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RESEARCH ARTICLE

Dynamics of fish dispersal during river-floodplain connectivity and its implications for community assembly

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Abstract In river-floodplain ecosystems, overbank flows interact with floodplain geomorphology to generate a network of transient inter-waterbody connections. Heterogeneity in the characteristics of these connections may interact with species-specific dispersal capacity to affect the maintenance of diversity and community assembly on the floodplain. We modelled the immigration and emigration rates of nine species of fish entering and leaving a large floodplain lake during a hydrological connection with the parent river. Dispersal rates were modelled as a continuous function of time-since-connection over 3 months, with the aim of testing for species-specific patterns in (a) the timing and magnitudes of lateral dispersal, and (b) the balance between total immigration into, and emigration from, the lake. Significant interspecific variation in the timing and magnitude of lateral dispersal was evident. Magnitude of lateral dispersal was not a function of local abundance for all species. Further, the balance between immigration to, and emigration from, the lake varied significantly across species, and over time within species. The immigration–emigration balance of a species was not related to its magnitude of lateral dispersal, but may be related to its behavioural and life-history traits. Spatial heterogeneity in the duration of inter-waterbody connections may interact with species-specific dispersal functions to shape assembly of floodplain communities. Accordingly, habitat heterogeneity among floodplain waterbodies is not strictly necessary for heterogeneity in fish community composition. These dynamics have implications for the maintenance of diversity in river-floodplain fish metacommunities under both natural and managed connectivity regimes.

Keywords Flood-Pulse Concept · Metacommunity processes · Movement ecology · Temporal ecology · Transient connectivity

Introduction

The fish communities of river-floodplain ecosystems are complex metacommunities (Fernandes et al. 2013; Stoffels et al. 2015; Winemiller et al. 2010), where local communities are linked by transient connections (Zeigler and Fagan 2014). Between floods, the local communities of a river-floodplain segment ($\sim$10–100 longitudinal km; sensu Fausch et al. 2002) occupy discrete waterbodies including the channel itself and other lentic waterbodies on the floodplain (Amoros and Bornette 2002). Given sufficient time since the last flood, local communities may be shaped by interactions between species' niches and the local environment, including interactions with other species (Layman and Winemiller 2004; Rodríguez and Lewis 1994, 1997; Winemiller et al. 2000). During floods,

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hydrological connectivity among waterbodies facilitates dispersal of fishes, such that after a flood, the structure of a local community may reflect both the effects of local processes and effects of dispersal processes throughout the broader region (Fernandes et al. 2013; Stoffels et al. 2015).

To date, most research on river-floodplain fish metacommunities has come in the form of temporally-static studies, most of which focus on the influence of local factors. Such studies have improved our understanding of the role of local processes, but our understanding of the role played by dispersal during lateral hydrological connectivity (LHC) events is very poor (Stoffels et al. 2015). Indeed, metacommunity studies that focus on the estimation of the rates of critical metacommunity processes are rare (e.g. dispersal and predation rates; Logue et al. 2011). With respect to river-floodplain systems, species-specific dispersal traits of fishes may interact with connectivity traits of the waterbody network to generate complex spatial dynamics (DeAngelis et al. 2010; Trexler et al. 2005).

During an LHC event, a critical trait of the waterbody network is the distribution of connection durations among pairs of waterbodies. Consider what will happen as water level increases on a floodplain where waterbodies vary in the flood-height required to create a hydrological connection with other waterbodies of the network (Girard et al. 2010; van de Wolfshaar et al. 2011). Those waterbodies connected at lower flood-heights will be connected early in the flood, while higher waterbodies will be connected later. During the recession of the flood, waterbodies connected at higher flood-heights will be disconnected first, while the last waterbodies to be disconnected will be those connected at the lowest flood-heights. It follows that floodplain waterbodies will incur hydrological connections of varied durations during a flood (Girard et al. 2010).

Dispersal traits of the fishes include the timing of lateral movement during an LHC event (e.g., early vs. late) and the magnitude of dispersal (e.g., high vs. low rates). A simple thought experiment leads one to speculate that dispersal traits like ‘timing’ must interact with spatial heterogeneity in the duration of inter-waterbody LHC to shape metacommunty structure; species that disperse early in the flood-pulse are likely to colonise waterbodies experiencing very brief connections, while those species dispersing later may colonise fewer waterbodies, specifically those waterbodies connected to the rest of the river-floodplain network for longer. Species-specific dispersal traits have long been considered an important driver of community assembly in marine and terrestrial systems (Levin 1992; Tilman and Kareiva 1998), as well as freshwater invertebrate (Funk et al. 2013; McCauley 2006; Townsend 1989; Urban 2004) and amphibian communities (Resetarits et al. 2005), but are very poorly studied in river-floodplain fish communities (Crook 2004a, b; DeAngelis et al. 2010; Kerezsy et al. 2013; Layman et al. 2010). The influence of species-specific dispersal on metacommunity structure goes beyond mass-effects (Mouquet et al. 2005), as the order in which species colonise a waterbody may then shape the outcomes of local species interactions through priority effects (Alford and Wilbur 1985; Shulman et al. 1983).

Thus it is possible species-specific dispersal rates may interact with variation in LHC duration to shape spatial patterns—and perhaps the maintenance of diversity—in river-floodplain metacommunities, even in the absence of habitat heterogeneity among waterbodies. Unfortunately, our knowledge of fish lateral dispersal in river-floodplain ecosystems is extremely poor (King et al. 2003; Nunn et al. 2010; Stoffels et al. 2014). Multispecies studies are particularly rare. This paucity of knowledge is surprising, given the fundamental importance of lateral movements to fish populations under the Flood Pulse Concept (Junk et al. 1989), which has been a dominant theoretical construct for river-floodplain ecologists for more than 25 years. Fernandes (1997) showed that direction of fish lateral dispersal varies through time and may be linked to the phenology of life-histories (also see Osorio et al. 2011), while more recent studies have shown that the magnitudes of fish lateral movements vary as a function of LHC duration and may be linked to the hydrology of the flood pulse (Conallin et al. 2012; Gorski et al. 2014; Lyon et al. 2010; Ru and Liu 2013).

Here we determine the dispersal-rate functions of nine fishes (Online Resource 1) moving between a lowland river and a large floodplain lake. We sought answers to the following questions: (1) Does the timing of peak immigration and emigration differ among species? If the answer to this question is ‘yes’, then spatiotemporal variation in LHC duration will be sufficient to generate heterogeneity in community composition in the absence of habitat heterogeneity. (2) How do species-specific dispersal-rate functions translate into cumulative numbers of individuals that have entered or exited the lake, and how does net cumulative immigration (immigration–emigration) vary through time and among species?

Materials and methods

Study site

This investigation took place within the Euston Lakes, a regulated system of waterbodies on the Murray River floodplain, New South Wales, Australia. The Murray River is the parent river of two large floodplain lakes relevant to this investigation: Dry Lake and Washpen Lake. Washpen Lake—the focus of this work—is connected to Dry Lake via an unnamed connection channel—the channel sampled here—and, in turn, Dry Lake is connected to the Murray River via Taila Creek (Online Resource 2). Dry Lake must fill before water flows into Washpen Lake, and under most flow conditions both lakes may only receive water when the Taila Creek regulator is open. In 2007 the Euston Lakes were selected for temporary disconnection from the Murray River and drying, as part of a Federal water-saving initiative during a drought. Accordingly, the Taila Creek regulator was closed for 2 years, from Sep 2007 through to Dec 2009. Due to the conservation significance of its resident fauna, Washpen Lake was maintained as a drought refuge during this time by periodically pumping water from Taila Creek. In late Dec 2009 the regulator was opened and water flowed from Dry Lake, through the connection channel into Washpen Lake. The connection channel between Dry Lake and Washpen Lake was 15 m wide and 1 m deep at our sampling points during connection, and water levels and flows in this channel did not vary noticeably throughout this study. Discharge in the Murray River remained constant throughout this managed LHC event; any lateral fish movement could not have been cued by in-channel flow pulses (see Online Resource 2 and Stoffels et al. (2014) for further information about the site and its hydrology before, during and after this study).

Sampling

We wished to form a time series of species- and direction-specific dispersal rates following reconnection between Washpen Lake and the Murray River. To this end, we sampled the fish community weekly following reconnection, from 7 January to 25 March 2010, thus giving 12 discrete sampling events over 78 days (3 months), from which dispersal rates can be estimated. Only 11 sampling events took place, as a large storm precluded access to Washpen Lake during Week 9. Fishes were sampled using small and large directional fyke nets using a setup very similar to that of Lyon et al. (2010). During each sampling event two large fyke traps were set within the connection channel; one to intercept all large-bodied fish immigrating to Washpen Lake and the other to intercept all large-bodied fish emigrating from Washpen Lake. Large fykes were set approximately 100 m apart within the connection channel, and were double-wing (each 10 m × 1.2 m), coarse mesh (28 mm stretched-mesh) fykes. These large fyke nets blocked the entire channel in both directions and directed fish into the trap. A subset of the smaller individuals that passed through the coarse mesh was then intercepted with eight small (2 mm mesh) fykes; four set in each direction. These fykes had two wings (each 2.5 m × 1.2 m) that funnelled fish into a trap, and a plastic grid over the trap entry to keep large aquatic vertebrates out of the trap. When set, these fine-mesh fyke nets had an opening width of 2 m. These small nets were positioned randomly within the connection channel during each sampling event, in between the two large fykes. Nets were set for a total of approximately 24 h during each of the 11 sampling events. Soak-time was recorded for each net so that we could standardise catch by the number of fish moving in each direction per unit time.

Analysis

We obtained species- and direction-specific dispersal rates for each of the 11 sampling events by summing the dispersal rate estimates obtained from both small and large fykes. Dispersal rate estimates from large fykes were obtained by standardising the catch to units of number of individuals per day (24 h), as each net blocked the entire connection channel. However, each small fyke only intercepted fish moving through a 2 m section (perpendicular to shoreline) of the channel. Four fykes were set in each direction so in total our small fykes sampled an 8 m section of the channel for each direction, which was 53 % of the 15 m channel width. Actual capture rates from small fykes (individuals per day) were adjusted upward (multiplying by 15/8) to compensate for the small fykes' incomplete coverage of the channel width. Because we positioned our small fyke nets randomly within the channel, we assumed that our small fyke samples are representative of small-bodied fish movement through the entire channel, even though we only sampled a subset of that channel.

Smoothing splines were used to estimate the continuous immigration- and emigration-rate functions of species i, as a function of time since LHC ($\dot{I}_i(t)$ and $\dot{E}_i(t)$, respectively). Dispersal rate data are often noisy, and in such situations smoothing splines are a preferred method (MathWorks 2006). $\mathrm{I}_i(t)$ and $\mathrm{E}_i(t)$ were not extrapolated beyond the domain of data collected, and so the domain for t was [1, 77] for all analyses. Because spatial replication of this LHC event was not possible (as is often the case for large-scale perturbation studies (Carpenter 1990; Hargrove and Pickering 1992; Oksanen 2001)) we constructed confidence intervals (95 %) around the dispersal rate functions $\dot{I}_i(t)$ and $\dot{E}_i(t)$ using the jackknife procedure (Manly 2007). We considered the immigration and emigration rates of a species to differ when their 95 % CIs did not overlap. Likewise, interspecific differences in immigration or emigration rates occurred when the corresponding confidence intervals did not overlap.

Three other continuous functions were derived from the confidence intervals of $\dot{I}_i(t)$ and $\dot{E}_i(t)$: the cumulative number of individuals of species i immigrated to the lake at time t, or cumulative immigration ($I_i(t)$), cumulative emigration ($E_i(t)$) and net cumulative immigration (immigration–emigration; $N_i(t)$). Means and confidence intervals for each of these functions were obtained using Monte Carlo simulation (1000 replicates each, based on resampling daily movement data). Confidence intervals (95 %) around $I_i(t)$, $E_i(t)$, and $N_i(t)$ were then obtained by treating the vector of 1000 daily abundance estimates as a sample from which bootstrap confidence limits could be estimated (Manly 2007, p. 42). As was the case for $\dot{I}_i(t)$ and $\dot{E}_i(t)$, significant differences occurred when 95 % CIs did not overlap. These algorthims are explained in greater detail in Online Resource 3, which also contains MATLAB (R. 2014b) programs for jackknifing smoothing splines and Monte Carlo simulations.

Finally, we calculated the index $N(I+E)^{-1}$, the 'relative immigration–emigration balance' (I–E balance, hereafter), for each species after 77 days of connectivity. This statistic is bounded between -1 (strong net emigration) and 1 (strong net immigration), and the closer to 0 a species gets, the more its immigration has been balanced by emigration. We plotted $N(I+E)^{-1}$ against the total dispersal after 77 days ($I+E$), to visualise the relationship between the magnitude of dispersal and I–E balance. Confidence intervals (95 %) around I–E balance and total dispersal were obtained by bootstrapping.

Results

We found significant differences in the timing of both peak immigration and emigration rates among species (Fig. 1). *C. carpio*, for example, exhibited peak immigration and emigration during the first 7 days of LHC (Fig. 1a), while for *C. s. fulvus* peak immigration occurred during the final days of sampling (week 11; Fig. 1g), and peak emigration occurred at approximately 50 days since LHC (Fig. 1g).

Strong interspecific differences existed in the magnitudes of dispersal rates among species (Fig. 1). The confidence intervals for peak immigration rates of bony herring *N. erebi* (a large-bodied species) and *C. s. fulvus* (a small-bodied species) illustrate these points: between 1500 and 5600 individuals per day, and between 79 and 89 individuals per day, respectively (Fig. 1c, g).

Figure 2 presents relative dispersal rates for each species, and groups species according to the similarity of their relative $\dot{I}_i(t)$ and $\dot{E}_i(t)$ functions. Interestingly, while peak immigration and emigration rates occurred at very similar

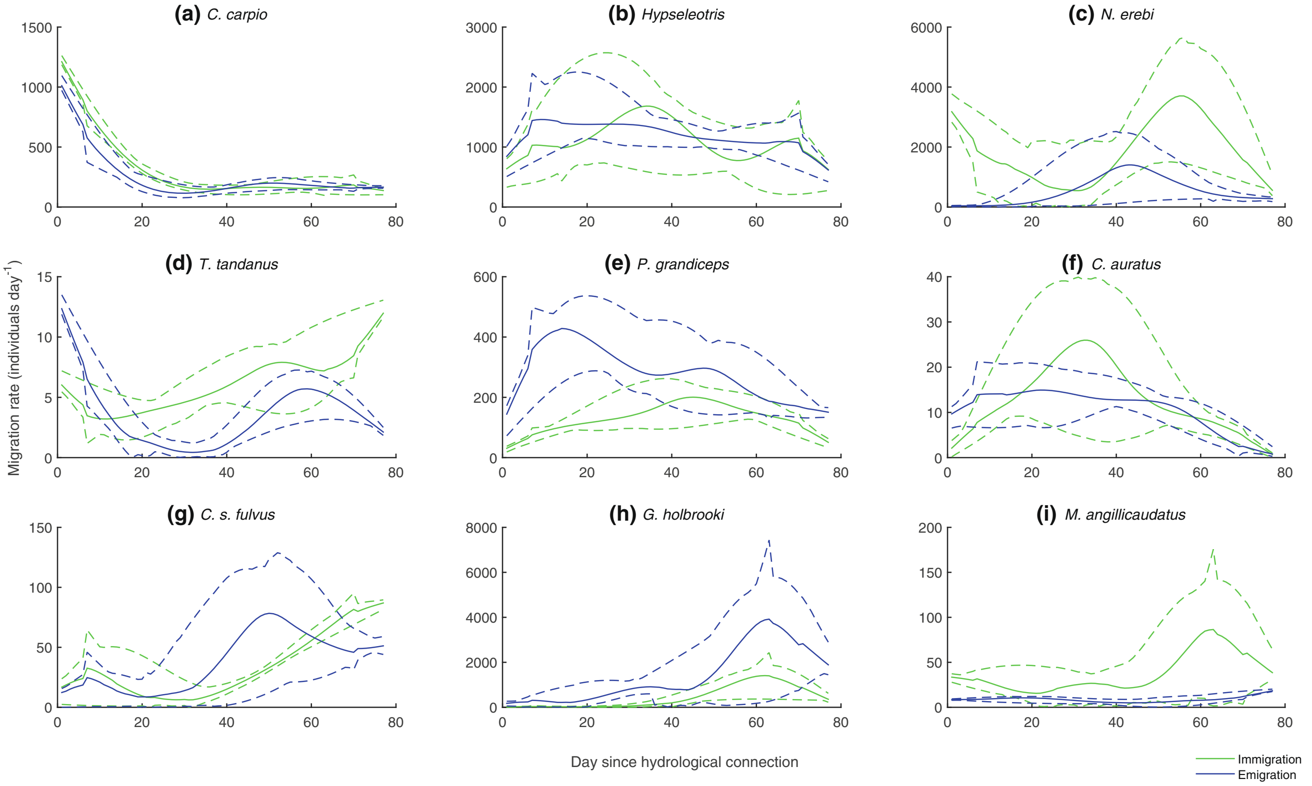
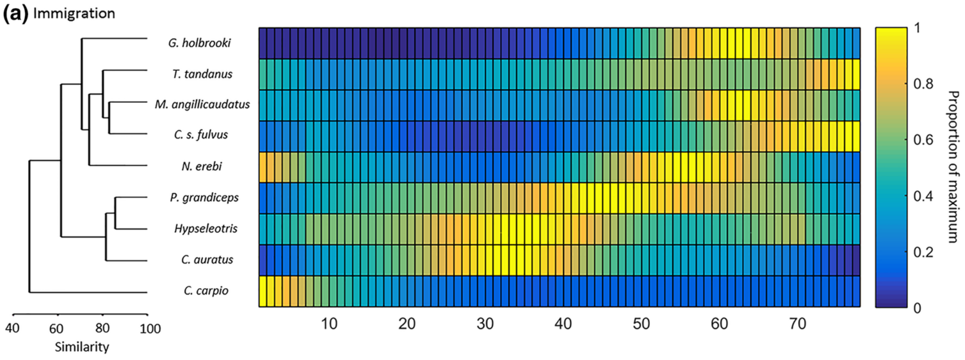


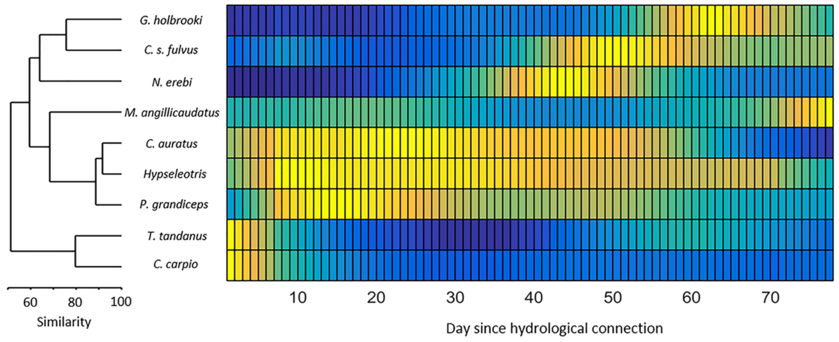
Fig. 1 Rates of immigration (*green*) and emigration (*blue*) from a floodplain lake as a function of time since hydrological connection for nine species of fish. *Solid lines* are mean dispersal rates and *dotted lines* are upper and lower 95 % confidence intervals (color figure online)

Fig. 2 *Colour matrices* showing relative lateral dispersal rates of nine species of fish over a 77-day hydrological connection between river and floodplain. Relative immigration (**a**) and emigration (**b**) rates are presented for each species. *Dendrograms on the left* group species according to the Bray–Curtis similarity of their relative dispersal-rate functions. Relative dispersal rate determined by dividing dispersal rates for each day by the maximum dispersal rate in the 77-day dataset for each species, each direction (immigration and emigration) (color figure online)

(a) Immigration



(b) Emigration



times for certain species (e.g., *C. carpio*), the timing of peak immigration and emigration was quite different for others (Fig. 2). For example, while freshwater catfish *T. tandanus* was grouped alongside *C. carpio* as a species emigrating early in the LHC event (Fig. 2b), with respect to immigration it was grouped with other species exhibiting delayed movement (Fig. 2a).

Differences among species in timing and magnitudes of immigration and emigration rates generated some particularly strong differences among species in the dynamics of the cumulative number of individuals entering or leaving Washpen Lake (Fig. 3). With respect to *T. tandanus* and *C. auratus*, for example, emigration exceeded immigration for the first 20 days (Fig. 3d, f), resulting in significant net emigration early in the LHC event (Fig. 4d, f). Thereafter, the balance between immigration and emigration shifted, such that both species exhibited a net gain in abundance after 20 days of connectivity (Figs. 3d, f; 4d, f). *C. s. fulvus* provides a similar example of how LHC duration affects the balance of gains and losses from a floodplain population. That is, after 20 days significant immigration of *C. s. fulvus* was observed, whereas between days 20 and 40 immigration was balanced by emigration. Thereafter, significant emigration occurred (Figs. 3g, 4g).

After 77 days of LHC, significant and strong interspecific variation in cumulative I–E balance was observed, but there was no obvious relationship between total dispersal and I–E balance (Fig. 5). Some species exhibited balanced dispersal (*Hypseleotris*, *C. carpio*, *C. s. fulvus*, and *C. auratus*) while others exhibited net immigration (*N. erebi*, *M. anguillicaudatus*, and to a lesser extent *T. tandanus*) or net emigration (mosquitofish *G. holbrooki, P. gandiceps*) (Fig. 5). I–E balance was not related to total dispersal magnitude (Fig. 5). For example, for each of *P. grandiceps*, *C. carpio*, *G. holbrooki*, *Hypseleotris* and *N. erebi*, between 3×10^4 and 20×10^4 individuals moved through the connection channel over 77 days, but these five species exhibited a great diversity of I–E balance (Fig. 5).

Discussion

Here we have shown that species-specific immigration and emigration dynamics may interact with the duration of a lateral hydrological connectivity event to affect assembly of local fish communities on floodplains. Perhaps the most striking implication of this result is that spatial habitat heterogeneity among waterbodies is not necessary for heterogeneity in fish community composition. Instead, heterogeneity in the duration of LHC among waterbodies may be sufficient to generate spatial heterogeneity in community assembly during overbank flows.

We found species-specific dispersal to have a very strong temporal component, and in other settings such temporal heterogeneity is a strong determinant of community assembly (McCauley 2006). To see this, consider a

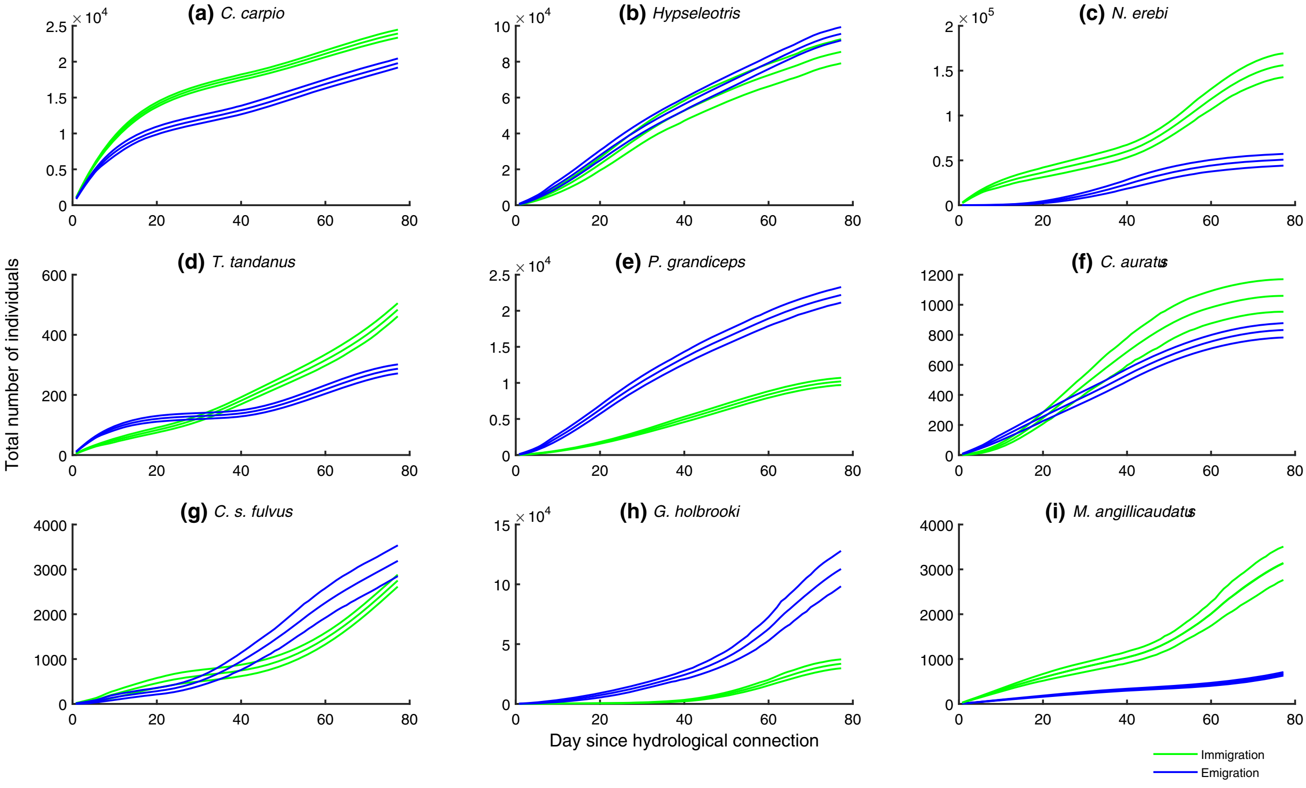


Fig. 3 Cumulative number of individuals that immigrated to (*green*), or emigrated from (*blue*), a large floodplain lake as a function of time since hydrological connection. Mean (±95 % CI) abundances are presented for nine species of fish (color figure online)

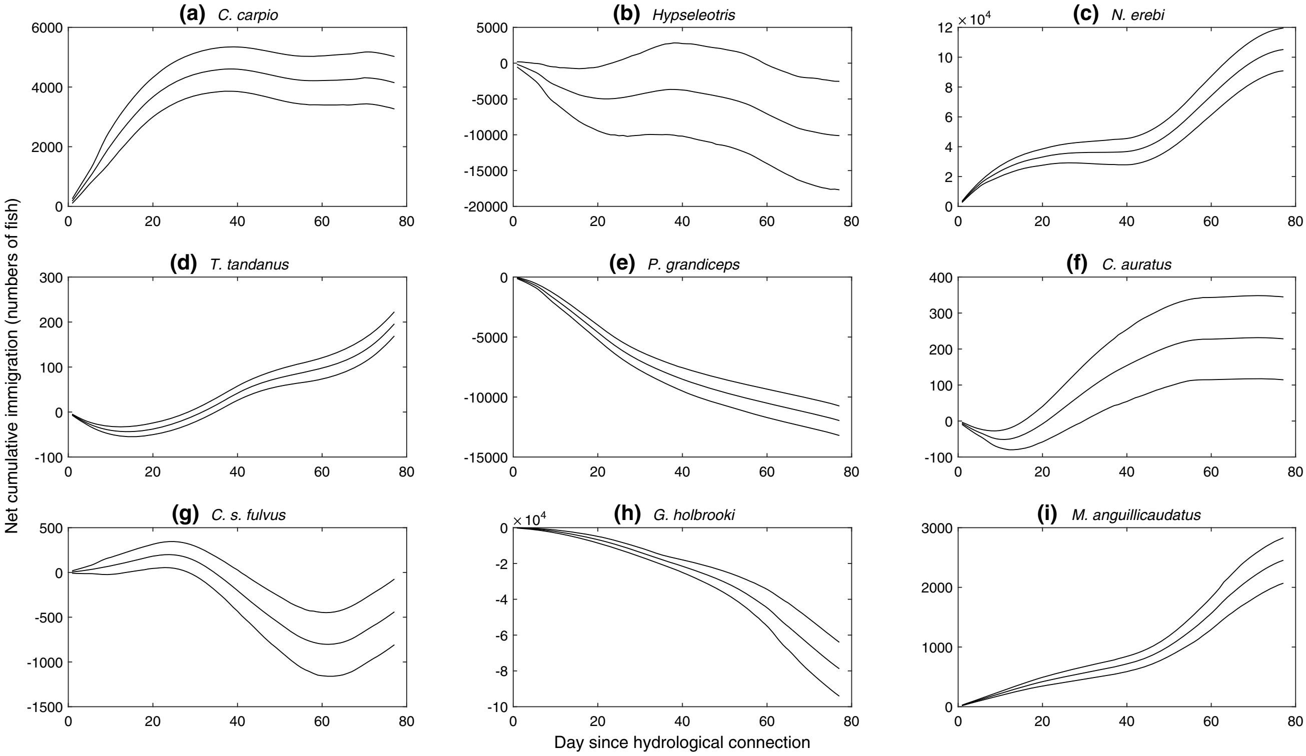


Fig. 4 Net cumulative immigration into a large floodplain lake as a function of duration of hydrological connectivity (net immigration = immigration − emigration). Mean (±95 % CI) net immigration *curves* are presented for nine fishes

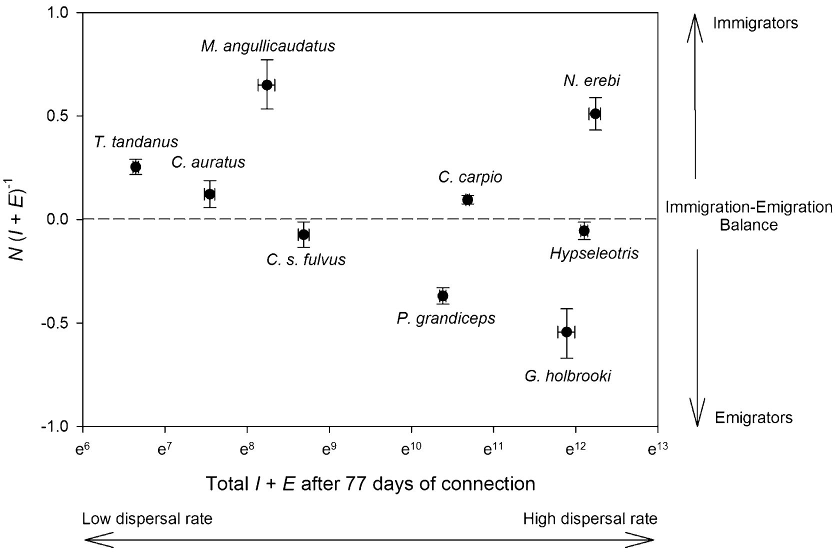


Fig. 5 Mean (±95 % CI) relative immigration–emigration balance as a function of mean (±95 % CI) total dispersal for nine species of fish moving between waterbodies during river-floodplain connectivity. Relative immigration–emigration balance is defined as $N(I + E)^{-1}$, where I and E are, respectively, cumulative immigration and emigration after 77 days of hydrological connectivity, and N is cumulative net immigration ($I - E$). The statistic $N(I + E)^{-1}$ is bounded on the interval (−1,1), and a value of *zero* indicates a balance between immigration and emigration. Total dispersal is simply the sum of cumulative immigration and emigration after 77 days of connectivity, and indicates the magnitude of lateral dispersal during river-floodplain connectivity

scenario in which we had a dry floodplain that experienced unidirectional immigration of fishes during an LHC event. Under this scenario our immigration functions suggest that, during an LHC event of less than 20 days, the community of a waterbody would be dominated by *C. carpio* and *N. erebi*, which both exhibit high immigration rates early in an LHC event. Extending the LHC by another 40 days would see *Hypseleotris* and *C. auratus* make a greater contribution to the community, while colonisation rates of species like *T. tandanus* and *C. s. fulvus* would be highest after 70 days of LHC (Fig. 2).

Of course, floodplain waterbodies are often not dry and individuals likely undertake bidirectional dispersal during an LHC event, so the dynamics of both immigration and emigration will affect the assembly of communities on floodplains. Indeed, certain species may exhibit high magnitudes of lateral dispersal during LHC, but make a relatively minor contribution to the assembly of a local community on a floodplain. *Cyprinus carpio* is a case in point; this species was quite rare in Washpen Lake prior to the managed LHC event studied here (Stoffels et al. 2014, 2015), so we can be confident that much of the emigration observed can be attributed to return movements of individuals that immigrated during an earlier phase of the one LHC event studied here. Despite the very high dispersal exhibited by this species, it exhibited strong I–E balance, implying most individuals that immigrated into Washpen Lake subsequently emigrated (Fig. 5). This observation accords with our knowledge of the species' life-history, whereby LHC is known to induce a strong spawning migration to floodplains, after which adults primarily return to the channel (Jones and Stuart 2009). At the other extreme, *T. tandanus* was the most numerous large-bodied fish in Washpen Lake prior to this LHC event (Stoffels et al. 2014, 2015), but exhibited very low dispersal during LHC, and net immigration after 77 days (Fig. 5). Again, this is concordant with our knowledge on the behaviour of this species, which is known to be reasonably sedentary. It follows that dispersal magnitudes between floodplain waterbodies are not necessarily a reflection of local abundance, and the influence of a species' dispersal on local communities will depend on its behavioural and life-history traits (a challenge noted in a more general context by Holt et al. 2005). This a significant point, as several models of animal movement through patchy landscapes assume emigration rate is positively related to local abundance (Gotelli and Taylor 1999; Schlosser and Angermeier 1995). Much more data on the factors affecting fish dispersal rate can be found from upland streams. Unfortunately, a relatively complicated picture emerges there, too, whereby fish dispersal rate appears to be a function of physiological (e.g., swimming capacity), behavioural (e.g., home range and territoriality) and life-history (e.g., spawning movements) traits (Albanese et al. 2009; Detenbeck et al. 1992; Dexter et al. 2014; Ensign et al. 1997; Petty and Grossman 2004; Sheldon and Meffe 1995).

Returning to river-floodplain systems, the underlying causes of interspecific variation in the timing of fish lateral movements is unknown. Certain researchers have suggested that rates of change in channel depth (rising or falling) or discharge might drive patterns in lateral movements (Castello 2008; Conallin et al. 2011; Fernandes 1997; Lyon et al. 2010; Nunn et al. 2010), but these studies tend to focus on the magnitudes of movement per se, rather than factors driving species-specific lateral movements. In our case, this managed LHC event did not coincide with any changes in discharge within the Murray River, or changes in depth of Washpen Lake (Stoffels et al. 2014). It follows that while variation in discharge and/or river height contributes greatly to the magnitude of lateral dispersal (Conallin et al. 2011; Stoffels et al. 2014), it is not necessary to drive species-specific timing in lateral dispersal. In an interesting study by Cucherousset et al. (2007), interspecific differences in physiological tolerance drove species-specific patterns of emigration from a floodplain waterbody with declining water quality. Harsh water quality in either the river or lake was not a factor here (Stoffels, unpublished data), but one wonders whether interspecific differences in sensory physiology might affect timing of lateral movements. Did *C. carpio*, for example, move onto the floodplain early because it can detect floodplain-derived cues earlier than other species? Such questions are not just of fundamental interest, as their answers affect how LHC is managed (Stoffels et al. 2014). We cannot, however, answer such questions—or the broader question of what drives species-specific lateral dispersal—without a fundamental understanding of the physiological, behavioural and life-history bases for species-specific movement in river-floodplain networks (Fullerton et al. 2010).

Species-specific dispersal functions will affect community assembly on the floodplain during LHC, but what are the consequences to metacommunity dynamics following LHC events? Two questions are particularly pertinent: (1) After LHC ceases and waterbodies become isolated, how persistent are the compositions of local fish communities following particular patterns of community assembly? (2) How do species-specific dispersal functions affect coexistence in river-floodplain metacommunities?

At this stage in our understanding of river-floodplain metacommunities, the answer to the first question appears to depend on context. In tropical river-floodplain systems with a predictable, annual flood pulse, effects of dispersal pulses on metacommunity structure may be transient on a short timescale of weeks to months (Fernandes et al. 2013; Rodríguez and Lewis 1994). That is, shortly after the flood-induced pulse of immigrants, local environments quickly interact with species' niches to filter the composition of local communities (Rodríguez and Lewis 1994). In temperate systems with a less frequent flood pulse, dispersal pulses may affect the structure of floodplain communities for several years (Stoffels et al. 2015). Irrespective of the time-scales involved, interactions between species-specific dispersal functions and heterogeneity in LHC duration among waterbodies will determine the set of species on which local environments may act. If we are to improve our understanding of the relative roles of regional and local drivers of river-floodplain metacommunities, then we will need to integrate measurements of multi-species dispersal rates during LHC events with measurements of community dynamics within and among waterbodies between LHC events.

With respect to the second question, species-specific dispersal during LHC events may facilitate species coexistence—hence biodiversity maintenance—if species trade-off capacity to colonise a waterbody with their capacity to evade any negative impacts of interspecific interactions like predation and competition. The most familiar example is that of the competition–colonisation trade-off that underpins the patch dynamics perspective of metacommunity theory (Mouquet et al. 2005). In the context of river-floodplain metacommunities, fishes that are able to colonise a waterbody earlier than others may find refuge from competition or predation—and hence increase regional population size—if those competitors and/or predators disperse later during an LHC event and are excluded from some waterbodies by transient connectivity. In addition to LHC duration, other features of connectivity among waterbodies might generate dispersal limitation and facilitate species coexistence. Consider, for example, the interaction between channel depth and fish dispersal capacity. Shallow connecting channels may allow passage of small-bodied species, but exclude the passage of larger piscivores. It follows that a trade-off between body size—one aspect of dispersal capacity in these systems—and trophic level may interact with heterogeneity in connection depth to facilitate coexistence between predators and prey in these metacommunities. If we are to determine how LHC affects species coexistence in river-floodplain fish metacommunities, then further research needs to determine: (a) interspecific trade-offs between dispersal capacity and the capacity to increase population size in the presence of other species (i.e., competition and piscivory); (b) how LHC hydrology affects connectivity properties (e.g., duration and depth distributions) of the river-floodplain network (surprisingly little is known on this matter; Girard et al. 2010).

Species-specific dispersal-rate functions have relevance to the management of LHC in regulated river-floodplain systems. In many temperate river-floodplain systems of the world, restoring a natural LHC regime is becoming increasingly difficult, due to the shortage of water for the environment and restrictions on overbank flows. In such systems LHC duration—and other hydrological characteristics of LHC events—are heavily managed (Beesley et al. 2012; Bond et al. 2014; Galat et al. 1998; Minckley et al. 2003; Stoffels et al. 2014). Throughout Australia's Murray-Darling Basin, for example, managers look to scientists for advice on operation of the large regulators that control LHC. Our results show that the duration of managed LHC events might shape regional fish communities by controlling patterns of immigration to, and emigration from, the floodplain. For example, two species that immigrated very late during the LHC (*T. tandanus and C. s. fulvus*) are threatened endemic species (Online Resource 1). Does this mean that these species only disperse laterally during long-duration LHC events, and are they rare because long-duration LHC events are rare? Another interesting case is provided by *C. carpio*, an alien species of great concern to managers (Koehn 2004). It exhibited its highest immigration and emigration rates very early in the connection, so does this mean that an LHC regime composed of frequent short LHC events will benefit this alien species more than endemic species? Managing LHC events to benefit endemic fishes more than alien species is a great challenge to river-floodplain ecologists (Conallin et al. 2012; Minckley et al. 2003; Stoffels et al. 2014), but we do not yet have sufficient knowledge about the lateral dimension of population and community processes in river-floodplain systems to answer such questions. The existence of species-specific dispersal functions leads us to speculate that there is no such thing as an 'optimal' LHC duration (or perhaps more accurately, that any such optimality would be entirely system- and context-specific), and that heterogeneity in LHC durations may be most beneficial to fish diversity in river-floodplain systems.

A key limitation of this study is that we have no replication. Any research approach comes with trade-offs, and while most examinations of metacommunities trade-off an understanding of process dynamics for description of broad-scale patterns (Logue et al. 2011), here we have made the reverse trade-off. Accordingly, while we have demonstrated the existence of species-specific dispersal functions, the generality of such multi-species dispersal behaviour is unknown. Our study is not unique in this regard; studies of the effects of large-scale perturbations are often very difficult to replicate in a single study, necessitating repetition in different contexts before generality can be determined (Hargrove and Pickering 1992). Encouragingly, in a recent study of the lateral dispersal of *C. carpio* and *N. erebi* (two species studied here), the relative timing of lateral movements were the same as those reported here (Stoffels, unpublished data). Another major limitation of this study is that dispersal rates were only examined for 3 months. Dispersal rates of certain species peaked during the last week of sampling, and so future studies might benefit from extending the duration of sampling during LHC events.

Understanding fish dispersal in a multispecies context is one of the major challenges facing contemporary fish ecology (Fullerton et al. 2010). We suggest that research on fish communities of river-floodplain systems may benefit from being cast within the framework of metacommunity theory, wherein the goal is not merely to understand the roles of dispersal or local habitat in isolation of each other, but to understand how these processes—and others—come together to drive the dynamics and maintenance of diversity.

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Compliance with ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Fish sampling was carried out under La Trobe University Ethics Approval AEC07-22-MD-V2.

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