.05$, as estimated by the forward selection procedure with Monte Carlo simulations (199 permutations) provided by CANOCO (ter Braak & Šmilauer 1998).

Next, we examined temporal variability in fish assemblage structure with nonmetric multidimensional scaling (NMDS) performed with the Primer version 5.0 software package (Primer; Clarke & Gorley 2001). NMDS is a particularly useful indirect gradient analysis because it provides operational flexibility in defining similarity among samples and converting it to distance that is accurately portrayed in low-dimension ordination space (Legendre & Legendre 2000). We chose the Bray–Curtis coefficient to construct the similarity matrices used in the NMDS ordinations because joint absences do not influence similarity. Species catch data were $\log(x+1)$ -transformed. The fit of an NMDS ordination, quantified by a value termed stress, is determined by how well the among sample distances in the ordination preserve the actual sample dissimilarities. Stress values of <0.05 are considered excellent, while a value of 0.2 is considered a threshold for potentially useful ordinations (Clarke & Warwick 2001). Stress values in our ordinations did not change from that of the original run (default value = 10) when we repeated the analysis several times and increased the number of random restarts, indicating the ordinations provided a good representation of sample dissimilarities (Clarke & Gorley 2001).

We applied two different generalised linear models (GLM) to the sample scores of the NMDS to evaluate temporal patterns of assemblage structure. The models we tested were developed based upon the results of the CCA (see Results) and previous knowledge of assemblage structure of juvenile and larval fishes in Yolo Bypass (Sommer et al. 2004b; Feyrer et al. 2006a). The first model examined seasonal patterns of assemblage structure and tested for differences according to month. The second model tested the effects of flood stage (flood basin inundated or not inundated), year and the flood stage \times year interaction. We applied these two models to each of the first three NMDS axes. For all analyses, we included species that occurred in $> 1\%$ of the samples. However, we excluded threadfin shad *Dorosoma petenense* from the analysis because the small body size allowed this abundant species to freely swim in and out of the trap, reducing our confidence in their catch trends.

Results

There was at least some inundation of the flood basin in each year of our study but the duration and intensity were highly variable (Fig. 2). The median date of flood basin inundation typically was in late January. During the first two study years, the inundation period was relatively short, but large expanses of the Yolo Bypass were covered. This was followed by relatively short and minor inundation events occurring around 2000 and 2001. The next few years had long inundation events that lasted for up to 6 months. There was high variability in the intensity of long events, with high flows in 2006 generating large expanses of the inundated seasonal habitat that were covered for much of the winter and spring. Water temperature was relatively consistent on a seasonal basis (Fig. 3). Seasonal low water temperatures of approximately 10 °C occurred in January, which was coincident with the median date of flood basin inundation. Water temperatures peaked in July at about 25 °C.

We collected a total of 18,336 individual fish comprised of 27 species (Table 1). Overall, the catch was dominated by resident alien fishes. Resident alien species white catfish *Ameiurus catus*, channel catfish *Ictalurus punctatus* and common carp *Cyprinus carpio* were the most abundant and comprised 74% of the total catch. Only forty-one per cent of the species were native, most of which were migratory. Splittail *Pogonichthys macrolepidotus* (3.8%), white sturgeon *Acipenser transmontanus* (2.3%) and Sacramento sucker *Catostomus occidentalis* (1.1%) were

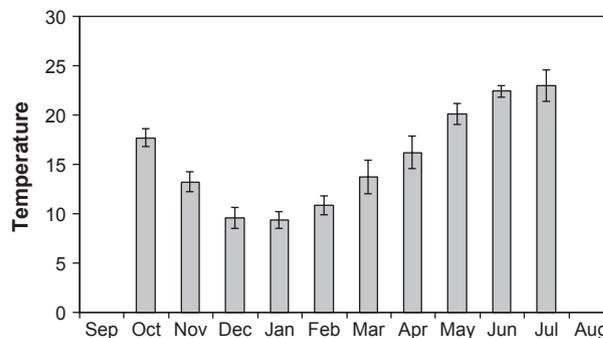


Fig. 3. Mean monthly (\pm one standard deviation) water temperature in Yolo Bypass. No data were collected in August or September.

the only native species which represented at least 1% of the total catch.

The forward selection procedure retained water temperature and stage as significant variables in the final CCA model. These two environmental variables explained 9.1% of the variation in the species data and 100% of the species–environment relation within the first two axes. The eigenvalues were 0.119 for axis one and 0.035 for axis 2. The CCA biplot demonstrated how the relative abundances of species were related water temperature and stage (Fig. 4). Most notably, the native migratory species splittail, white sturgeon and Sacramento pikeminnow *Ptychocheilus grandis* clustered together as a group associated with increasing values of stage, suggesting they are most abundant during flood pulses. Most of the other species scored either near the origin or in the negative range for the stage vector, suggesting that

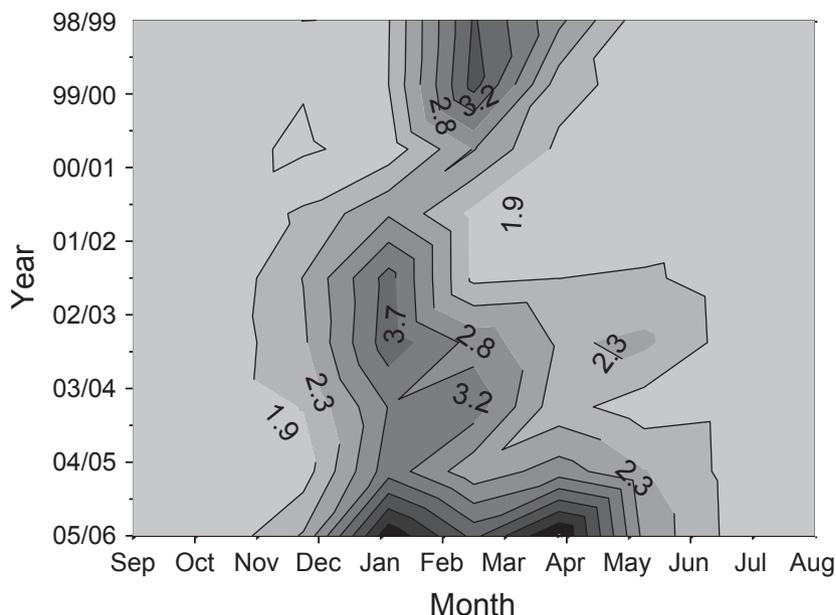


Fig. 2. Filled contour plot depicting seasonal and annual variability in stage (m) in Yolo Bypass. Floodplain inundation initiates at stage values greater than 1.9 m.

Large-bodied fish migration and residency in a flood basin

Table 1. List of fish species collected in Yolo Bypass fyke trap sampling, 1998–2006. Status is either native (N) or alien (A), and resident (R) or migratory (M). Relative abundance and frequency of occurrence are both expressed as percentages.

Species	Code	Status	Relative abundance	Frequency of occurrence in samples
White Catfish	<i>Ameiurus catus</i>	A, R	46.3	79
Channel Catfish	<i>Ictalurus punctatus</i>	A, R	14.7	53
Common Carp	<i>Cyprinus carpio</i>	A, R	13.5	75
Striped Bass	<i>Morone saxatilis</i>	A, R	9.8	76
Splittail	<i>Pogonichthys macrolepidotus</i>	N, M	3.8	19
Black Crappie	<i>Pomoxis nigromaculatus</i>	A, R	3.5	34
White Sturgeon	<i>Acipenser transmontanus</i>	N, M	2.3	6
Threadfin Shad	<i>Dorosoma petenense</i>	A, R	1.7	16
Sacramento Sucker	<i>Catostomus occidentalis</i>	N, M	1.1	20
Sacramento Blackfish	<i>Orthodon microlepidotus</i>	N, M	0.7	14
American Shad	<i>Alosa sapidissima</i>	A, M	0.6	7
White Crappie	<i>Pomoxis annularis</i>	A, M	0.5	8
Sacramento Pikeminnow	<i>Ptychocheilus grandis</i>	N, M	0.3	6
Chinook Salmon	<i>Oncorhynchus tshawytscha</i>	N, M	0.3	8
Brown Bullhead	<i>Ameiurus nebulosus</i>	A, R	0.2	5
Black Bullhead	<i>Ameiurus melas</i>	A, R	0.2	5
Goldfish	<i>Carassius auratus</i>	A, R	0.1	3
Bluegill	<i>Lepomis macrochirus</i>	A, R	0.1	2
Hitch	<i>Lavinia exilicauda</i>	N, M	0.1	1
Largemouth Bass	<i>Micropterus salmoides</i>	A, R	<0.1	1
Longfin Smelt	<i>Spirinchus thaleichthys</i>	N, M	<0.1	<1
Steelhead	<i>Oncorhynchus mykiss</i>	N, M	<0.1	<1
Yellow Bullhead	<i>Ictalurus natalis</i>	A, R	<0.1	<1
Yellowfin Goby	<i>Acanthogobius flavimanus</i>	A, R	<0.1	<1
Prickly Sculpin	<i>Cottus asper</i>	N, R	<0.1	<1
Threespine Stickleback	<i>Gasterosteus aculeatus</i>	N, R	<0.1	<1
Warmouth	<i>Lepomis gulosus</i>	A, R	<0.1	<1

flood basin inundation was not important in determining their abundance. American shad *Alosa sapidissima*, an anadromous alien species, was most strongly associated with high water temperature. This

observation was consistent with their persistent appearance only in early summer during their upstream migration.

The NMDS ordination provided a 3-dimensional solution with a stress value of 0.17. Our first GLM found that month was a significant factor for scores of NMDS axes 1 ($P < 0.001$, $F = 14.01$, d.f. = 10) and 2 ($P < 0.001$, $F = 19.04$, d.f. = 10) but not 3 ($P = 0.05$, $F = 1.89$, d.f. = 10). For axis 1 scores, months varied in a form that closely matched the manner in which temperature varied across months, suggesting that temperature was an important factor affecting seasonal variability in fish assemblage structure (Fig. 5). There was no discernable pattern to the variability in scores for axis 2. Similarly, our second GLM produced different results for each set of axis scores. For axis 1, flood stage was the only significant factor ($P < 0.001$, $F = 50.76$, d.f. = 1). For axis 2, year ($P < 0.001$, $F = 6.74$, d.f. = 6), flood stage ($P < 0.001$, $F = 13.09$, d.f. = 1) and the interaction term ($P < 0.001$, $F = 3.29$, d.f. = 6) were all significant factors. There were no significant factors for axis 3 scores. The significant interaction term found in axis 2 scores was because the 1999/2000-year fish assemblage structure during the nonflood period closely resembled that of the typical flood period-fish assemblage structure normally found in Yolo Bypass (Fig. 6).

Discussion

Our results for large-bodied fishes are consistent with previous sampling in Yolo Bypass showing that the temperate flood basin supports a diverse assemblage of fishes (Sommer et al. 2001b, 2004b; Feyrer et al. 2006a). While there are fewer data on large-bodied fishes in floodplains than for smaller species, high species diversity appears to be a common pattern in many types of seasonal floodplains, perhaps in part because of the complex mosaic of habitats and seasonal variability (Rodriguez & Lewis 1994; Bunn & Arthington 2002). As expected, the fishes observed in our study comprised two broad groups, resident and migratory types. Moreover, our finding that there were distinctly different migration strategies between groups is consistent with studies from several other areas (Ross & Baker 1983; Winemiller & Kelso-Winemiller 1994).

Unfortunately, data on the Sacramento River large-bodied fish communities are scarce beyond the past half-century, so we were unable to determine the degree to which the observed relative numbers of native fishes in Yolo Bypass were comparable to historical conditions. There is excellent evidence that most of the native large-bodied fishes have declined (Moyle 2002), but the degree to which their relative

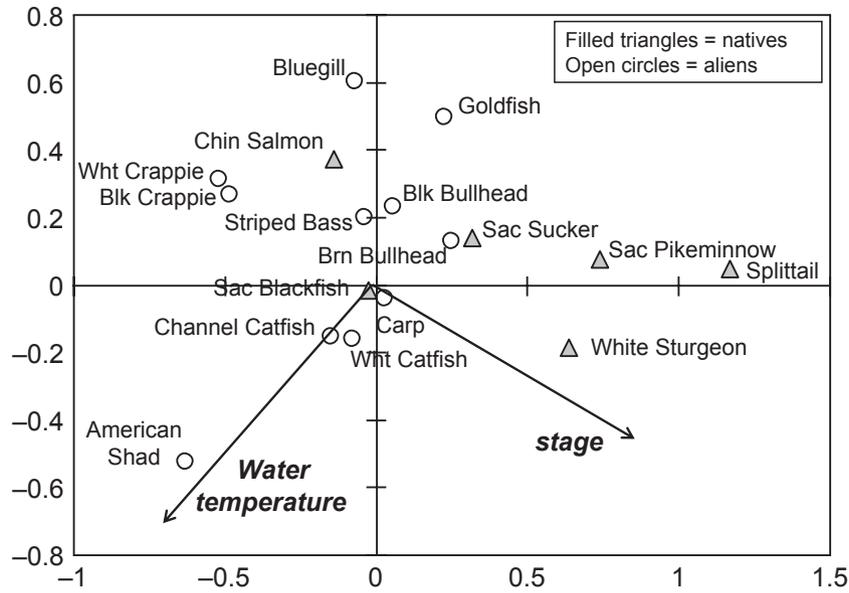


Fig. 4. Canonical correspondence analysis biplot depicting the relationship among species relative abundances and environmental variables. Species details are provided in Table 1. Symbols for the species are filled triangles for natives and open circles for aliens.

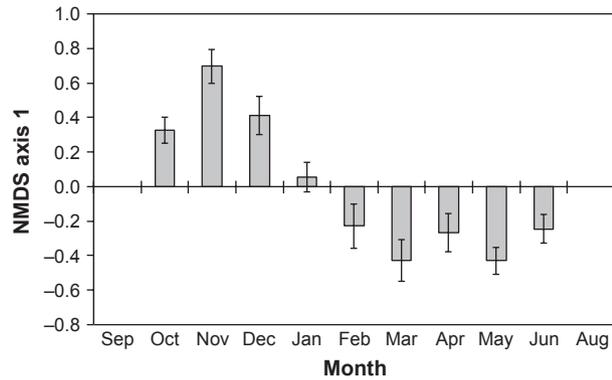


Fig. 5. Sample scores from NMDS axis 1 summarised as monthly averages (\pm one standard error).

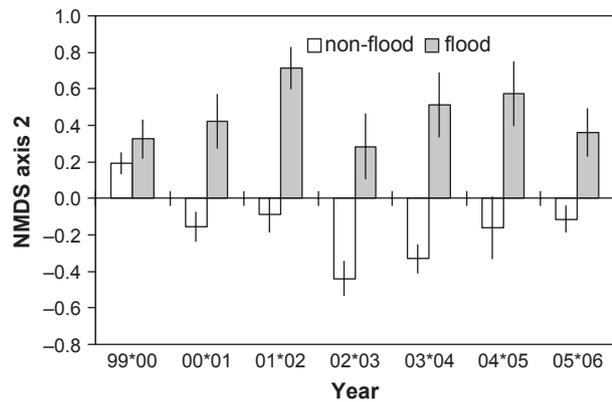


Fig. 6. Sample scores from NMDS axis 1 summarised as averages (\pm one standard error) by year and flood stage (floodplain inundation versus no floodplain inundation).

abundance has shifted is unclear. At the very least, a major change is that the fish community no longer contains two historically abundant native fishes.

Thicktail chub *Gila crassicauda* were one of the most abundant fishes used by Native Americans in this basin and supported a historical fishery until the species went extinct in the 20th century. Similarly, Sacramento perch *Archoplites interruptus* have been extirpated from the Sacramento River. One of the most notable results of our study was the prevalence of alien fishes. The Sacramento watershed has been extensively invaded by numerous alien fishes, especially in its lower reaches (Moyle 2002; Brown & Moyle 2005), so it was not surprising that alien fishes would be prevalent. However, it has been hypothesised that more natural hydrographs and habitat variability should tend to discourage alien fishes (Bunn & Arthington 2002; Moyle et al. 2003). Despite the dynamic nature of the floodplain environment in Yolo Bypass, we found that large-bodied fish assemblages were dominated by alien species. This point is best illustrated by catfishes and common carp, which dominated our fyke trap catches. Native species were most abundant during winter and spring periods of flood basin inundation, but rarely reached greater abundances than the alien species. The major role of alien species in the large-bodied fish assemblage is generally consistent with previous studies in floodplains of California (Crain et al. 2004; Sommer et al. 2004b; Feyrer et al. 2006a). This observation suggests that the extant assemblage of alien species is capable of persisting through flood events and that hydrological variation alone is not enough to eliminate invasive species (Moyle et al. 2003). Our finding for Yolo Bypass is not surprising as the flood basin has a diverse mosaic of habitats including perennial channels and ponds that provide

year-round refuges for alien fishes (Feyrer et al. 2004).

These results do not mean, however, that natural hydrographs and temperate floodplain habitat are not beneficial to native fishes. There is excellent evidence from California streams that re-establishing natural hydrographs can improve the status of native fishes and depress populations of alien fishes (Kiernan & Moyle 2012; Kiernan et al. 2012). We hypothesise that seasonal temperate floodplain habitat may give native fishes an additional competitive edge. Specifically, seasonally inundated areas provide spawning and rearing habitat to several types of native fishes (Sommer et al. 2001a; Feyrer et al. 2006a). Perhaps the best example is splittail, which migrate into Yolo Bypass in winter to spawn (Sommer et al. 1997; Feyrer et al. 2006b). The floodplain then provides rearing habitat for the young fish. Alien fishes spawn later in mid- to late-spring, after the Yolo Bypass typically has drained (Sommer et al. 2004b). Adaptive benefits of floodplain habitat include large increases in shallow water rearing habitat (Power et al. 1995) and enhanced levels of phytoplankton, zooplankton and drift invertebrates (Hein et al. 1999; Mueller-Solger et al. 2002; Sommer et al. 2004a). Hence, there appears to be at least a seasonal niche for native fishes that migrate into Yolo Bypass. Temperate floodplain may provide a similar adaptive advantage to native fishes in other parts of north America (Modde et al. 2001) and in other heavily invaded ecosystems worldwide (Bunn & Arthington 2002). We acknowledge, however, that there may be unique cases in which river–floodplain connectivity may not enhance native fishes. For example, river–floodplain connectivity can sometimes enhance the spread of alien fishes, putting rare and sensitive resident native fishes at risk (Scheerer 2002).

The strong response of a suite of native fishes to flow pulses is noteworthy. There are numerous studies describing the migration of individual species (Lucas & Baras 2001), but studies examining the upstream movements of entire assemblages are rare. In this case, we observed that most of the native fishes responded to flow events. This pattern is somewhat expected as floodplains are strongly pulsed ecosystems (Tockner et al. 2010), and other studies have observed increased catch rates and spawning of migratory fishes during seasons of high water (Gorski et al. 2010; Ru & Liu 2013). The mechanisms behind the fish responses are open to debate because separation of the specific cues that trigger migration is an especially difficult task (Lucas & Baras 2001). Flow pulses cause numerous environmental changes including temperature, light, water quality and food availability (Tockner et al. 2010), each of which could trigger changes in fish behaviour. Among

fishes, the best-studied group is salmonids, which show strong olfactory responses during migration (Dittman & Quinn 1996). In our study, however, Chinook salmon *Oncorhynchus tshawytscha* abundance was not associated with inundation or flow events as with the other native migratory species. This may be because most of the catch was fall-run Chinook salmon, a race known to migrate upstream relatively early before winter and spring flow events (Moyle 2002). Our results for most of the migratory natives are, nonetheless, consistent with other studies (Moyle 2002; Sommer et al. 2011). Both adult Sacramento pikeminnow (Moyle 2002) and Sacramento sucker (Villa 1985; Moyle 2002) show peak movements in the upper Sacramento River region during winter to early spring, when flows are often higher. Another western minnow (Colorado pikeminnow *Ptychochilus lucius*) undertakes spawning migrations in response to spring flow events (Irving & Modde 2000). Similarly, razorback sucker *Xyrauchen texanus*, a western relative of Sacramento sucker, migrates in response to Colorado River flow (Tyus & Karp 1990). The localised movements of sturgeon are not well understood (Parsley et al. 2008), but there is evidence that white sturgeon show general upstream movements during high-flow spring months (Kohlhorst et al. 1991; Moyle 2002). Overall, these findings suggest that a response to flow is a relatively common pattern in migratory native fishes (Welcomme 1979; Ross & Baker 1983; Rodriguez & Lewis 1994).

Together with other studies, our results have local and broader implications for the management of river–floodplain systems. Although our results revealed that periodic flood basin inundation may not be sufficient to eliminate alien fishes, the strong linkage between native fish communities and flow pulses highlights the importance of temperate river–floodplain connectivity for the conservation of native fishes. For native fishes such as splittail, flood pulses and floodplain connectivity play a profound role in their life cycles as they depend on seasonal habitat for spawning and rearing (Sommer et al. 1997; Feyrer et al. 2006b). It is also clear that temperate floodplain needs to be recognised as a major migration corridor and thus also as a potential fish passage issue. The native migratory fishes in our study including white sturgeon, Sacramento pikeminnow, splittail, Sacramento sucker and four races of Chinook salmon all spawn in riverine habitats upstream of our study area (Moyle 2002). Unfortunately, connectivity with upstream spawning habitat is poor under most conditions. While Yolo Bypass is inundated from the Sacramento River in the majority of years, the average length of overflow (i.e., connectivity) is only about 3 weeks (Sommer et al. 2001b). There is no upstream passage during the

remainder of the year, when the floodplain corridor is essentially a dead-end. As a consequence, one of the best opportunities to improve the ecological functioning and habitat use of the Yolo Bypass system would be to improve connectivity between the Sacramento River and its flood basin. Our study therefore reinforces the notion that improved river–floodplain connectivity should be an important conservation goal for migratory fishes (Hoggarth et al. 1999; Bunn & Arthington 2002).

Acknowledgements

This study would not have been successful without the contributions of staff from California Department of Water Resources and the California Department of Fish and Game. We owe particular thanks to many scientific aides that helped collect these data under difficult conditions. Funding was provided by the Interagency Ecological Program and CALFED Bay-Delta Program.

References

- Agostinho, A.A. & Zaliwski, M. 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. *Hydrobiologia* 303: 141–148.
- Bowen, Z.H., Bovee, K.D. & Waddle, T.J. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society* 132: 809–823.
- ter Braak, C.J.F. & Šmilauer, P. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Ithaca, New York: Microcomputer Power.
- Brown, L.R. & Moyle, P.B. 2005. Native fishes of the Sacramento-San Joaquin drainage: a history of decline. In: Rinne, J.N., Hughes, R.M. & Calamusso, B., eds. *Historical changes in large river assemblages of the Americas*. Symposium 45, Bethesda, Maryland: American Fisheries Society, pp. 75–98.
- Bunn, S.E. & Arthington, A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30: 492–507.
- Clarke, K.R. & Gorley, R.N. 2001. *Primer v5: user manual/tutorial*. Plymouth, United Kingdom: Primer-E Ltd.
- Clarke, K.R. & Warwick, R.M. 2001. *Change in marine communities: An approach to statistical analysis and interpretation*. 2nd edn. United Kingdom: Primer-E Ltd. Plymouth.
- Copp, G.H. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes* 26: 1–27.
- Crain, P.K., Whitener, K. & Moyle, P.B. 2004. Use of a restored central California floodplain by larvae of native and alien fishes. In: Feyrer, F., Brown, L.R., Brown, R.L. & Orsi, J.J., eds. *Early life history of fishes in the San Francisco Estuary and Watershed*. Symposium 39, Bethesda, Maryland: American Fisheries Society, pp. 125–140.
- Dittman, A. & Quinn, T. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology* 199: 83–91.
- Feyrer, F., Sommer, T., Zeug, S.C., O'Leary, G. & Harrell, W. 2004. Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA), with implications for the conservation of native fishes. *Fisheries Management and Ecology* 11: 335–344.
- Feyrer, F., Sommer, T. & Harrell, W. 2006a. Importance of flood dynamics versus intrinsic physical habitat in structuring fish communities: evidence from two adjacent engineered floodplains on the Sacramento River, California. *North American Journal of Fisheries Management* 26: 408–417.
- Feyrer, F., Sommer, T. & Harrell, W. 2006b. Managing floodplain inundation for native fish: production dynamics of age-0 splittail in California's Yolo Bypass. *Hydrobiologia* 573: 213–226.
- Gorski, K., Winter, H.G., Leeuw, D., Minin, A.E. & Nage-lkerke, L.A.J. 2010. Fish spawning in a large temperate floodplain: the role of flooding and temperature. *Freshwater Biology* 55: 1509–1519.
- Goulding, M. 1980. *The fishes and the forest – explorations in Amazonian natural history*. Berkeley: University of California Press.
- Halyk, L.C. & Balon, E.K. 1983. Structure and ecological production of the fish taxocene of a small floodplain system. *Canadian Journal of Zoology* 61: 2446–2464.
- Harrell, H.L. 1978. Responses of the Devils River (Texas) fish community to flooding. *Copeia* 1978: 60–68.
- Hein, T., Heiler, G., Pennetzdorfer, D., Riedler, P., Schagerl, M. & Schiemer, F. 1999. The Danube Restoration Project: functional aspects and planktonic productivity in the floodplain system. *Regulated Rivers: Research and Management* 15: 259–270.
- Henderson, P.A. & Hamilton, H.F. 1995. Standing crop and distribution of fish in drifting and attached floating meadow within an Upper Amazonian varzea lake. *Journal of Fish Biology* 47: 266–276.
- Hoggarth, D.D., Dam, R.K., Debnath, K. & Halls, A.S. 1999. Recruitment sources for fish stocks inside a floodplain river impoundment in Bangladesh. *Fisheries Management and Ecology* 6: 287–310.
- Irving, D.B. & Modde, T. 2000. Home-range fidelity and use of historic habitat by adult Colorado pikeminnow (*Ptychocheilus lucius*) in the White River, Colorado and Utah. *Western North American Naturalist* 60: 16–25.
- Kiernan, J.D. & Moyle, P.B. 2012. Flows, droughts, and aliens: factors affecting the fish assemblage in a Sierra Nevada California stream. *Ecological Applications* 22: 1146–1161.
- Kiernan, J.D., Moyle, P.B. & Crain, P.K. 2012. Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications* 22: 1472–1482.
- Kimmerer, W.J. 2002. Physical, biological and management responses to variable freshwater flow into the San Francisco Estuary. *Estuaries* 25: 1275–1290.
- King, A.J., Humphries, P. & Lake, P.S. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 773–786.
- Kohlhorst, D.W., Botsford, L.W., Brennan, J.S. & Caillet, G.M. 1991. Aspects of the structure and dynamics of an

- exploited central California population of white sturgeon (*Acipenser transmontanus*). In: Williott, P., ed. *Acipenser*. Bordeaux, France: Cemagref Publishers, pp. 277–293.
- Kurmayer, R., Keckeis, H., Schrutka, S. & Zweimuller, I. 1996. Macro- and microhabitats used by 0+ fish on a side-arm of the River Danube. *Archiv für Hydrobiologie* 113 (Suppl): 425–432.
- Kwak, T.J. 1988. Lateral movement and use of floodplain habitat by fishes of the Kankakee River Illinois. *American Midland Naturalist* 120: 241–249.
- Legendre, P. & Legendre, L. 2000. *Numerical ecology*. Developments in environmental modeling, 20, Amsterdam: Elsevier Science.
- Lucas, M.C. & Baras, E. 2001. *Migration of freshwater fishes*. Oxford: Blackwell Science.
- Modde, T., Muth, R.T. & Haines, G.B. 2001. Floodplain wetland suitability, access, and potential use by juvenile razorback suckers in the Middle Green River, Utah. *Transactions of the American Fisheries Society* 130: 1095–1105.
- Molls, F. 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. *Journal of Fish Biology* 55: 1187–1200.
- Moyle, P.B. 2002. *Inland fishes of California*. Berkeley: University of California Press.
- Moyle, P.B., Crain, P.K., Whitener, K. & Mount, J.F. 2003. Alien fishes in natural streams: fish distribution, assemblage structure, and conservation in the Cosumnes River, California, USA. *Environmental Biology of Fishes* 68: 143–162.
- Mueller-Solger, A.B., Jassby, A.D. & Mueller-Navarra, D.C. 2002. Nutritional quality for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta, USA). *Limnology and Oceanography* 47: 1468–1476.
- Opperman, J.J., Galloway, G.E., Fargione, J., Mount, J.F., Richter, B.D. & Secchi, S. 2009. Sustainable floodplains through large-scale reconnection to rivers. *Science* 326: 1487–1488.
- Parsley, M.J., Popoff, N.D., van der Leeuw, B.K. & Wright, C.D. 2008. Seasonal and diel movements of white sturgeon in the Lower Columbia River. *Transactions of the American Fisheries Society* 137: 1007–1017.
- Pikitch, E.K., Doukakis, P., Lauck, L., Chakrabarty, P. & Erickson, D.L. 2005. Status, trends and management of sturgeon and paddlefish fisheries. *Fish and Fisheries* 6: 233–265.
- Power, M.E., Parker, G., Dietrich, W.E. & Sun, A. 1995. How does floodplain width affect floodplain river ecology? A preliminary approach using simulations. *Geomorphology* 13: 310–317.
- Puckridge, J.T., Sheldon, F., Walker, K.F. & Boulton, A.J. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* 49: 55–72.
- Rodriguez, M.A. & Lewis, W.M. 1994. Regulation and stability of fish assemblages of neotropical floodplain lakes. *Oecologia* 99: 166–180.
- Ross, S.T. & Baker, J.A. 1983. The response of fishes to periodic spring floods in a southeastern stream. *American Midland Naturalist* 109: 1–14.
- Ru, H.-J. & Liu, X.-Q. 2013. River-lake migration of fishes in the Dongting Lake area of the Yangtze floodplain. *Journal of Applied Ichthyology* 29: 594–601.
- Scheerer, P.D. 2002. Implications of floodplain connectivity on the conservation of an endangered minnow, Oregon chub, in the Willametter River, Oregon. *Transactions of the American Fisheries Society* 131: 1070–1080.
- Schomaker, C. & Wolter, C. 2011. The contribution of long-term isolated water bodies to floodplain fish diversity. *Freshwater Biology* 56: 1469–1480.
- Service, R. 2007. Delta blues, California style. *Science* 317: 442–445.
- Sommer, T., Baxter, R. & Herbold, B. 1997. Resilience of splittail in the Sacramento-San Joaquin Estuary. *Transactions of the American Fisheries Society* 126: 961–976.
- Sommer, T., Nobriga, M.L., Harrell, W., Batham, W. & Kimmerer, W.J. 2001a. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 325–333.
- Sommer, T., Harrell, W., Nobriga, M., Brown, R., Moyle, P., Kimmerer, W. & Schemel, L. 2001b. California's Yolo Bypass: evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. *Fisheries* 26: 6–16.
- Sommer, T., Harrell, W., Mueller-Solger, A., Tom, B. & Kimmerer, W. 2004a. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14: 247–261.
- Sommer, T., Harrell, W., Kurth, R., Feyrer, F., Zeug, S.C. & O'Leary, G. 2004b. Ecological patterns of early life stages of fishes in a river-floodplain of the San Francisco Estuary. In: Feyrer, F., Brown, L.R., Brown, R.L. & Orsi, J.J., eds. *Early life history of fishes in the San Francisco Estuary and Watershed*. Symposium 39, Bethesda, Maryland: American Fisheries Society, pp. 111–123.
- Sommer, T., Mejia, F., Nobriga, M., Feyrer, F. & Grimaldo, L. 2011. The spawning migration of delta smelt in the upper San Francisco Estuary. *San Francisco Estuary and Watershed Science* 9:16.
- Tockner, K., Pusch, M., Borchardt, D. & Lorang, M.S. 2010. Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology* 55(Suppl. 1): 135–151.
- Tyus, H.T. & Karp, C.A. 1990. Spawning and movements of razorback sucker, *Xyrauchen texanus*, in the Green River Basin of Colorado and Utah. *Southwestern Naturalist* 35: 427–433.
- Villa, N.A. 1985. Life history of the Sacramento sucker, *Catostomus occidentalis*, in Thomes Creek, Tehama County, California. *California Fish and Game* 71: 88–106.
- Welcomme, R.L. 1979. *Fisheries ecology of floodplain rivers*. London, England: Longman Group Limited.
- Whipple, A.A., Grossinger, R.M., Rankin, D., Stanford, B. & Askevold, R.A. 2012. *Sacramento-San Joaquin Delta Historical Ecology Investigation: Exploring Pattern and Process*. Prepared for the California Department of Fish and Game Ecosystem Restoration Program. San Francisco Estuary Institute-Aquatic Science Center Publication 672, Richmond CA. Available at: http://www.sfei.org/sites/default/files/Delta_HistoricalEcologyStudy_SFEL_ASC_2012_highres.pdf
- Winemiller, K.O. & Jepsen, D.B. 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology* 53(Suppl. A): 267–296.
- Winemiller, K.O. & Kelso-Winemiller, L.C. 1994. Comparative ecology of the African pike, *Hepsetus odoe*, and tigerfish, *Hydrocynus forskahlii*, in the Zambezi River floodplain. *Journal of Fish Biology* 45: 211–225.