

## **Fish larvae and recruitment patterns in floodplain lagoons of the Australian Wet Tropics**

Paul C. Godfrey<sup>AB</sup>, Angela H. Arthington<sup>AF</sup>, Richard G. Pearson<sup>CD</sup>, Fazlul Karim<sup>E</sup> and Jim Wallace<sup>D</sup>

<sup>A</sup>Australian Rivers Institute, Griffith University, Nathan, Queensland 4111, Australia.

<sup>B</sup>NRA Environmental Consultants; Cairns, Queensland, Australia 4870

<sup>C</sup>College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia.

<sup>D</sup>Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER), James Cook University, Townsville, Queensland 4811, Australia.

<sup>E</sup>Land and Water, Commonwealth Scientific and Industrial Research Organisation, Black Mountain Laboratories, Canberra, ACT 2601, Australia.

<sup>F</sup>Corresponding author. Email: [a.arthington@griffith.edu.au](mailto:a.arthington@griffith.edu.au)

### **Running Head**

Fish larvae in tropical floodplain lagoons

## **Abstract**

Floodplain lagoons in the Queensland Wet Tropics bioregion, Australia, are important and threatened habitats for fish. As part of studies to assess their ecological condition and functions, we examined patterns of occurrence of fish larvae, juveniles and adults in 10 permanent lagoons on the Tully-Murray floodplain. Lagoons contained early life-history stages of 15 of the 21 native species present, including 11 species that complete their life cycle in fresh waters and 4 that require access to saline habitats for larval development. Lagoon connectivity to the rivers, distance from the coast and flood dynamics influenced temporal variation in fish abundance, population size-structures and recruitment patterns. This study and the literature show that wet, post-wet and dry season habitats are utilised by small opportunists (e.g., species of *Melanotaenia* and *Hypseleotris*), equilibrium species (*Glossamia aprion*) and larger periodic strategists (neosilurid catfishes). Movement between coastal, riverine and floodplain habitats is important for completion of diadromous life cycles. Maintenance of natural seasonal patterns of flow and connectivity, and active protection of permanent floodplain lagoons from riparian and land-use disturbance, will be essential if their roles in fish recruitment are to be sustained.

## **Additional keywords:**

hydrology, connectivity, fish life history, conservation, floodplain management

## Introduction

Tropical floodplain rivers and wetlands are among the most dynamic, heterogeneous and productive of all ecosystems on Earth (Junk *et al.* 1989; Bayley 1995; Power *et al.* 1995; Winemiller 2008) and their high biodiversity and valued ecosystem services (e.g., fish production) make them priority areas for protection under the Convention on Biodiversity (CBD 2011). Research over recent decades has led to significant advances in understanding spatial patterns of floodplain fish communities in relation to natural environmental drivers, especially hydrology, connectivity with main channels of rivers, water quality and biotic interactions (e.g., Junk *et al.* 1989; Winemiller 1996, 2004; Rodríguez and Lewis 1997; Tejerina-Garro *et al.* 1998; Zeug *et al.* 2005; Pains da Silva *et al.* 2010). The effects of floodplain land use and water management on fish spatial patterns have also been investigated (e.g., Bayley 1991, 1995; Agostinho *et al.* 2004, 2009; Tockner *et al.* 2010; Arthington *et al.* 2014; King *et al.* 2015). In contrast, investigations of early life stages of fish and life history strategies in floodplain river systems are scarce, particularly in the tropics (Bishop *et al.* 2001; Agostinho *et al.* 2004; Zeug and Winemiller 2007).

The critical role of hydrology in river-floodplain systems is well established. The flood-pulse concept (Junk *et al.* 1989) describes how annual floodplain inundation stimulates booms of primary and secondary production that are exploited by fish through processes of feeding, growth and recruitment (e.g., Sparks 1995; Agostinho *et al.* 2004; Winemiller, 1989, 2004). Flood dynamics exert a major influence on the life history of many tropical fish species, stimulating spawning and providing fish with access to floodplain environments, which may function as residence habitats, breeding sites and/or larval and juvenile nursery areas (Junk *et al.* 1989; Agostinho *et al.* 2004, 2009; Winemiller 2004, 2008; Welcomme *et al.* 2006). Fish life history strategies vary in tropical floodplain rivers (Zeug and Winemiller 2007). Some species migrate from main river channels to use temporary floodplain habitats for spawning and feeding, while others reside and recruit in a range of permanent and semi-permanent habitats including lakes, lagoons and anabranches (Welcomme *et al.* 2006). Understanding the role of floodplain habitats for breeding and as nursery areas for larval and juvenile fishes is critical to floodplain management and implementation of effective conservation policies.

In Australia, understanding of the influence of floods on fish recruitment has developed largely from research in dryland floodplain rivers of temperate and arid regions (Humphries

*et al.* 1999; Balcombe *et al.* 2007; King 2004; King *et al.* 2009), but there is growing interest in floodplain processes in tropical areas (Bishop *et al.* 2001; Blanchette *et al.*; 2014; King *et al.*, 2015; Jardine *et al.* 2015). Floodplain rivers in northern Australia are characterised by wet season floods that play an important role in regulating the dynamics of instream habitats and fish populations (Kennard 1995; Bishop *et al.* 2001; Pusey *et al.* 2009). Flooding typically increases the extent of aquatic habitat for fish and facilitates fish movement between river channels and floodplain waterbodies for activities including foraging, spawning and larval recruitment (Bishop *et al.* 2001, Pusey *et al.* 2009). In the Alligator Rivers Region in Australia's wet-dry tropics, most fish species spawn and recruit during the wet season which coincides with increases in habitat, food resources and connectivity among habitat patches, although small-bodied species (e.g., members of Melanotaeniidae and Atherinidae) also breed and recruit in the dry season in channels and floodplain waterbodies (Bishop *et al.* 2001).

To date, the ecology of early life-history stages of fishes has not been investigated in floodplain habitats of Australia's Wet Tropics where the flow regimes of rivers are predictable with respect to annual yield and timing of monthly flow (Pusey *et al.* 2004, 2008; Kennard *et al.* 2010) and where there is regular connectivity between elements of the freshwater landscape via channels and overland flows (Karim *et al.* 2012, 2014; Pearson *et al.* 2013).

Representing only 0.26% of Australia's land area, the Queensland Wet Tropics bioregion (QWT) supports an exceptionally rich fauna, including over 40% of Australia's freshwater fish species (Pusey *et al.* 2008; Unmack 2013). Most species are restricted to lowland areas (Rayner *et al.* 2008) where high-order rivers and associated floodplain wetlands are afforded little protection by terrestrial reserves, which are focused mainly on upland areas in the Wet Tropics World Heritage Area (Januchowski-Hartley *et al.* 2011). We investigated fish assemblages of floodplain wetlands of the Tully and Murray rivers, located approximately centrally in the QWT, with particular focus on permanent lagoonal habitats, which are the scarcest type of wetlands in the region (QDERM 2012).

Floodplain lagoons contribute to the high biodiversity of the QWT (Pusey *et al.* 2008; Pearson *et al.* 2013) and provide important habitat for fish species in the Tully-Murray system (Pusey and Kennard 1996; Vallance and Hogan 2004; Veitch and Sawynok 2005).

The ecological condition and fish assemblages of these wetlands in relation to riverscape, habitat and water quality variables have been described elsewhere (Pearson *et al.* 2013; Arthington *et al.* 2014). The present study extends those investigations by focusing on the life history stages of fish collected from the lagoons in relation to temporal variation in habitat and hydrological conditions. We aimed to: (i) determine which fish species use the lagoons as larvae and early juveniles, (ii) describe temporal patterns of abundance and population size-structure of selected species, (iii) compare these patterns with those in systems with contrasting flow regimes, and (iv) consider the role of permanent floodplain lagoons in the life history strategies of Wet Tropics fishes.

We sampled during the immediate post-wet and dry seasons as past studies have documented fish breeding and recruitment in Australian tropical rivers at these times (Beumer 1979, Orr and Milward 1984, Kennard 1995, Bishop *et al.* 2001, Pusey *et al.* 2002, 2004, Godfrey 2011). Patterns of presence and abundance of larvae and early-juveniles were interpreted in terms of likely recruitment events. We used published information and personal data from related studies to identify larvae, juveniles and mature individuals and to estimate the age of captured fish to help identify recruitment events. On the basis of field observations and previous studies (e.g., Pusey *et al.* 2002; Arthington *et al.* 2014), we expected that: (i) there would be species-specific changes in abundance and population size structure over time related to each species' life-history strategy; and (ii) factors including connectedness of lagoons, position in the landscape (e.g., proximity to waterways and the coast) and hydrology (frequency and extent of flood inundation) would influence fish recruitment patterns. We review the role of floodplain lagoons as nursery areas for larval and juvenile fishes, and discuss the implications of our findings for floodplain management and conservation of fish diversity in the QWT.

## **Materials and methods**

### *Study area*

The Tully-Murray catchment is located in the centre of the QWT (Fig. 1). The topography of the catchment varies from steep rainforest-covered mountains, to a low-relief floodplain which is heavily developed for agriculture, with some remnant forest near the coast (Armour *et al.* 2009; Pearson *et al.* 2015). Floodplain wetlands in the QWT have been substantially depleted by agricultural development (Johnson *et al.* 1999; EPA 1999), with ~46% of the remaining wetlands being located on the Tully-Murray floodplain (Johnson *et al.* 1999). The

combined Tully-Murray floodplain supports an extensive network of permanent and ephemeral palustrine wetlands. Typically these wetlands are deep, elongated water bodies in current or past drainage channels. The main natural wetlands (“lagoons”) are complemented by a network of smaller natural and artificial water bodies, some of the latter developed on farms as sediment and nutrient sinks, and flood detention basins (Veitch and Sawynok, 2005). They are probably unique as they occur in the wettest part of Australia and are permanently or regularly connected by flood waters and channel flows (Karim *et al.* 2012; 2014; Pearson *et al.* 2013). The Tully and Murray rivers are the two main gauged waterways in this area, both discharging into the Great Barrier Reef lagoon. Most floodplain lagoons connect to either the Tully River or the Murray River via a network of natural streams and drains (Veitch and Sawynok 2005; Karim *et al.* 2014).

The climate of the region is tropical, with average monthly maximum air temperature ranging from 24.9°C in July to 31.5°C in December, and annual rainfall between about 2000 and 4000 mm, with ~80% occurring during the wet season (December to May). Over-bank flooding normally occurs only in the wet season, with peak flows typically occurring in January, linking the two rivers and inundating the intervening Tully-Murray floodplain (Wallace *et al.* 2009; Pearson *et al.* 2013). Floodwaters eventually drain back to the main river channels or to the coast via distributary channels. After floods, lagoons are sustained by inflows from small catchments and groundwater (McJannet *et al.* 2012a, 2012b). Flows in the stream and drainage network decline during the dry season, when some of the lagoons become disconnected from the river channels (Karim *et al.* 2014).

The hydrographs during the study period (May 2008 – May 2009) were representative of the long-term flow regime of the Tully and Murray rivers, with elevated flows occurring from late December 2007 to mid-April 2008 and from late December 2008 to mid-May 2009 (Fig. 2). Multiple overbank floods occurred between December 2007 and March 2008, and between January and April 2009, with the floods during the 2008/2009 wet season of larger magnitude and longer duration (15 days) than those in the 2007/2008 wet season (12 days) (Fig. 2). The biophysical characteristics of the lagoons varied over the period of study. In a companion study, Pearson *et al.* (2013) showed that lagoons differed significantly, with about 75% of the variance in environmental data explained by six axes of a PCA relating to size (0.6-18.7 ha), depth (1.5-5.7 m), and distance to river mouth (17.3-43.4 km). There was

pronounced spatio-temporal variation in environmental variables with a strong seasonal signal for water quality variables including temperature, conductivity and pH. Water temperature followed the austral pattern with maxima occurring in November 2008 (median: 32.4°C) and minima in July 2008 (median: 22.6°C). Conductivity and pH were highest in November 2008 (conductivity: 85  $\mu\text{s}/\text{cm}$ ; pH: 6.7) and lowest in May 2009 (conductivity: 47  $\mu\text{s}/\text{cm}$ ; pH: 5.7), reflecting the seasonal patterns of rainfall and catchment run-off (Pearson *et al.* 2013). Similar seasonal patterns were recorded in the nearby Mulgrave River (Rayner *et al.* 2008).

### *Sampling design*

Fish were sampled in 10 lagoons that provided a range of conditions of basin morphology, position in the landscape (proximity to the coast, distance of wetlands from river channels), frequency and extent of inundation during floods and connectivity to the Tully and Murray rivers (Fig. 1). All lagoons were sampled in May and September 2008 and May 2009 to capture the response of fish to seasonal biophysical changes. The May samples represented the immediate post-wet season, characterised by receding inflows/outflow, and the September sample represented stable dry-season conditions and reduced wetland connectivity (Fig. 2). Five of the lagoons were also sampled in July 2008 (early dry season) and four in November 2008 (late dry season) to enhance understanding of the temporal patterns of larval/juvenile fishes (Table 1). The subset of lagoons sampled in July and November was selected for their representativeness of the full set of study lagoon in terms of morphology, within-lagoon habitats, distance from Tully/Murray River and hydrologic connectivity with the stream/drain network (Pearson *et al.* 2013; Arthington *et al.* 2014). Time constraints did not permit sampling of all 10 lagoons in July and November.

Fish were sampled using a combination of fyke netting and electrofishing in marginal areas of each lagoon (Table 1); these methods are effective in sampling the early life-history stages of fishes in the region (Orr and Milward 1984; Kennard 1995; Pusey *et al.* 2004; Godfrey 2011). Fyke nets had 5 supporting hoops (0.5 m diameter) and two wings, each 2 m long x 1.5 m deep, and a stretched mesh size of 2 mm (Arthington *et al.* 2014). Pairs of fyke nets were set back-to-back around each lagoon in water up to 2 m deep, with the cod end held above the surface to prevent air-breathing vertebrates (e.g., turtles) from drowning. Each pair was set no closer than 50 m to the next pair. Pairs of nets were also set at the one or two locations where the lagoon connected to the channel network. The nets were set at midday

and retrieved after 24 hours. Catch per unit effort (CPUE) on each sampling date represented the abundance of each species collected per net per 24 hours.

A back-pack electrofisher (Smith-Root model 7) was used to collect fishes from aquatic macrophytes and leaf litter, with locations selected to include the range of vegetation types present (Arthington *et al.* 2014). Sampling involved moving the activated anode through the selected habitat covering all available depths and microhabitats and was followed by a dip net (50 cm gape, square bottom, mesh size of 250  $\mu\text{m}$ ) to collect the fish stunned (after King and Crook 2002) over 10 x 30-s (power-on time) electrofishing periods in each habitat type (Arthington *et al.* 2014). The electrofisher was operated from an aluminium dinghy to avoid encounters with estuarine crocodiles. The number of electrofishing periods performed and habitats sampled was used for calculation of CPUE, representing the average abundance of species over the  $n$  number of 30-s electrofishing periods in each lagoon (Table 1).

Captured fish were identified, measured (standard length, SL, in mm) and counted before being released alive at the point of capture, except for exotic species, which were euthanized in accordance with permits issued under the Queensland Fisheries Act 1994, and a subset of larvae, which were preserved in formalin for subsequent identification in the laboratory using published and unpublished descriptions (Ivanstovff *et al.* 1988; Neira *et al.* 1998; Dotsu *et al.* 2000; Humphrey *et al.* 2003; Close *et al.* 2005; Godfrey 2011). Specimens were categorized as pre-flexion larvae (no curvature at tip of notochord), flexion larvae (upward flexion at tip of notochord), post-flexion larvae (notochord flexion complete, caudal fin rays developing), metalarvae (caudal fin rays developed and pelvic fin forming), juveniles or adults (full complement and position of adult characters, including scales, fin rays and spines) (Leis and Trnski 1989; Serafini and Humphries 2004). For PERMANOVA, pre-flexion and flexion groups were combined as “early-stage larvae”, with post-flexion larvae referred to as “late-stage larvae”. Published age and growth data for the collected species or similar species (Supplementary Table 1) and our collective experience of the fish species were used to categorise 0.5-5 or >6 month old recruits depending on the species and its age at capture in the study lagoons (Table 2). Juveniles and adults were separated for species for which information on length at sexual maturity was available (Pusey *et al.* 2004). Medium and larger bodied species (e.g., eels) were separated into length classes in the absence of information on length at sexual maturity (Table 2).

### *Data analysis*

The eight most commonly captured species, plus *Lates calcarifer* (a species of commercial/recreational importance) and *Denariusa bandata* (a species of regional conservation significance) were selected for analysis. Combined catches were used in the analyses following adjustments for number of fyke nets and electrofishing periods used and habitats available in each lagoon. Larval and juvenile CPUE data and length-frequency distributions for the selected species were compared across five sampling times, using data pooled across Barrett's, Kyambul, Selby's and Digman's lagoons for each sampling occasion (Table 1). CPUE and length-frequency distributions for *H. compressa*, a diadromous species that undertakes upstream juvenile migrations (Pusey *et al.* 2004; Godfrey 2011), were also compared across lagoons and times to document recruitment events in relation to connectivity.

Spatial and temporal variation in CPUE of individual species was examined using univariate permutational analysis of variance (PERMANOVA) in the Primer 6 package (Clarke and Gorley 2006; Anderson *et al.* 2008). Two analyses were performed on  $\log(x+1)$  transformed CPUE using Euclidean distances as the similarity measure: i) a one-way design comparing larval and juvenile CPUE of all individual species between times (fixed factor); and ii) a two-way design comparing juvenile *H. compressa* CPUE between sites (fixed factor) and times (fixed factor). PERMANOVA pairwise tests were performed where significant differences were detected. All tests were based on 4,999 permutations. Statistical analysis was not attempted for juvenile *Anguilla reinhardtii* and *Lates calcarifer* owing to the small sample numbers. Additionally, we constructed length-frequency histograms for each species and sampling occasion to visualise temporal shifts in modal size of small size-classes, indicating larval/juvenile recruitment and growth.

## **Results**

### *Fish assemblage composition*

Sampling yielded a total of 19,762 individuals from 22 fish species (21 native, 1 exotic), including six native species that require access to saline habitat for spawning and/or larval development and 15 that are exclusively freshwater species (Table 1). The entirely freshwater native species collected as larvae included nine species: *Nematalosa erebi*, *Craterocephalus stercusmuscarum*, *Melanotaenia splendida*, *Pseudomugil gertrudae*, *Ambassis agassizii*,

*Denarius bandata*, *Glossomia aprion*, *Hypseleotris* sp. 1 and *Mogurnda adspersa*. Juveniles of a further two exclusively freshwater species – *Neosilurus ater* and *N. hyrtlii* – were also recorded in floodplain lagoons. In only four cases (*Melanotaenia maccullochi*, *Ophisternon* cf. *gutturale*, *Hephaestus fuliginosus* and *Giurus margaritacea*) were exclusively freshwater species detected in the lagoons as adults but not as larvae. Four of the six diadromous species recorded in the lagoons were collected as early life-history stages: *Redigobius bikolanus*, *Anguilla reinhardtii* and *Lates calcarifer* were collected as juveniles while *Hypseleotris compressa* were recorded as post-flexion larvae and juveniles (Table 2).

The total catch included 527 larvae and 18,531 juvenile/adult individuals (Table 2). Two eleotrids – *Hypseleotris compressa* and *Hypseleotris* sp. 1 – dominated the early life-history collections, contributing 80% and 12% of the total number collected, respectively. Approximately 95% of the *H. compressa* collected were juveniles and 2% were post-flexion larvae, while 89% of the *Hypseleotris* sp. 1 recorded were juveniles and 10% were post-flexion larvae. *Craterocephalus stercusmuscarum*, *D. bandata* and *M. splendida* comprised between 1% and 3% of total CPUE, with larvae and juveniles contributing more than 70% of the total number of each species. The remaining species each contributed less than 1% of the total catch, with the early life-history stages comprising between 1% and 98% of the total abundance of each species: *A. reinhardtii* (4%), *N. erebi* (61%), *N. ater* (98%); *N. hyrtlii* (50%); *P. signifier* (1%), *A. agassizii* (49%), *G. aprion* (79%) and *M. adspersa* (93%).

#### *Abundance and population size structure*

Six exclusively freshwater species (*C. stercusmuscarum*, *M. splendida*, *D. bandata*, *G. aprion*, *M. adspersa* and *Hypseleotris* sp. 1) were recorded in the lagoons as larval, juvenile and adult forms (Table 2). Abundances of early-juvenile *M. adspersa* (<20 mm SL), *C. stercusmuscarum* (<18 mm SL), *M. splendida* (<18 mm SL) and larval *D. bandata* varied significantly between sampling occasions as indicated by PERMANOVA. Monthly pairwise comparisons for each species revealed that significant differences were between months within the same or different seasons (Table 3), with *M. adspersa* more abundant in May 2009 (immediate post-wet) compared with May, September (dry season) and November (dry season) 2008 (Fig. 3a); *C. stercusmuscarum* were less abundant in May 2008 compared with other months (Fig. 3b); *M. splendida* were less abundant in November 2008 compared with other months (Fig. 3c); and larval *D. bandata* were more abundant in November compared to

September and May 2009 (Fig. 3d). Temporal variation in abundances of larval and early-juvenile forms was also significant for *G. aprion* and *Hypseleotris* sp. 1 (Table 3). Monthly pairwise comparisons were significant between post-wet and dry-season months, with *G. aprion* more abundant in November 2008 compared to May 2008 and 2009, while *Hypseleotris* sp. 1 were more abundant in July, September and November 2008 compared to May 2008 and 2009 (Fig. 3e-f).

*Neosilurus ater* and *N. hyrtlui* were recorded in the lagoons only as juveniles and adults (Table 2, Figure 3g-h). Juvenile (<80 mm SL) abundances of *N. ater* varied significantly over time (Table 3), with more individuals captured in May 2008 and 2009 (Fig 3g). Seasonal patterns in juvenile abundance of *N. hyrtlui* appeared to mirror those of *N. ater*, although the differences were not significant (Table 3, Fig. 3h). The juveniles caught in May 2008 and 2009 were predominately of smaller length classes (*N. ater*: May 2008, 60-80 mm; May 2009, 60-80 mm; *N. hyrtlui*: May 2008, 40-60 mm; May 2009, 60-80 mm) (Fig. 3g-h). There was an increase in modal length class from May 2008 to November 2008 (*N. ater*: May, 60-80 mm; November, 120-140 mm SL; *N. hyrtlui*: May 2008, 40-60 mm SL; November, 100-120 mm (Fig. 3g-h)), representing a maturation period.

*Anguilla reinhardtii*, *L. calcarifer* and *H. compressa* recruited to the lagoons as young-of-the-year juveniles (Table 2), reflecting separation of saline larval environments and freshwater juvenile habitats. *Anguilla reinhardtii* of similar sizes (69-76 mm SL) were captured in May, July and November 2008 (Table 2, Fig. 3i), indicating colonisation over an extended period or multiple colonisation events. *Lates calcarifer* displayed seasonally influenced recruitment as indicated by the capture of individuals in the 100-150 mm length class in May 2008 (Fig. 3j). As we did not sample through the 2007/2008 wet season, it is unclear whether this pattern represents discrete post-wet season recruitment.

Abundances of juvenile (<20 mm SL) *H. compressa* varied significantly between sampling times although not consistently across lagoons (Table 4). Abundances varied between sampling times in 2008 in Barrett's, Selby's and Digman's lagoons, with higher numbers in September in Barrett's and Selby's lagoons, and in July in Digman's lagoon (Table 4, Fig. 4a-c). There was an increase in modal length of *H. compressa* from May to November 2008 in Barrett's, Kyambul, and Selby's lagoons (Fig 4a-c), and from July to November 2008 in Digman's lagoon (Fig. 4d), indicating growth of fish within these lagoons. Abundances

varied significantly between May 2008 and 2009 in Barrett's, Selby's and Digman's lagoons (Table 4), with more individuals caught in May 2009 in each lagoon. Modal size and size classes of *H. compressa* caught in May 2009 were smaller than in May 2008 in all four lagoons.

There were differences in size of the smallest juvenile *H. compressa* captured in each lagoon with the most downstream lagoon, Barrett's, containing smaller individuals (10-11 mm) than Selby's (12-13 mm), Digman's (12-13 mm) and Kyambul (14-15 mm) lagoons located upstream in the catchment (Fig. 4a-d). The larval form of *H. compressa* was only caught in Barrett's Lagoon (Fig. 4a-d).

## Discussion

### *Fish fauna of the lagoons*

This study has shown that freshwater lagoons on the Tully-Murray floodplain contribute to larval and juvenile fish nursery habitats in this Wet Tropics river system. The 15 native species collected as early life-history stage fishes in the lagoons represent a moderate proportion of the 38 native species recorded in the Tully and Murray rivers and wetlands (Hogan and Graham 1994; Pusey and Kennard 1996; Vallance and Hogan 2004; Veitch and Sawynok 2005; Arthington *et al.* 2014). Nine species (*A. agassizii*, *C. stercusmuscarum*, *D. bandata*, *G. aprion*, *Hypseleotris* sp. 1, *M. splendida*, *M. adspersa*, *N. erebi* and *P. gertrudae*) were collected as larvae, demonstrating the larval nursery function of these lagoons. This finding is important because some species (e.g., *P. gertrudae* and *D. bandata*) are of conservation significance in the QWT (Pusey *et al.* 2005), and others QWT (i.e., *Hypseleotris* sp. 1 and *Ambassis agassizii*) are uncommon towards the northern end of their geographical range in the QWT (Pusey *et al.* 2004). Floodplain wetlands in the QWT have been substantially depleted by agricultural development and remain poorly protected in terrestrial reserves and national parks (Johnson *et al.* 1999; Pearson *et al.* 2013; Arthington *et al.* 2014). Further loss or degradation would threaten the availability of important fish nursery habitats.

The Tully-Murray lagoons supported the early-juvenile stages of diadromous species such as *H. compressa*, *A. reinhardtii* and *L. calcarifer* (an iconic sport and table fish) and migratory species which move between elements of the freshwater landscape (e.g. *N. ater* and *N.*

*hyrtlui*). *Hypseleotris compressa*, *A. reinhardtii* and *L. calcarifer* migrate between coastal marine habitats and fresh water as part of their life cycle (Russell and Garrett 1985; Shiao *et al.* 2002; Pusey *et al.* 2004; Godfrey 2011). The presence of these fishes in the Tully-Murray lagoons illustrates connectivity along the continuum of habitats, as observed elsewhere in northern Australia (Kennard 1995; Bishop *et al.* 2001; Pusey and Kennard 2009; Pearson *et al.* 2013; Arthington *et al.* 2014).

#### *Temporal variability in fish abundance and recruitment*

Temporal variability in the presence and abundance of larval and juvenile fishes in the study lagoons was pronounced, with species-specific changes in presence and abundance over time. Larval or early-juvenile forms of opportunistic species (*C. stercusmuscarum*, *M. splendida*, *D. bandata* and *M. adspersa*) and the equilibrium species *G. aprion* (see Sternberg and Kennard 2014) were collected in post-wet and dry seasons, with abundances varying substantially over time for each species. Collections of early-juvenile cohorts of *C. stercusmuscarum*, *M. splendida*, *D. bandata* and *M. adspersa* in all sampling times suggests an aseasonal or protracted spawning period in the lagoons, which is consistent with observations for these species in other northern Australian rivers (Beumer 1979; Bishop *et al.* 2001; Pusey *et al.* 2004). Opportunistic species (i.e., small, early maturing, frequent spawning/reproductive intervals and low batch fecundity, Winemiller and Rose 1992) may be compelled to breed often because they are short-lived, and they typically spawn and recruit moderately under most conditions including, for example, in newly created or disturbed habitats (Winemiller 1996). Opportunism within the Tully-Murray fish assemblage may be viewed as an adaptation to temporal changes in microhabitat habitat conditions (e.g., litter accumulations, macrophyte cover), water levels in the lagoons and variable connectivity of freshwater habitats (Pearson *et al.* 2013; Arthington *et al.* 2014).

Larvae or early-juvenile *G. aprion* were captured in all sampling seasons with highest abundances in the late dry season, suggesting stronger dry-season recruitment. This pattern concurs with the recruitment schedule of *G. aprion* in other north Australian rivers (Kennard 1995, Bishop *et al.* 2001; Pusey *et al.* 2004; Godfrey 2011). Bishop *et al.* (2001) recorded reproductively active *G. aprion* and early juveniles throughout the year in the Alligator Rivers region, northern Australia, and suggested that the presence of still-water conditions was important for the transfer of eggs from the female to the buccal cavity of the male. The

late dry season of 2008 in the Tully-Murray corresponded with low stable river flows and lagoon water levels which presumably contributed to the strong recruitment at that time.

Larval and early-juvenile *Hypseleotris* sp. 1 were captured in the Tully-Murray lagoons on all sampling occasions, with abundances higher in July, September and November 2008, suggesting that there was elevated dry-season spawning activity and recruitment. The spawning stimulus for *Hypseleotris* sp. 1 is unknown but the reproductive period for this species in the Mary River in south-east Queensland corresponds with the dry season and the period of low and stable discharge and increasing temperature and photoperiod between July and September (late winter and early spring) (Pusey *et al.* 2004).

*Neosilurus ater* and *N. hyrtlui* exhibited seasonal variations in juvenile abundances, with peaks during the post-wet season (May 2008 and May 2009). Some key elements of the breeding biology of these catfishes, including spawning phenology and migration behaviour, have been studied in northern Australian rivers (Pusey *et al.* 2004). Orr and Milward (1984) reported spawning by *N. ater* and *N. hyrtlui* on rising water levels at the start of the wet season in the Ross River, to the south of the QWT. In the Tully-Murray system juveniles captured in May 2008 and 2009 were estimated to be 3-5 months old, which corresponded to periods of the 2007/2008 and 2008/2009 wet seasons when there were multiple overbank floods (Pearson *et al.* 2013). It is likely that spawning and larval development occurred during these periods, although wet season sampling would be required to confirm this. We did not record larvae of *N. ater* and *N. hyrtlui* in the study lagoons despite using electrofishing, which is a proven method for collecting them (Orr and Milward 1984). Spawning sites of both species in the Ross and upper Burdekin rivers, north-east Australia, include tributaries of the main channel (Pusey *et al.* 2004). Orr and Milward (1984) noted that spawning migration into tributaries during wet season flows is likely to provide an environment that reduces the risk of larval mortality from respiratory stress, predation, infection and disease and/or starvation. Sampling of lagoons and channels/drains on the Tully-Murray floodplain during March 2009 (mid wet-season) showed that the juvenile *N. ater* and *N. hyrtlui* caught in the channels/drains (range: 41-125 mm SL) were smaller than those from lagoons (range: 51-160 mm SL) (Godfrey, unpublished data), suggesting that channels/drains may serve as larval habitat for *N. ater* and *N. hyrtlui*. Early wet-season sampling may confirm this.

There was temporal variability in the presence and abundance of the 0+ juvenile forms of diadromous species – *A. reinhardtii*, *H. compressa* and *L. calcarifer* – captured in the study lagoons, with the results suggesting that colonisation by *A. reinhardtii* and *H. compressa* occurred in multiple events and/or over an extended period throughout the immediate post-wet and dry seasons. The limited data for *L. calcarifer* suggest that recruitment occurred in the wet season and/or immediate post-wet season. Recruitment information on *A. reinhardtii*, *L. calcarifer* and *H. compressa* is available for QWT rivers (Russell and Garrett 1985; Shiao *et al.* 2002; Pusey *et al.* 2002, 2004, Godfrey 2011). Upstream movement of *A. reinhardtii* eelers in QWT rivers occurs throughout the year but timing is variable (Godfrey 2011), perhaps as a result of variability in the timing of *A. reinhardtii* glass eel invasion into the tropical rivers of eastern Australia (Shiao *et al.* 2002). For *H. compressa*, the patterns of distribution and timing of occurrence of post-flexion larvae (>6.0 mm SL) and early-juveniles indicate that the migration of life stages between estuaries and fresh waters coincides with the decline in wet season discharge and dry-season base flow (Godfrey 2011). Meanwhile, advanced 0+ juveniles (~120 mm SL) of *L. calcarifer* move from supralittoral habitat of estuaries to permanent habitats at the end of the wet season (Russell and Garrett 1985). Our results are generally consistent with previous studies, although we found that these species colonised the study lagoons later in the calendar year (*L. calcarifer*) or were further developed (*A. reinhardtii* and *H. compressa*) because the lagoons were located further upstream of larval saline habitats.

There was substantial inter-annual variation in the abundances of juvenile *H. compressa*, with more juveniles collected in May 2009 than in May 2008, possibly because of the improved access for juveniles to the study lagoons caused by the longer durations of overbank flooding and connectivity in the Tully and Murray catchments during the 2008/2009 wet season (Karim *et al.* 2012; Pearson *et al.* 2013). The magnitude of wet-season flows also influences recruitment and year-class strength of *L. calcarifer* in northern Australia (Staunton-Smith *et al.* 2004; Stewart-Koster *et al.* 2011), probably because elevated flows enhance juvenile access to nursery areas (Staunton-Smith *et al.* 2004).

#### *Influence of connectivity, landscape position and hydrology on fish recruitment*

Connectivity of each lagoon to the stream network, wetland position in the landscape and flood dynamics were important influences on fish assemblages and recruitment patterns in QWT floodplain wetlands, as observed in other studies (Kennard 1995; Gomes and

Agostinho 1997; Arthington *et al.* 2014). The contrast in dry-season *H. compressa* recruitment patterns between Digman's Lagoon and other lagoons probably reflected accessibility for this species, which undertakes upstream juvenile migrations from the estuary (Pusey *et al.* 2004; Godfrey 2011). Access to lagoons over the dry season is a function of connectivity between the lagoons and the Tully and Murray rivers via natural and man-made channels (Karim *et al.* 2014; Arthington *et al.* 2014). The influence of channel connectivity was apparent in the present study with *H. compressa* recruiting to Selby's and Kyambul lagoons during the early, mid and late dry-season 2008. These lagoons maintain regular connection with the Murray River because of local catchment runoff and groundwater contributions to base flows in the natural stream network, and their close proximity to the river (Karim *et al.* 2014). In contrast, colonisation of Digman's Lagoon ceased by the mid dry-season 2008, probably because the constructed drain that connects the lagoon with the Murray River had ceased flowing (Pearson *et al.* 2010; Karim *et al.* 2014).

In the QWT, distance from the river mouth is important in determining the distribution, abundance and population size-structures of diadromous species that must migrate from saline larval habitats to freshwater juvenile habitat. As a consequence, locations closer to the estuary typically contain such species at a higher proportion of the total species richness and smaller juveniles compared to locations higher in the catchment (Pusey *et al.* 2002, 2004; Godfrey 2011; Arthington *et al.* 2014). This was reflected by the population size-structure of *H. compressa* in the Tully-Murray lagoons, with Barrett's Lagoon, which is closest to the coast, containing smaller juveniles than more upstream lagoons. Similar patterns in population size structures have been observed for other diadromous species in coastal rivers on Okinawa Island, Japan (Maeda and Tachihara 2005) and elsewhere (Keith 2003).

*Neosilurus ater* and *N. hyrtlui* showed consistent temporal patterns of elevated juvenile abundance in the post-wet season, probably reflecting the occurrence of flooding during the 2007/2008 and 2008/2009 wet season which stimulated spawning and juvenile recruitment. In floodplain systems, the degree of predictability of floods influences the development of morphological, behavioural, and physiological adaptations of aquatic organisms to flooding (Junk *et al.* 1989; Bayley 1991; Jardine *et al.* 2015). Seasonal spawning by fishes (i.e., the periodic strategy – Winemiller and Rose 1992) optimise fitness in environmentally predictable river systems (Junk *et al.* 1989; Winemiller 1996, 2004, 2008). The flow regime of the Tully and Murray rivers is highly predictable with respect to annual yield and timing of

monthly flow (Pusey *et al.* 2004, 2008), with overbank flows occurring virtually every year and typically only in the wet season (Pearson *et al.* 2013). This predictable pattern of flooding is likely to result in the offspring of seasonal spawners encountering favourable conditions for recruitment in most years.

### *Conservation and Management Implications*

One of the greatest threats to fish biodiversity for the QWT region is the loss of floodplain wetlands (Pusey *et al.* 2004, 2005). Between one half and two thirds of wetlands in the Johnstone, Moresby and Russell/Mulgrave River systems were destroyed between 1951 and 1992 (Russell and Hales 1993; Russell *et al.* 1996a, 1996b). The extent of damage is probably now much greater given that there was little abatement in the rate of land reclamation in the 1990s (Pusey *et al.* 2005). Such losses pose a particular threat to the survival of *Denarius bandata*, *Pseudomugil gertrudae* and *Melanotaenia maccullochi* because of their highly fragmented distributions and preference for lentic environments (Valance and Hogan 2004; Pusey *et al.* 2005; Veitch and Sawynok 2005; Arthington *et al.* 2014). The Tully-Murray floodplain wetlands play a particularly important role in the conservation of freshwater fish diversity in the QWT given that these lagoons constitute a high proportion of the remnant wetland remaining in the QWT (Pearson *et al.* 2013). QWT wetlands have been severely depleted as a result of altered hydrological conditions and land clearing (Arthington *et al.* 1997; Queensland Government 2003; Pusey *et al.* 2007), and loss to sea-level rise of around 30 m in the last 10 000 years (Hopley 1983). The remaining freshwater wetlands may be regarded as remnants that have survived past natural marine incursions and more recent human impacts (Pearson *et al.* 2013).

The ability of diadromous fish species to move between coastal, riverine and floodplain habitats in the Tully-Murray system is critical to completion of their life cycles. The regular overbank and channel connectivity in the Tully and Murray rivers and wetlands (Karim *et al.* 2012, 2014) probably contributes to the presence of migratory species in lagoon faunas and high similarity among lagoonal fish assemblages (Arthington *et al.* 2014).

Recruitment strategies of fishes in the Tully-Murray system involve adaptations to natural seasonal variations in flow and the availability and accessibility of suitable aquatic habitats. Seasonal patterns of flow generate wet, post-wet and dry season habitats utilised by opportunistic, equilibrium and periodic species (Winemiller and Rose 2002). Floodplain

lagoons are of particular importance as nursery habitat, providing suitable water quality, complex cover and abundant food resources (Pearson *et al.* 2013; Arthington *et al.* 2014). Maintenance of the natural seasonal patterns of flow and wetland connectivity in QWT rivers is critical to maintaining their present ecological integrity (Pearson *et al.* 2013) and sustaining freshwater fish diversity in this region (Pusey *et al.* 2005, 2008; Arthington *et al.* 2014).

Although the construction of further large dams seems unlikely, other factors such as weirs and water abstraction can influence flow volumes and seasonal patterns of importance to fish mobility and recruitment, especially if low flows become more critical under future climatic influences (e.g., King *et al.* 2015). Furthermore, the early life-history stages of fish are easily prevented from moving among habitats by seemingly insignificant barriers, including accumulations of aquatic vegetation or debris and the possible further introduction of small barriers, such as road crossings and culverts (Kapitzke 2007; Kroon and Phillips 2016).

Given that the floodplain wetlands present when Europeans first arrived in the Wet Tropics region were only a fraction of those that would have occurred on the extended floodplains at the height of the Pleistocene (Hopley 1983; Pearson *et al.* 2013), the more recent removal of wetlands and land-use development in catchments impose significant added pressure upon the few remaining floodplain waterbodies. There is clearly a need for active protection of these wetland remnants if their role as nursery habitats and importance for fish recruitment are to be sustained into the future.

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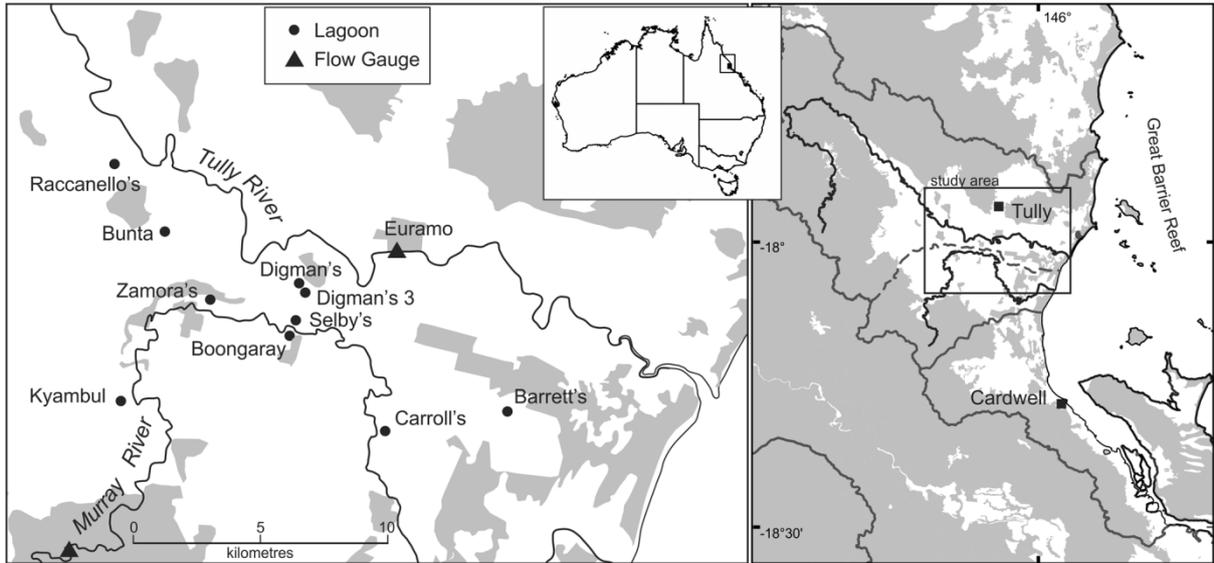
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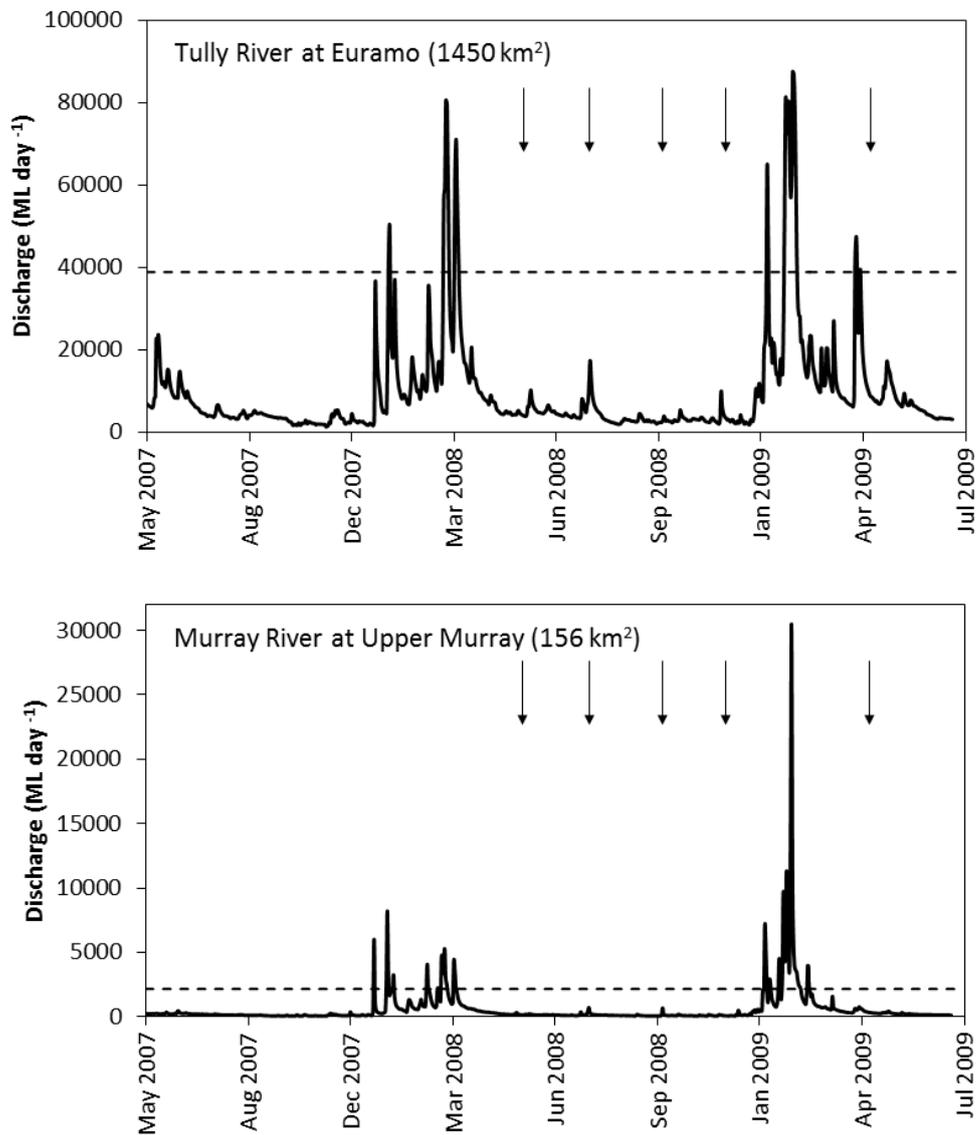
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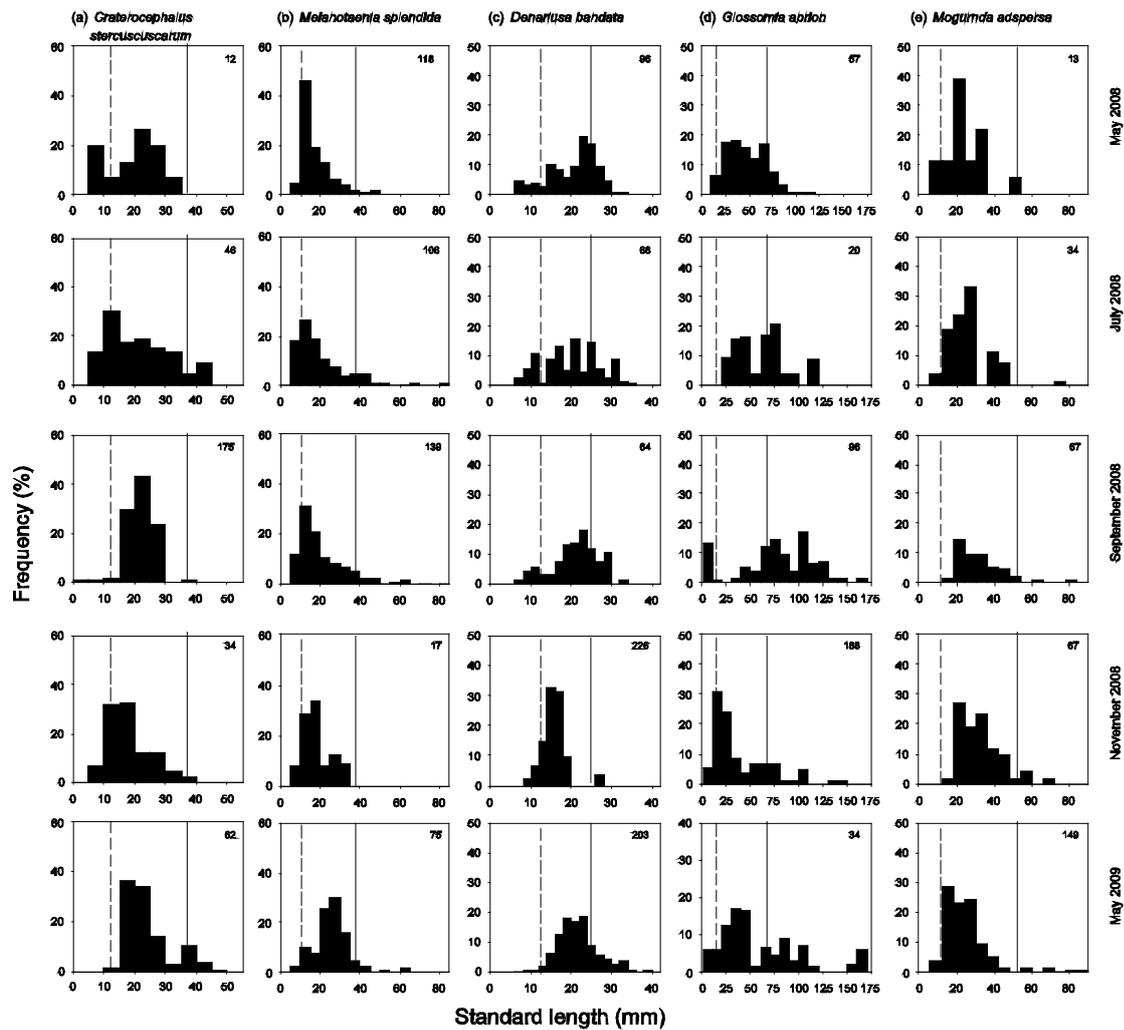
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**Figure 1.** Location of the Tully-Murray floodplain (centre and right panels), the 10 study lagoons (left panel) and the Euramo (Tully River) and Upper Murray River flow gauging stations (left panel). Black lines on right-hand map indicate the rivers; grey lines indicate catchment boundaries; dashed line shows boundary between Tully and Murray catchments. Shading represents forest. Figure adapted from Pearson *et al.* (2013).



**Figure 2.** Daily discharge at the Euramo (Tully River) and Upper Murray flow gauges (see Fig.1) prior to and during this study. Values in parentheses indicate the catchment area upstream of each gauge. Sampling occasions (arrows) and flood thresholds (dashed lines) are indicated. Data provided by the Queensland Department of Environment and Resource Management.



**Figure 3.** Length frequency histograms (mm standard length) for selected species from four Tully-Murray lagoons (Barrett's, Kyambul, Selby's and Digman's) during May, July, September and November 2008, and May 2009. Vertical lines on each plot indicate estimates of minimum length at metamorphosis (dash) and length at maturity (solid). Unadjusted abundance for each species on each sampling event is shown in the top right corner of each plot.

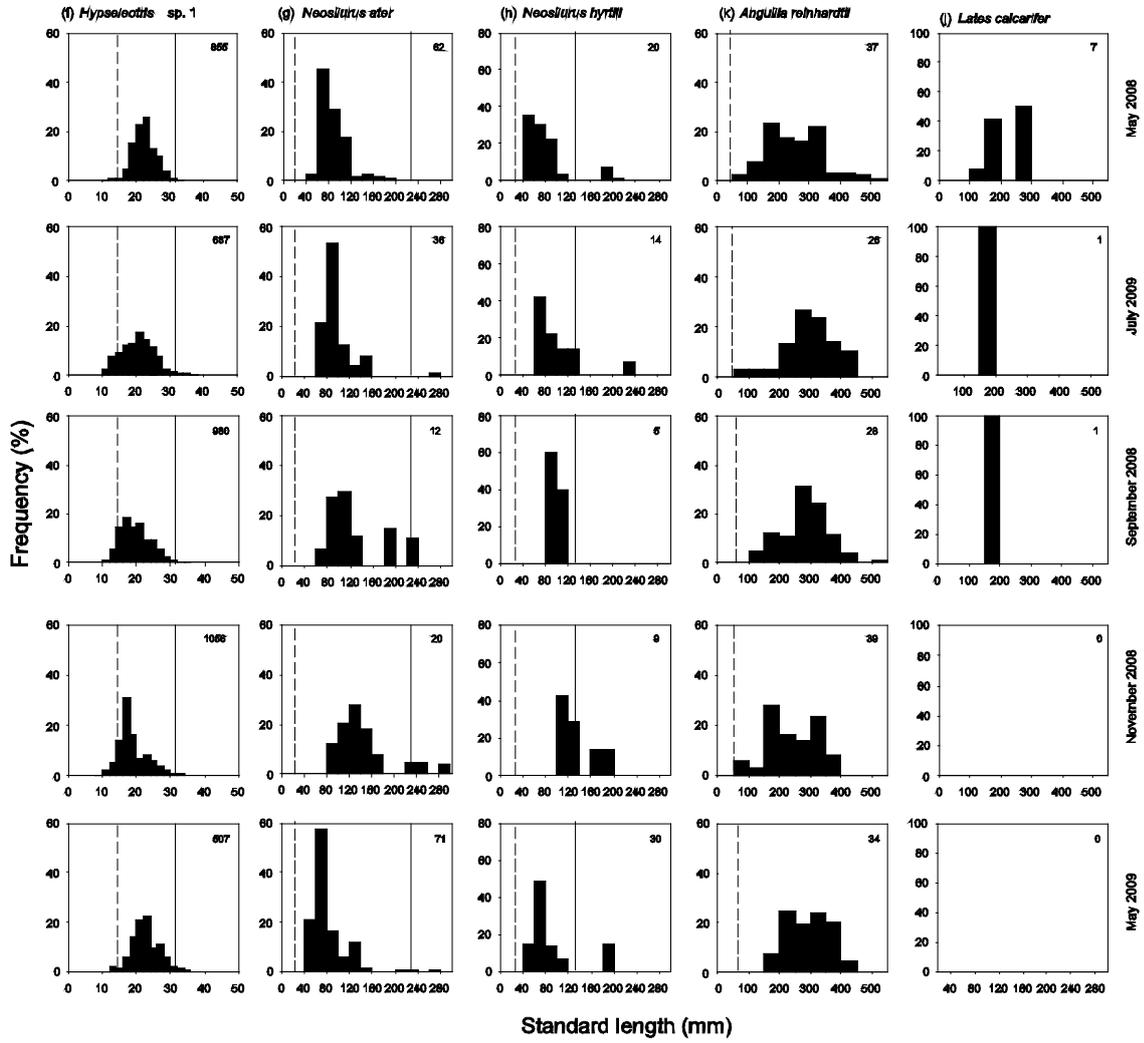
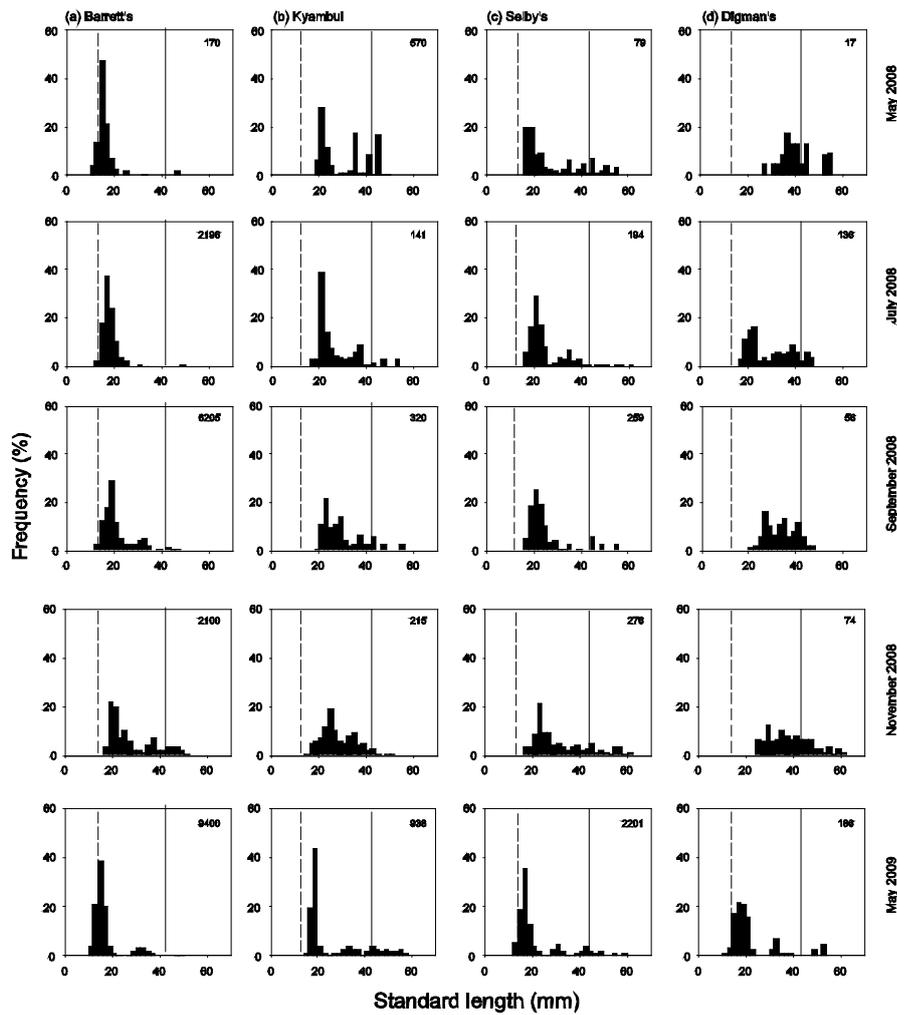


Figure 3. (cont'd)



**Figure 4.** Length frequency histograms (mm standard length) for *Hypseleotris compressa* from Barrett's, Kyambul, Selby's and Digman's lagoons during May, July, September and November 2008, and May 2009. Vertical lines on each plot indicate estimates of minimum length at metamorphosis (dash) and length at maturity (solid). Unadjusted abundance for each species on each sampling event is shown in the top right corner of each plot.

**Table 1.** Number of fyke net (Fy) and electrofishing (El) replicates per lagoon and sampling occasion. - = not sampled.

Survey	May 2008		July 2008		September 2008		November 2008		May 2009	
Sampling date	7-17 May		29 Jul-2 Aug		23 Sep-2 Oct		25-29 Nov		14-25 May	
Lagoon	El	Fy	El	Fy	El	Fy	El	Fy	El	Fy
Barrett's	30	4	20	6	20	8	30	8	20	8
Kyambul	30	8	20	5	25	8	30	8	20	8
Selby's	30	8	30	6	30	8	30	8	30	8
Digman's 1	30	8	30	6	30	8	30	8	30	8
Zamora's	20	7	20	6	20	8	-	-	20	8
Bunta	30	8	-	-	30	8	-	-	30	8
Raccanello's	30	8	-	-	30	8	-	-	30	8
Carroll's	20	8	-	-	20	8	-	-	20	8
Digman's 2	20	8	-	-	20	8	-	-	20	8
Boongaray	20	8	-	-	20	8	-	-	20	8
Total	260	75	120	29	245	80	120	32	240	80

**Table 2.** Standardized catch per unit effort (combined fyke net and electrofishing catches) of each species in lagoons of the Tully-Murray floodplain, sampled on five occasions between May 2008 and May 2009. Number of lagoons sampled on each occasion is shown in parentheses below the sampling date. Stage = developmental stage, PF= pre-flexion larvae; F = flexion larvae; POF/T = post-flexion/transitional larvae; Juv = Juvenile. Habitats are estuarine/marine (E/M) and freshwater (FW) (Pusey *et al.* 2004, Godfrey 2011).

Family Species	Stage/ size class (mm standard length)	Larva l habit at	Standard length (mm)	May 2008 (10)	July 2008 (5)	Septembe r 2008 (10)	Novemb er 2008 (4)	May 2009 (10)
<b>Anguillidae</b>								
<i>Anguilla reinhardtii</i> Steindachner, 1867	<100	E/M	69-76	0.07	3.30	-	0.03	-
	100-300		111-300	5.40	6.91	6.93	7.62	6.18
	301-600		305-550	9.95	2.00	16.23	3.54	9.75
<i>Anguilla obscura</i> Günther 1872	100-300	E/M	275-300	-	-	-	-	0.68
	301-600		450-475	0.24	-	0.27	-	-
<b>Clupeidae</b>								
<i>Nematalosa erebi</i> Günther, 1868	POF/T	FW	21-38	0.49	-	-	-	-
	Juv		44-105	1.24	0.50	-	-	1.03
	Adult		200-260	-	-	0.86	0.28	0.18
<b>Plotosidae</b>								
<i>Neosilurus ater</i> (Perugia, 1894)	Juv	FW	49-233	19.84	14.09	7.56	5.23	25.84
	Adult		235-295	-	-	-	0.49	0.45
<i>Neosilurus hyrtlui</i> (Steindachner, 1867)	Juv	FW	52-120	4.35	3.00	2.01	1.18	4.52
	Adult		125-225	4.64	1.98	1.31	2.53	4.34
<b>Atherinidae</b>								

<i>Craterocephalus stercusmuscarum</i> (Günther, 1867)	PF	FW	5.0-6.3	0.05	-	0.07	-	-
	POF/T		7.0-11.0	6.00	1.07	0.15	0.45	<0.00
	Juv		11.9-35.0	112.98	9.85	149.51	6.52	103.37
	Adults		36.0-46.0	3.66	1.81	1.48	0.18	11.93
<b>Melanotaenidae</b>								
<i>Melanotaenia maccullochi</i> (Ogilby, 1915)	Juv/adult	FW	26-32	-	-	-	-	4.62
<i>Melanotaenia splendida</i> (Peters, 1866)	PF	FW	4.0-6.4	-	1.27	-	0.03	-
	F		6.3-7.7	0.03	1.20	0.20	-	-
	POF/T		7.3-13.0	1.41	0.31	2.85	0.47	0.27
	Juv		13.0-37.0	31.84	5.00	51.91	1.28	66.95
	Adult		38.0-84.0	1.67	3.73	4.08	-	0.82
<b>Pseudomugilidae</b>								
<i>Pseudomugil gertrudae</i> Weber 1911	POF/T	FW	6-9	0.03	-	0.05	-	-
	Juv/adult		10-25	0.52	2.10	0.20	-	32.74
<b>Synbranchidae</b>								
<i>Ophisternon cf. gutturale</i> (Richardson, 1845)	<100	FW	90-99	0.03	-	-	0.17	-
	100-300 mm		100-210	0.07	0.05	0.11	0.10	0.18
<b>Scorpaenidae</b>								
<i>Notesthes robusta</i> (Günther, 1860)	Adult	E/M	120	-	-	0.27	-	-
<b>Chandidae</b>								
<i>Ambassis agassizii</i> (Steindachner, 1867)	POF/T	FW	10.0-12.0	-	-	-	2.25	-

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	Adult		25.6-34	6.20	3.16	28.45	4.70	12.57
<i>Denariusa bandata</i> (Whitley, 1948)	POF/T	FW	6.5-12.5	0.38	0.47	0.73	2.93	0.66
	Juvenile		12.0-24.5	42.63	19.48	32.43	40.26	75.74
	Adult		25.0-41.0	5.63	10.43	9.47	8.90	13.81
<b>Centropomidae</b>								
<i>Lates calcarifer</i> (Bloch, 1790)	Juvenile	E/M	140-180	3.27	0.54	0.05	-	-
	(100-300)							
	Juvenile		300	0.05	-	-	-	-
	(300-600)							
<b>Terapontidae</b>								
<i>Hephaestus fuliginosus</i> (Macleay, 1883)	Adult	FW	295	-	-	0.03	-	-
<b>Apogonidae</b>								

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<i>Glossomia aprion</i> (Richardson, 1842)	POF/T	FW	8-12	0.23	-	7.75	6.65	0.20
	Juv		13-49	22.17	8.20	13.27	26.70	28.49
	Adult		50-170	9.62	4.10	15.29	3.42	10.16
<b>Gobiidae</b>								
<i>Redigobius bikolanus</i> (Herre, 1935)	Juv/adult	E/M	16-42	1.62	1.00	3.56	0.63	0.92
<b>Eleotridae</b>								
<i>Giurus margaritacea</i> (Valenciennes, 1837)	cf. Adult (<100)	cf. FW	64-95	0.07	-	-	-	0.37
	cf. Adult (100-300 mm)		101-230	0.17	0.43	0.50	-	0.33
<i>Hypseleotris compressa</i> (Kreffft, 1864)	POF/T	E/M	10.3-14.0	8.49	4.37	12.29	3.23	234.44
	Juv		12.5-41.3	774.33	1436.80	4479.67	1180.90	7398.46
	Adult		41.3-59.5	110.02	24.98	34.22	32.10	80.53
<i>Hypseleotris</i> sp. 1	POF/T	FW	10.0-13.0	10.81	22.00	136.97	39.20	13.88
	Juv		14.0-30.7	361.57	192.03	1088.06	184.39	389.06
	Adult		30.8-39.0	0.87	7.43	3.80	3.64	3.77
<i>Mogurnda adspersa</i> (Castelnau, 1878)	POF/T	FW	7.0-12.0	0.18	0.03	-	-	0.22
	Juv		13.0-53.0	2.52	4.64	7.18	3.09	32.43
	Adult		54.0-96.0	0.54	-	1.52	0.10	0.89
<b>Poeciliidae</b>								
<i>Xiphophorus maculatus</i> (Günther, 1866)	Metalarvae	FW	8-10	0.03	-	2.14	-	0.13
	Juv/adult		11-40	3.81	7.94	53.31	1.22	13.69

**Table 3.** One-way univariate PERMANOVA results examining differences in larval and juvenile abundances of selected fish species across sampling times. Bold text indicates significant value ( $P < 0.05$ ). Also shown are the results of PERMANOVA pairwise comparison tests (t-test), with different superscript letters indicating significant differences ( $P < 0.05$ ) between months.

Species	Developmental stage/ length categories (standard length, mm)	d.f	MS	Pseudo-F	p	Pairwise comparisons				
						May 08	July 08	Sept 08	Nov 08	May 09
<i>Neosilurus ater</i>	Juveniles 49-80	4, 197	1.7471	4.9432	<b>0.0014</b>	a	a	b	b	a
<i>Neosilurus hyrtlii</i>	Juveniles 52-80	4, 197	0.2205	1.3576	0.2510					
<i>Craterocephalus stercusmuscarum</i>	Late stage larvae	4, 197	0.0230	1.3617	0.2332					
	Juveniles <18	4, 197	0.8440	2.7235	<b>0.0306</b>	a	b	b	b	b
	Early stage larvae	4, 197	0.0743	1.6994	0.0974					
<i>Melanotaenia splendida</i>	Late stage larvae	4, 197	0.0350	0.5637	0.7440					
	Juveniles <18	4, 197	0.4365	2.4835	<b>0.0406</b>	a	ab	b	a	ab
<i>Denariusa bandata</i>	Late stage larvae	4, 197	0.2213	4.0417	<b>0.0022</b>	ab	ab	a	b	a
	Juveniles <15	4, 197	1.6994	2.5765	<b>0.0290</b>	ab	ab	a	b	ab
<i>Glossamia aprion</i>	Late stage larvae	4, 197	1.7512	7.2420	<b>0.0002</b>	a	a	a	b	a
	Juveniles 15-25	4, 197	1.7823	12.69	<b>0.0002</b>	a	a	a	b	a
<i>Hypseleotris compressa</i>	Late stage larvae	4,197	1.3275	2.1209	0.0666					
<i>Hypseleotris</i> sp. 1	Late stage larvae	4, 197	8.0182	5.7387	<b>0.0004</b>	a	b	b	b	a
	Juveniles <15	4, 197	11.0080	7.8259	<b>0.0002</b>	a	b	b	b	a
<i>Mogurnda adspersa</i>	Late stage larvae	4, 197	0.0009	0.5827	0.5554					
	Juveniles <20	4, 197	1.3506	3.864	<b>0.0034</b>	a	ab	a	a	b

**Table 4.** Two-way univariate PERMANOVA results examining differences in juvenile *Hypseleotris compressa* (<20 mm SL) abundances across lagoons and sampling times. Also shown are the results of PERMANOVA pairwise comparison tests (t-test). Bold text indicates significant value (P <0.05). – = no *H. compressa* collected.

PERMANOVA

Source	df	MS	Pseudo-F	p
Time	4	36.013	13.719	<b>0.0002</b>
Lagoon	3	111.93	42.64	<b>0.0002</b>
Time x Lagoon	12	8.9624	3.4142	<b>0.0002</b>
Residual	18	2.625		

Pairwise comparisons of times and lagoons

Comparison	Barrett's		Kyambul		Selby's		Digman's	
	<i>t</i>	p	<i>t</i>	p	<i>t</i>	p	<i>t</i>	p
May 2008 vs. July	2.9997	<b>0.0122</b>	1.6211	0.1246	2.2791	<b>0.0434</b>	1.7299	<b>0.0236</b>
May 2008 vs. September	3.8840	<b>0.0028</b>	1.2373	0.2302	2.5005	<b>0.0254</b>	-	-
May 2008 vs. November	2.2257	<b>0.0410</b>	2.0179	0.0588	0.0188	0.9840	-	-
May 2008 vs. May 2009	2.3930	<b>0.0308</b>	1.7887	0.0884	4.7125	<b>0.0004</b>	5.0034	<b>0.0002</b>
July vs. September	0.7849	0.4372	0.7007	0.5040	0.3664	0.7290	1.3989	0.2150
July vs. November	0.5378	0.5988	0.0004	1.0000	2.1816	<b>0.0446</b>	1.7299	<b>0.0254</b>
July vs. May 2009	0.3624	0.7190	3.7214	<b>0.0034</b>	2.6122	<b>0.0180</b>	3.3689	<b>0.0030</b>
September vs. November	1.3600	0.1898	0.8645	0.4024	2.4300	<b>0.0242</b>	1.0000	1.0000
September vs. May 2009	1.1591	0.2528	3.5083	<b>0.0034</b>	2.3356	<b>0.0306</b>	4.8202	<b>0.0002</b>
November vs. May 2009	0.1721	0.8622	4.5990	<b>0.0014</b>	4.6160	<b>0.0004</b>	5.0034	<b>0.0002</b>

**Supplementary Table 1.** Published life-history information for species recorded in the present study. Data from field research are drawn from studies from northern and eastern Australia. Fish lengths are standard length unless stated. TL = total length; CFL = caudal fork length.

	Field or aquaria based study	River/region	River type	Spawning period	Length at hatching	Length at metamorphosis	Age and growth details	Length at sexual maturity	Age at sexual maturity	Reference
<i>Anguilla reinhardtii</i>	Field	Albert River, south-east Queensland	Lowland river / estuary	-	-	-	Onset of metamorphosis (from leptocephalus to glass eel) occurred on average by 124 days post-hatch; glass eels reached 50-55 mm TL in □ 150-180 days	-	-	McKinnon <i>et al.</i> (2002)
“	Field	Various, north-east Australia	Lowland river / estuary	Aseasonal	-	<50 mm TL	Age and length at recruitment into rivers ranged from 174-188 days post-hatch and ~50 Metamorphosis occurred approximately four weeks post-hatch; fish reached 75-85 mm TL by 9-11 weeks post-hatch	-	-	Shiao <i>et al.</i> (2002)
<i>Neosilurus ater</i>	Field	Ross River, Townsville	Tributary stream	February to March (wet season)	5.7-6.0 mm TL	~25 mm TL		-	-	Orr and Milward (1984)

“	Field	Alligator Rivers region, Northern Territory	Floodplain river	Early wet season (November to December)	-	-	-	Males: 260 mm TL Females: 280 mm TL	2 years (?)	Bishop <i>et al.</i> (2001)
<i>Neosilurus hyrtlii</i>	Field	Ross River, Townsville	Tributary stream	February to March (wet season)	5.7-6.0 mm TL	~25 mm TL	Metamorphosis occurred approximately four weeks post-hatch; fish reached 85-95 mm TL by 9-11 weeks post-hatch	-	-	Bishop <i>et al.</i> (2001)
“	Field	Alligator Rivers region, Northern Territory	Floodplain river	Early wet season (November to December)	-	-	-	Males: 135 mm TL Females: 135 mm TL	12 months (?)	Bishop <i>et al.</i> (2001)
<i>Craterocephalus stercusmuscarum</i>	Field	Alligator Rivers region, Northern Territory	Floodplain river	Aseasonal: late dry season (September to	-	-	-	Males: 27 CFL Females: 29 CFL	<12 months	Bishop <i>et al.</i> (2001)

				October) and mid wet season (January to March); variable across years						
“	Field	Johnstone River, North Queensland	Tributary stream	Dry season (September to November)	4.8-6.4 mm	9-11 mm	-	Males: 36 mm SL Females: 46 mm SL (lowland lineage)	<12 months	Pusey <i>et al.</i> (2004)
	Aquaria	-	-	-	4-4.5 mm TL (1-3 days after hatching)	-	Fish grew from 4.0-4.5 mm TL to 11.0-14.3 mm TL in 40 days	-	-	Ivanstovff <i>et al.</i> (1988)

<i>Melanotaenia splendida</i>	Field	Johnstone River, North Queensland	Tributary stream	Mainly dry season (September to November) with wet-season reproduction in habitats protected from high flows	3.9-4.5 mm	10-14 mm	-	Males: 38 mm Females: 44 mm	<12 months	Pusey <i>et al.</i> (2004)
	Field	Barron River, North Queensland	Riverine	-	-	-	Fish reached 14 mm by 95 days post-hatch and 18 mm by 176 days post-hatching	-	-	Richard Hunt/DNR M 2011. Unpublished data
	Aquaria	-	-	-	3.7 mm	-	Larvae reached 6.74 mm SL 14 days after hatching	-	-	Humphrey <i>et al.</i> (2003)
<i>Ambassis</i>	Field	Mary	Riverine	Septemb	-	-	-	Males:	-	Pusey <i>et</i>

<i>agassizii</i>		River, south-east Queensland		er to December					28.1 mm Females: 25.6 mm		<i>al.</i> (2004)
	Field	Brisbane River, south-east Queensland	Riverine	October to November	3.0 mm TL	-			-	12 months	Milton and Arthington (1986)
	Aquaria	-	-	-	-	-	Fish reached 12 mm SL by 60 days post-hatch		-	-	Leggett 1984
<i>Denariusa bandata</i>	Field	Alligator Rivers region, Northern Territory	Floodplain river	Aseasonal	-	>7 mm CFL	Modal length of population increased from 16-17 mm CFL to 31-32 mm CFL over an eight month period		Males: 25 mm CFL Females: 31 mm CFL	<12 months	Bishop <i>et al.</i> (2001)
<i>Lates calcarifer</i>	Field	Norman River, North Queensland	Floodplain river	Peak between' October and January	-	-	-		~300 mm TL	≥3 years	Davis (1982)

	Field	Various, North Queensland	-	Peak between October and February	-	-	0+ fish reached 120 mm TL by April.	-	-	Russell and Garrett (1985)
	Field	Papua New Guinea	-	October to February, with a peak between November and January	1.5 mm TL	-	-	-	-	Moore (1982)
	Aquaria	-	-	-	-	>8.7 mm TL	-	-	-	Russell <i>et al.</i> (1989)
<i>Glossamia aprion</i>	Field	Alligator Rivers region, Northern Territory	Floodplain river	Late dry season and early wet season	7 mm CFL	-	-	Males: 60 mm CFL Females: 70 mm CFL	<12 months	Bishop <i>et al.</i> (2001)
	Field	Mulgrave River, North	Riverine	-	-	9-12.5 mm	-	-	-	Godfrey (2011)

<i>Hypseleotris compressa</i>	Field	Queensland Alligator Rivers region, Northern Territory	Floodplain river	Mid wet season (January to March)	-	-	-	-	-	Bishop <i>et al.</i> (2001)
	Field	South-east Queensland	-	Concentrated in summer and autumn	-	-	-	Males: 41.3 mm Females: 62.4 mm	12 months (?)	Pusey <i>et al.</i> (2004)
	Field	Mulgrave River, North Queensland	Lowland river	-	<6 mm	11.5-14.25 mm	-	-	-	Godfrey (2011)
	Aquaria	-	-	-	1.35 mm	4.3-6.5 mm	Fish observed to increase in size from 1.35 mm TL to 18.3 mm TL in 89 days		-	Dotsu <i>et al.</i> (2000)
<i>Hypseleotris</i> sp. 1	Field	Mary River, south-	Riverine	Concentrated between	-	-	-	Males: 30.8 mm Females:	12 months	Pusey <i>et al.</i> (2004)

		east Queensla nd		Septemb er and January					32.4 mm		
<i>Mogurnda adspersa</i>	Field	Wet Tropics rivers, North Queensla nd	Various	Concentr ated in the dry season (October to Novemb er)	-	7.8-10 mm	-		Males: - Females: 54 mm SL	6 months	Pusey <i>et al.</i> 2004; Close <i>et al.</i> 2005
	Aquar ia (?)	-	-	-	3.2-5.0 mm TL	-	-		-	-	Pusey <i>et al.</i> (2004)
	Aquar ia	-	-	-	-	-	Fish were reported to grow to 10 mm after six weeks, 25 mm after two months and 50 mm at six to seven months			6 months	Hansen (1988); Tappin (1997)
	Aquar ia	-	-	-	-	-	Fish reached 12-27 mm TL after 41 days post- hatch				Starrs <i>et al.</i> (2013)