River regulation and recruitment in a protracted-spawning riverine fish

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Abstract. We present and test an extension of the “match/mismatch” hypothesis that attempts to explain the persistence, under conditions of flow alteration, of small, short-lived, native, riverine, fish species. The premise is that flow alteration typically changes environmental conditions, such as temperature and prey abundance, which may affect survival during the larval period of fishes. This “window-of-opportunity hypothesis” states that, if optimal conditions for recruitment vary temporally within a year, the probability that a proportion of the larvae of protracted-spawning species will encounter a period of optimal conditions is greater than for larvae with only a brief spawning period, and so the former will have a recruitment advantage. We determined whether all hatching events contributed equally to juvenile recruitment of the protracted-spawning Australian smelt (*Retropinna semoni*) during one breeding season in three pairs of heavily regulated and largely free-flowing unregulated rivers in the Murray-Darling Basin, Australia, and related patterns in the hatch dates of recruits to temperature or prey biomass for one pair. For all rivers, heavily regulated or not, recruits present at the end of the breeding season most commonly hatched in the latter part of the breeding season. Mortality of those fish hatched in the first part of the season likely explains this trend. Furthermore, while hatching times were similar for all rivers, each river showed a distinct pattern of hatching and recruitment, which may relate to the temperature range within which epigenetic processes are aligned. Patterns of zooplankton biomass differed between the largely free-flowing Ovens and regulated Goulburn rivers and likely had different sources: within the channel and within the storage lake, respectively. For the Ovens River, recruits hatched subsequent to the period when the first significant increase in zooplankton biomass occurred. We hypothesize that temperature may largely influence the “window” during which recruitment can take place but that prey density, responding to river-specific interactions between temperature and discharge, plays a role in the timing and magnitude of recruitment of Australian smelt. We conclude that the match/mismatch hypothesis may be applicable to rivers, that the window-of-opportunity hypothesis has some currency and deserves further investigation, and that river regulation may have significant impacts on fish recruitment.

Key words: Australia; fish larvae; food availability; freshwater fish; match/mismatch hypothesis; Murray-Darling Basin; recruitment; *Retropinna semoni*; river regulation; window-of-opportunity hypothesis.

INTRODUCTION

Populations persist through time by the production of new individuals to replace members lost through mortality or emigration. Recruitment each year is usually determined by the number of new individuals that survive to join the juvenile or adult population. Survival through a given life period is controlled by physicochemical factors, such as temperature and dissolved oxygen, predation, inter- and intraspecific

interactions and the quantity and accessibility of one or more key resources required for that period (White 2001). However, because of fluctuating environmental conditions, the amount and availability of these resources vary inter- as well as intra-annually, which means that some years, and some periods within a year will be more favorable for survival than others (Jobling 1995). Because most animal species have distinct breeding seasons, unless environmental conditions are predictable, a likely response to intra-annual variation in environmental conditions is considerable fluctuations in interannual recruitment.

Recruitment variability and year-class strength in fish are thought to be largely determined during the very early life stages, particularly larval development (Houde 1997, Horwood et al. 2000, Brander et al. 2001).

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Abundant and rapid changes in morphology, ecology, and behavior during this time mean that mortality rates are generally highest and most variable (Bradford and Cabana 1997). The time taken to reach recruitment is strongly influenced by the growth rates during each life history period, and these growth rates are in turn influenced by genetics and environmental factors such as food availability and temperature (Jobling 1995). For any given level of development, well-fed larvae generally grow faster and reach recruitment earlier than poorly-fed ones. Similarly, temperature has a positive influence on growth rates, typically to an upper threshold.

One of the most enduring fish recruitment hypotheses is the “match/mismatch” hypothesis (MMH), which states that inter-annual variation in recruitment of temperate fish populations is due to the relatively fixed time of spawning not always coinciding with the highly variable time of peak production of larval food (Cushing 1990). Larvae have only a short window, usually in the order of a few days, within which to locate food, or risk starving (Hjort 1914). Modeling and empirical studies have investigated aspects of this hypothesis for various marine groups (Gotceitas et al. 1996, Chick and Van Den Avyle 1999, Beaugrand et al. 2003, Bos et al. 2006, Fiksen and Jørgensen 2011, Giménez 2011), although none, to our knowledge, for riverine fishes.

In temperate areas, where climate varies seasonally, it is generally accepted that fish breed at a time that coincides with optimal conditions for the survival of their young (Trippel et al. 1997). Therefore, any anthropogenic changes, such as those associated with river flow regulation may adversely affect recruitment rates. River regulation has undoubtedly played a role in the decline in abundance and distribution of the world’s freshwater fishes, and has variously been linked to disruption to spawning and migration cues, temperature depression, disconnection from the floodplain, and associated changes to spawning and nursery conditions (Lloyd et al. 2003, Lytle and Poff 2004, Driver et al. 2005, Roberts et al. 2008, Tonkin et al. 2008a, King et al. 2009, Liermann et al. 2012). The mechanisms, however, are largely elusive (Lloyd et al. 2003, Lytle and Poff 2004). The persistence of some species, however, goes against this trend. In the southeastern Murray-Darling Basin, Australia, two opportunistic native species, the Australian smelt (*Retropinna semoni*) and flathead gudgeon (*Phlypnodon grandiceps*), thrive, despite dramatic changes to the flow regimes (Humphries et al. 2002, 2008). It has been hypothesized that they can cope with alterations to the flow regime because of their extended spawning period, which increases the probability of a “match” with optimal recruitment conditions (Humphries et al. 2002). A prediction from the MMH is that, as spawning duration decreases, inter-annual recruitment variability should increase (Mertz and Myers 1994). A longer spawning period would potentially increase the likelihood of larvae surviving during what may be a relatively brief period of optimal recruitment conditions. Con-

versely, the lack of success of species with relatively short spawning periods may be due to the limited opportunity these species have to produce larvae that coincide with peaks in optimal conditions.

This extension of the MMH, from the inter-annual to intra-annual context, we call the “window-of-opportunity hypothesis” (WOOH; Fig. 1). It builds on many marine studies that explore the influence that the timing of fish production and the production of their prey have on fish recruitment (e.g., Beaugrand et al. 2003, Sanvicente-Añorve et al. 2006, Burrow et al. 2011) and assumes that there is a relatively high level of stochasticity in prey production and so uncertainty in the timing of peak food abundance. Note that hereon “recruitment” refers to juvenile recruitment, or fish that advance through all larval stages to the juvenile stage. The WOOH states: *in any one year, if optimal conditions for recruitment vary temporally, fish that spawn over a protracted period have a recruitment advantage over those that spawn only for a brief period*. This is because the probability that a proportion of the larvae of protracted-spawning species will encounter a period when conditions are optimal for recruitment is greater than for larvae with only a brief spawning period. While the WOOH is not limited to rivers, the physicochemical environment of freshwaters, and especially rivers and flow, is more variable than the marine environment, and the influences on conditions optimal for recruitment are therefore expected to be different.

In the present study, we investigated aspects of the WOOH in six lowland rivers of the Murray-Darling Basin, Australia. The primary aim was to determine if most Australian smelt recruits originated from a restricted window relative to the hatching distribution, reflecting differential survival of young and greater contribution of some hatching events than others to recruitment. This species was chosen because it can spawn for many months, it is widespread in the Murray-Darling Basin and it thrives under regulated conditions. We also compared the timing of hatching between pairs of rivers (one having regulated flows and one having mostly unregulated flows) in three regions of the Murray-Darling Basin, the premise being that river regulation alters the rearing environment for young fishes and thus may result in different patterns of spawning, hatching and recruitment. We chose three regions of the Murray-Darling Basin to investigate broad-scale patterns and established paired rivers of similar geomorphologies, sizes, discharge volumes, and ones likely to have had similar fish faunas prior to regulation. We also recorded discharge and temperature, and collected potential prey to explore relationships with fish recruitment in the rivers. The specific aims of the study were to (1) determine whether all hatching events contributed equally to recruitment of Australian smelt during one breeding season in six rivers; (2) determine whether hatching and recruitment are synchronous between regulated and mostly free-flowing rivers; and

FIG. 1. Schematic of the window-of-opportunity hypothesis, showing the relationship between timing of spawning and recruitment for (a) brief and (b) protracted spawners when conditions are uniform throughout the year and for (c) brief and (d) protracted spawners when conditions are variable throughout the year.

(3) determine if environmental variables or food availability are related to recruitment of Australian smelt in a subset of rivers.

METHODS

Study areas and reaches

We conducted our study in the southern, lower, and northern regions of the Murray-Darling Basin, south-eastern Australia (Fig. 2). Each region included a pair of rivers, one that was heavily regulated and that received high flows over the spring/summer spawning and recruitment period (regulated rivers), and one that received relatively natural, and typically much lower, flows over the same period (free-flowing rivers). The Goulburn River, Murrumbidgee River, and Dumaresq River were our regulated systems and the Ovens/King system, the Lindsay River and the Mole River our free-flowing systems of the southern, lower, and northern regions, respectively. The regulated Goulburn River receives regulated flows from several major weirs and dams, including Lake Eildon, whereas the free-flowing Ovens River has only one small impoundment that has little effect on discharge. The major difference in flow regime between the regulated Murrumbidgee and the free-flowing Lindsay systems is that the latter typically experiences a protracted period of low discharge, whereas the former experiences a protracted period of high discharge as an anastomosing channel of the River Murray, over much of the summer/early autumn period. The regulated Dumaresq River receives regulated releases from Glenlyon Dam on an upstream tributary, and its discharge tends to be erratic. The free-flowing Mole River experiences natural peak discharge over summer,

but discharge remains relatively stable throughout this period, with rainfall events causing only relatively brief fluctuations. These produce large velocity and depth changes within the channel.

Because the Murray-Darling Basin encompasses more than 1 million square kilometers, and several climatic zones, it was impossible to find three identical, relatively free-flowing rivers and three similar, regulated rivers. Nevertheless, the nature of the regulation for the three regulated rivers is such that runoff occurring prior to, or in, spring each year is captured and later released during spring and/or summer, substantially enhancing discharge above what would be natural, whereas for the three free-flowing rivers, runoff prior to, or in, spring, runs into and down the river and discharge is typically low over summer (Fig. 3).

Three reaches (length range 450–2000 m, typically encompassing three run-pool sequences, depth range 0.5–3 m) were selected from each of the regulated and free-flowing rivers because they were proximate to each other, within the same altitudinal range and the fish faunas were known to be similar (Fig. 2). The inclusion of multiple reaches meant that variation within each system could be included, and that any small-scale movement of larval or juvenile fish into and out of a reach would be between environmental conditions similar to one of the other reaches being sampled. Furthermore, studies on movement of inland populations of the study species, Australian smelt, have indicated limited movement (Woods et al. 2011), and sporadic sampling in the Northern Region confirmed the virtual absence of this species dispersing as either larvae or juveniles (G. G. Wilson, *unpublished data*).

FIG. 2. Map of the Murray-Darling Basin, showing the northern, lower, and southern study regions, rivers (R, regulated rivers; F, free-flowing rivers), and study reaches included in the present study. The map of Australia is reproduced courtesy of the Murray-Darling Basin Commission.

Study species

The Australian smelt (*Retropinna semoni*: Retropinnidae; McDowall 1996), is endemic to Australia and was primarily chosen because of its wide distribution, its abundance, its protracted spawning season and the fact that it is pelagic throughout its life, making it vulnerable to capture using the same methods throughout its life. The species is in fact a complex of several genetically distinct species: lower River Murray, upper Murray and Darling River, and coastal forms (Hammer et al. 2007). These species are yet to be formally described, are virtually identical morphologically and ecologically, and the present study likely includes more than one species. Australian smelt in the lower River Murray matures at about 40 mm, is semelparous, and breeds at one year of age (S. J. Leigh, *unpublished manuscript*). The timing and duration of spawning vary with locality, but Australian smelt generally breeds for a protracted period (Milton and Arthington 1985, Humphries et al. 2002; S. J. Leigh, *unpublished manuscript*): fish can spawn as early as August and continue until April, but usually February in the southern Murray-Darling Basin (Humphries et al. 2002). It is a multiple batch spawner, with synchronous oocyte development producing discrete batches of eggs every 3–4 days. However, it is unknown how many

batches of eggs an individual female may lay over the spawning period. The protracted spawning season may result from the same females spawning many batches over a long period, or from successive females spawning for shorter periods. Australian smelt eggs are 0.8–1.0 mm in diameter, negatively buoyant, and strongly adhesive (Milward 1969; S. J. Leigh, *unpublished manuscript*). Spawning occurs in shallow littoral areas of slow-flowing stream pools, with eggs attached to the base of vegetation, debris or sediment (Milton and Arthington 1985). Embryos take approximately 9 days to develop and hatch at water temperatures of 13–19°C (Milward 1969). Newly hatched larvae are approximately 5 mm long, and residual yolk is absorbed within 2–3 days. The diet of larvae comprises primarily small zooplankters, rotifers, cladocerans, and chironomids, with terrestrial-derived prey increasing in importance as fish enter the juvenile stage (King 2005).

Fish

Field sampling was undertaken monthly from August 2006 to February 2007, using a range of gears designed to catch larval and juvenile Australian smelt. A pilot study indicated that the techniques that best collected larvae and juveniles of Australian smelt were seine and

FIG. 3. (a) Long-term mean monthly hydrographs and (b) daily hydrographs for the six rivers in the three regions of the Murray-Darling Basin between July 2006 and April 2007. In each case, solid lines represent rivers with heavily regulated discharges (R, regulated rivers), and dashed or dotted lines represent rivers with largely free-flowing discharges (F, free-flowing rivers). For the lower middle panel, the left-hand y-axis is for Mullaroo Creek, and the right-hand y-axis is for Lindsay River.

throw nets. Thus, a minimum of five random, replicate hauls of a 2×8 m seine net (2-mm mesh with a 500- μ m cod-end) were carried out monthly per reach during the day. The seine was deployed by two operators from the bank, and circled a known area. A 30 cm diameter, 1 m long (500- μ m mesh), conical throw net was also used during the day. This net was attached to a 5 m rope and was thrown and retrieved from the bank five times per replicate. Five random, replicate samples were taken from each reach.

Zooplankton

Zooplankton was collected using a 25 cm diameter, 53- μ m mesh, conical, tow net deployed from a boat. Five random, 30 s tows were taken at each reach, when moving at a constant speed, zig-zagging across the river, with volumes of water filtered quantified. All samples were preserved in 95% ethanol.

Temperature, discharge, and water quality

StowAway Onset (Onset, Pocasset, Massachusetts, USA) temperature loggers were deployed at each reach, and set to record water temperature hourly. Daily discharge data were obtained from either Thiess Environmental (Melbourne, Australia) or the New South Wales Department of Water and Energy (data available online).⁶ Duplicate spot temperature, dissolved

oxygen, conductivity, pH, and turbidity measurements were made at each reach in each month, using either a Horiba Water Quality Checker 10 (Horiba, Kyoto, Japan) or a Hydrolab Quanta (Hach Hydromet, Loveland, Colorado, USA).

Age

Fish samples were sorted in the laboratory. Australian smelt were separated from the other species and were the focus for all further analyses. Larvae of this species were staged using Serafini and Humphries (2004). Results were pooled by river. The lengths of most fish were measured to 0.1 mm using vernier calipers or a microscope micrometer, although in the case of large samples a maximum of 50 fish per reach was measured. A maximum of 30 Australian smelt larvae and juveniles per month per river were aged from daily increments on sagittal otoliths using standard methods (Tonkin et al. 2008b). Both sagittae were removed, placed on a glass slide in Crystalbond adhesive (Aremco Products, Valley Cottage, New York, USA), and one otolith was polished using fine lapping film until a flat surface was achieved and increments were discernible to the hatching check near the primordium. Otoliths were examined under a compound microscope and photographs were taken of every otolith (see Plate 1). Increments were counted directly from the otolith and from the image, and an average taken. All otoliths were read by two readers,

⁶ <http://waterinfo.nsw.gov.au>

PLATE 1. Magnified section (~ 0.2 mm) of an otolith of a 100-day-old Australian smelt, showing daily growth rings. Photo credit: P. Humphries.

and if the two estimates differed by more than 5%, the otolith was discarded.

Validation of daily increment formation and hatch checks for Australian smelt has been demonstrated by Tonkin et al. (2008b). Length–age relationships were explored for each species for the entire breeding period, to integrate growth rates and incorporate changes in temperature. Although Gompertz equations were applied in a previous study of the growth of juvenile Australian smelt (Tonkin et al. 2008b), these were unable to be fitted to length–age data because many juveniles exceeded the theoretical maximum length obtained by fish (L_∞), thus making it impossible to back-calculate ages for these individuals. Not using these individuals would have invalidated the study. Instead, sigmoidal models, which approximate the Gompertz model and gave virtually identical fits, were used and in most cases gave excellent fits to the data. These were used to back-calculate ages from all fish and took the form

$$A = \frac{a}{1 + \exp[-(L - L_0)/b]}$$

where A is age, L is length, and L_0 , a , and b are constants that define the shape of the curve in terms of point of inflexion and upper and lower asymptotes, respectively.

Timing of hatching and recruitment

Estimated ages from length–age relationships were rounded to the nearest whole number and hatch dates

determined as the date of capture minus estimated age. Frequency histograms of lengths and hatch dates were constructed for the fish collected in each month using area plots in Microsoft Excel (Microsoft, Redmond, Washington, USA). However, because the error around each constant in the length–age models was sometimes substantial, we included the predicted ages for the model and an estimate of the 95% confidence limits of the constants to give a more comprehensive estimate of hatch date using centered period-three moving averages. Also, because in some cases the lengths of all fish in large samples were not measured but total numbers needed to be included in recruitment assessments, the lengths of randomly selected measured fish were used to bring numbers to 100%. This did not alter the shape or extent of frequency distributions. Juveniles collected at the end of the breeding season in January and February were used as a measure of recruitment.

Recruitment relationships with food, temperature, and discharge

Plankton samples were processed only for the Ovens River at Warby Range Road and for the Goulburn River at Northwood Road, due to time constraints. However, the above two sites were the source of most larvae and juvenile recruits sampled in these rivers. The particulate organic matter analysis method of meiofauna biomass and size structure of Masson et al. (2004) was followed. Briefly, each sample was divided in half and

FIG. 4. Mean monthly (a) temperature, (b) dissolved oxygen, (c) conductivity, (d) pH, and (e) turbidity measurements from three reaches in the three regions of the Murray-Darling Basin between August 2006 and March 2007. In each case, solid lines represent rivers with heavily regulated discharges and dashed lines represent rivers with largely free-flowing discharges.

both were filtered through a series of four sieves with decreasing mesh size (500, 212, 106, and 53 μm) to obtain four size fractions (+500, 212–500, 106–212, and 53–106 μm) (Seda and Dostalkova 1996). Each fraction was then resuspended in 600 mL distilled water and organisms removed from one of the pairs of fractions under a dissecting microscope. The remaining material and the other intact half were then filtered through pre-washed and pre-weighed (filter mass) (GF/C Whatman; Maidstone, UK) glass fiber filters and rinsed with distilled water to remove any residual fixative. They were dried at 60°C for 24 hours, desiccated and re-weighed using a micro-balance (dry mass). The difference between the two (fraction with organisms and fraction with organisms removed) gave the dry mass of organisms in each fraction.

Relationships between discharge and temperature and zooplankton biomass were explored using the means of the previous week's and month's temperature and discharge vs. dry mass of zooplankton in each size fraction. Values from the week and month previous to sampling can indicate if proximate or more distant environmental variables, respectively, affect plankton biomass. Generalized linear models for each size fraction were carried out to investigate the influence of discharge and temperature. Discharge and temperature were both $\log_{10}$ -transformed, but data for dry mass of zooplankton did not need to be transformed to meet the assumptions of the statistical tests. Analyses were performed in Microsoft Excel, SPSS 18 (SPSS, Chicago, Illinois, USA), and SigmaPlot 12.0 (SPSS).

TABLE 1. Sigmoidal length–age models and statistics for Australian smelt larvae and juveniles collected from the six rivers in the three regions of the Murray-Darling Basin between August 2006 and February 2007.

River	Region	River type	<i>n</i>	<i>R</i> ²	<i>a</i>	<i>b</i>	<i>L</i> ₀	<i>P</i> (<i>a</i> , <i>b</i> , <i>L</i> ₀)
Ovens	Southern	F	56	0.90	123.62 ± 16.49	5.04 ± 0.77	21.71 ± 1.65	all <0.0001
Goulburn	Southern	R	53	0.94	150.75 ± 18.58	6.20 ± 0.69	22.59 ± 1.88	all <0.0001
Lindsay	Lower	F	88	0.90	124.35 ± 8.87	4.93 ± 0.56	18.55 ± 0.96	all <0.0001
Mullaroo	Lower	R	124	0.86	178.12 ± 13.18	5.30 ± 0.54	21.44 ± 0.93	all <0.0001
Mole	Northern	F	40	0.51	130.31 ± 35.54	5.12 ± 2.52	15.98 ± 2.92	<0.001, 0.05, <0.0001
Dumaresq	Northern	R	113	0.77	121.46 ± 10.81	3.69 ± 0.53	19.04 ± 0.83	all <0.0001

Notes: River types are: R, regulated; F, free-flowing. *L*₀, *a*, and *b* are constants that define the shape of the curve in terms of point of inflexion and upper and lower asymptotes, respectively. Values are means ± SE. The parameter *n* is number of fish.

RESULTS

Environmental data

Historical discharge regimes and daily temperature and discharge patterns during the study period were not uniform across regions (Fig. 3). However, during spring and summer, in each region, discharge was much greater in each regulated river than in its largely free-flowing pair. Water temperature patterns were generally very similar for the pairs of rivers, but temperatures increased faster during spring and reached higher levels in the lower and northern than the southern region (Fig. 4). For example, water temperatures were close to or exceeded 20°C in October in the lower and northern region rivers, but did not reach this level until December in the southern region rivers. Spot measurements of dissolved oxygen and pH showed little consistent differences between pairs of rivers in each region (Fig. 4b, d). Conductivity was typically higher in the free-flowing Ovens than in the regulated Goulburn, in the free-flowing Lindsay than in the regulated Mullaroo, and in the regulated Dumaresq than in the free-flowing Mole (Fig. 4c). Turbidity was also consistently higher in the free-flowing Ovens than in the regulated Goulburn and in the regulated Mullaroo than in the free-flowing Lindsay (Fig. 4e).

Hatch-date distributions

Generally, sigmoidal length–age models provided good fits to the data and allowed for a high level of precision (80–94%) in predicting age from length and all were highly significant (Table 1, Fig. 5). The free-flowing Mole River model, however, was the worst fit, with an *R*² of only 0.51. In some cases, such as for the regulated Mullaroo and Dumaresq rivers, the model underestimated ages of very small larvae. For all rivers, however, while the variance around the model increased with length of fish, this variance was evenly distributed above and below the fitted line. This indicates that over- and under-estimates of age should be relatively evenly distributed for back-calculations of the larger sizes.

Australian smelt spawned, hatched and recruited in each river during the 2006–2007 breeding season, as shown by the collection of protolaryvae, length frequencies, and age estimated from back-calculated hatch dates

(Figs. 6–8). The presence of protolaryvae only approximated the period of hatching but probably represented well the peak time of hatching, but did not give a comprehensive estimate of the period of hatching. Our length-frequency histograms and back-calculation age distributions indicated the likelihood that hatching occurred sometimes before and possibly after protolaryvae were collected. Thus, we estimated that hatching occurred for between 4 and 6 months across the rivers. Hatching commenced first in the regulated Mullaroo and Dumaresq in July and possibly as early as June in the free-flowing Mole River. However, it was clear that hatching commenced later in the Southern Region rivers, probably in August, and in the free-flowing Lindsay River, in July. Hatching finished latest in the regulated Goulburn and Dumaresq rivers, in January and December, respectively.

Distributions of hatch date and recruitment

Length frequencies suggested that for most rivers there were only one or two cohorts of larvae produced or that persisted throughout the study period (Fig. 7). The exception to this was the regulated Goulburn River where fish larvae likely hatched continuously over much of a 6-month period. Again, in all cases, except the Goulburn, there was usually one length mode and occasionally two (e.g., January in the regulated Dumaresq) that predominated throughout the season.

The patterns observed and conclusions drawn from the presence of protolaryvae and from length-frequency histograms were broadly supported by back-calculated hatching dates of Australian smelt from the rivers (Fig. 8). Thus, there were generally only one or occasionally two cohorts that persisted throughout the season in most rivers. Back-calculated hatching dates for the regulated Goulburn in October–January, however, indicated the presence of at least two or three cohorts, albeit in low numbers.

In the case of all rivers, irrespective of region or discharge patterns, back-calculated hatch date distributions in each month differed from the start of the breeding period to the end of the breeding period (Fig. 8). Without exception, none of the earliest hatched larvae, collected usually in October or November, was present in January or February samples, whereas later

FIG. 5. Length–age models for Australian smelt collected from the six rivers in the three regions of the Murray-Darling Basin between August 2006 and February 2007.

hatching individuals were disproportionately represented in these later samples. This was most evident in fish from the Goulburn, Lindsay, Mole, and Dumaresq rivers and least evident in fish from the Ovens River, although even in the Ovens River, fish (albeit very few in number) that hatched in August did not persist through time. That being said, hatch-date distributions did not change dramatically in the Ovens River after November, whereas for the other rivers they did. Interestingly, the peak in hatch-date distributions did not change between October and December in the Mullaroo and Dumaresq rivers, but shifted slightly in January and February.

Relationships between environmental variables, hatching, and recruitment

In each case, the temperature range during the hatching period of fish collected in January and

February was always narrower than that of the entire hatching period and was always considerably warmer than when hatching commenced (Fig. 9). Hatching of the recruiting fish usually occurred when water temperatures were between approximately 17° and 24°C.

Comparing the hatch date distributions of Australian smelt recruits with the biomass of zooplankton in the free-flowing Ovens (at Warby Range Road) and the regulated Goulburn (at Northwood Road) rivers, it is evident that the peak in recruitment (January and February juvenile hatch-date distributions) in the Ovens, which was between late October and late November coincided with the first appreciable rise in biomass of the smallest size fraction (53–106 μm) of zooplankton (Fig. 10). This was not the case, however, with the Goulburn, where juvenile hatch-date distributions also peaked between late October and late November, but there

FIG. 6. Estimates of hatching time from collection of protolarvae and back-calculated dates (black) and from back-calculated hatching dates only (gray) for Australian smelt collected from each river in the three regions of the Murray-Darling Basin between August 2006 and February 2007.

was a peak in zooplankton biomass in mid-October. However, biomass of zooplankton of the two smallest size fractions in this river remained between 3 and 5 mg/L in November and December. The other size fractions are not shown because they did not differ significantly over time and were always at or below the lowest biomass levels of the two smallest size fractions (Warby Range Road, for 212–500 and >500 μm fractions, 0.795 ± 0.053 and 0.714 ± 0.033 mg/L [mean $\pm$ SE], respectively; Northwood Road for 212–500 and >500 μm fractions, 2.648 ± 0.196 and 2.971 ± 0.197 mg/L, respectively).

Mean biomass of zooplankton in the smallest size fraction was significantly and positively related to mean water temperature for the previous month for the free-flowing Ovens River at Warby Range Road (Fig. 11a). Although the relationship fit well for the smallest size fraction ($R^2 = 0.92$, $P < 0.001$), it was nonsignificant for the 106–212 μm size fraction. There was also a significant but negative relationship between mean discharge for previous month and mean biomass of both the smaller size fractions of zooplankton in the Ovens River ($R^2 = 0.96$ and 0.88 , $P < 0.001$). These relationships were negative power relationships. The

FIG. 7. Length frequencies of Australian smelt collected from three reaches on each of the six rivers in the three regions of the Murray-Darling Basin between August 2006 and February 2007. Frequencies represent the results from a minimum of 15 seines from each river per month. Values in parentheses are the numbers of fish.

Note: The y-axes have different scales.

FIG. 8. Back-calculated hatch date frequencies of Australian smelt collected from the six rivers in the three regions of the Murray-Darling Basin between September 2006 and February 2007. Frequencies represent the results from a minimum of 15 seines from each river per month. Values in parentheses are the numbers of fish. Numbers above curly brackets are the numbers of fish for small values that are hard to discern. Vertical dashed lines bracket the period during which fish hatched.

Note: Axes have different scales.

relationships between zooplankton mass and temperature and discharge for the regulated Goulburn River were very different (Fig. 11b). There was no significant relationship between temperature, either of the previous week or month, and zooplankton biomass of any size fraction. The greatest biomass of zooplankton occurred at intermediate temperatures in October. Zooplankton density for the two smallest size fractions, however, was best described by a second-order quadratic function ($R^2 = 0.99$ and 0.82 , $P < 0.001$), increasing from the lowest densities when discharge was approximately $23 \text{ m}^3/\text{s}$ to the highest densities when discharge was approximately $52 \text{ m}^3/\text{s}$.

DISCUSSION

Window-of-opportunity hypothesis

Our study stemmed from the observation that riverine fishes can be classified broadly as brief (1 or 2 months) or protracted (many months to all year round) breeders (Winemiller 1989, Humphries et al. 1999), and that one possible explanation for the apparent proliferation of some species, despite intense river regulation, is that

their protracted breeding periods give larvae a greater chance of access to resources essential for recruitment. These resources would potentially be missed by species that breed for only brief periods and is the basis of the extension of the match/mismatch hypothesis, that we call the window-of-opportunity-hypothesis (WOOH). Our results confirm that Australian smelt is a protracted breeder, the length of the breeding period in 2006–2007 varying between 4 and 6 months in the six rivers and three regions of the Murray-Darling Basin. Our results also provide support for the WOOH, because the distribution of hatching dates of Australian smelt recruits was a subset of overall distribution of hatching dates throughout the breeding period, and environmental conditions considered conducive for recruitment varied significantly over the same time (Fig. 12). These results are explored in detail in the following subsections.

Contributions of hatching dates to recruitment of Australian smelt

During the breeding period, and for each of the six rivers, all hatching events did not contribute equally to recruit-

FIG. 9. Daily temperatures at noon from the six rivers in the three regions of the Murray-Darling Basin between 1 September 2006 and 1 January 2007, showing temperature ranges during the entire hatching period (dotted rectangle) and temperature ranges during the hatching period of recruiting Australian smelt (shaded region).

ment. In each case, the juvenile recruits present at the end of the period (January and February) were estimated to have hatched in the latter part of the distribution of hatch dates. The first hatching events, which ranged from relatively insignificant to substantial, did not produce recruits that were present in January and February. In some cases (the free-flowing Ovens), the hatch-date distributions were consistent for several months, but showed evidence of a truncation only in February, whereas in other cases (the regulated Dumaresq), there was a gradual shift in the hatch-date distribution with successive months. There are several possible explanations for this truncation of hatch-date distributions: that it is a statistical artifact resulting from systematic gradual underestimation of hatch dates as the breeding season progressed and fish grew, that fish hatching earlier in the season emigrated from the three reaches in each river, or that the trend represents mortality of those fish hatched in the first part of the season.

The first explanation is unlikely because the residuals of the data, especially for large fish, generally were evenly distributed above and below values predicted by the model, indicating as much over- as under-estimation of hatch dates. The second explanation is possible, but still unlikely, as studies suggest that wholly freshwater Australian smelt move little as larvae or juveniles

(Humphries et al. 2002), and our study showed no evidence of influxes of fish hatching at quite different times in any of the rivers. Thus, the third explanation is the most plausible and concurs with marine and estuarine studies on the timing of production and recruitment (Dolbeth et al. 2010, Burrow et al. 2011, Giménez 2011, Shoji et al. 2011). Recruitment can often be limited to a subset of the spawning time, usually but not always associated with warm temperatures and upwelling of nutrients and associated abundance of zooplankton (Marin et al. 2003, Bos et al. 2006, Sponaugle et al. 2006, Kristiansen et al. 2011, Sakabe et al. 2011).

Recruitment studies of fish in rivers typically investigate spawning or hatching without reference to, or direct estimates of, recruitment (e.g., Balcombe et al. 2006, King et al. 2009, Konečná et al. 2009, Rolls and Wilson 2010, Walsh et al. 2010, Stefferud et al. 2011). It is, however, likely that similar processes to those in estuarine and marine environments, temperature and food, contribute to recruitment of riverine fishes, although relationships may be more complex because of environmental stochasticity. Of the few studies that have investigated the timing of spawning and/or hatching vs. recruitment in rivers, Falke et al. (2010)

FIG. 10. Mean $\pm$ SE biomass of the two smallest size classes (53–106 and 106–212 μ m) of zooplankton for the (a) Ovens River at Warby Range Road and (b) Goulburn River for Northwood Road, between August 2006 and February 2007.

showed that recruitment was maximal for brassy minnows (*Hybognathus hankinsoni*) that spawned in the middle of the breeding season when temperatures were warm in the Arikaree River, Colorado, but that hydrology also played an important role.

Synchrony of hatching and recruitment in regulated and free-flowing rivers

In our study, hatching and recruitment trends, recruitment being strongest for fish hatching in the latter part of the breeding season, were broadly the same for the regulated and the free-flowing systems. However, the detailed patterns in hatching and recruitment were dissimilar for each pair of rivers. Indeed, while hatching times were similar for all rivers in all regions, each river showed a distinct pattern of hatching and recruitment. For example, while the hatch-date distribution of the largely free-flowing Ovens River fish tended to be always relatively narrow, after October, that of the heavily regulated Goulburn River was wider, and showed evidence of at least two cohorts until late in the breeding season. In another example, whereas very few young Australian smelt were collected in the largely free-flowing Lindsay River beyond November and recruitment was relatively poor, recruits were abundant throughout the breeding season in the nearby heavily regulated Mullaroo Creek.

Flow regulation has been implicated strongly in the decline of freshwater fishes around the world, but often the mechanisms are unclear (Bunn and Arthington 2002,

Lloyd et al. 2003, Lytle and Poff 2004, Roberts et al. 2008, King et al. 2009). If species are obligate floodplain spawners and regulation changes components of flooding, or if pre-spawning migration or post-spawning larval dispersal are life history requirements, then impacts on spawning and recruitment are likely and the factors involved relatively obvious (e.g., Sanchez et al. 2006, Dudley and Platanina 2007, Tonkin et al. 2008a). However, most studies of the effects of river regulation on fish populations simply link recruitment to temperature or flow, without directly addressing mechanisms likely to influence spawning and especially recruitment; and most only imply that spawning and/or recruitment are somehow directly affected by flow or temperature (Driver et al. 2005, Roberts et al. 2008) or raise potential influencing factors, such as food abundance or availability, growth rates, habitat availability, migration, or dispersal potential (Freeman et al. 2001, Bowen et al. 2003, Balcombe et al. 2006, Stuart and Jones 2006, Tonkin et al. 2008a, King et al. 2009). To properly understand and manage rivers and conserve their fish, it is vital to understand the mechanisms that directly drive spawning, hatching, and recruitment success and how these mechanisms relate to aspects of flow regulation (Schiemer et al. 2003, 2004). Peñáz (1996) has suggested that river regulation disrupts cues for movement and spawning and results in less coordinated spawning and perhaps more protracted spawning. The last of these is the most relevant to our study, and seems to fit with our observations of Australian smelt spawning in the Goulburn River, but does not fit well with our observations in the other regulated rivers. Schiemer et al. (2004) specifically related decreased temperatures below hydropower dams to reduced growth rates in riverine fish and the potential impact that this may have during the critical period of growth during larval development. Because temperatures were not substantially different between the regulated and largely free-flowing rivers in the year of our study (e.g., normally the regulated Goulburn River would be much cooler [McMahon and Finlayson 1995]), temperature is unlikely to be the explanation. However, temperature may play a role in spawning, hatching, and recruitment in other ways, as we explore next.

Environment–recruitment relationships

For all rivers, the period during which we estimated Australian smelt recruits hatched included a narrower and warmer band of temperatures than during the entire hatching period. Thus, while hatching started when temperatures were as cool as 10°C, but more normally at 15°C, the temperatures at which the majority of recruits hatched was generally between 17° and 23°C. While temperature is well known to influence the timing of spawning (Jobling 1995), there is also evidence to support the importance of temperature in influencing growth rate and survival during early life history (Limburg et al. 1999, Kamler 2002, Schiemer et al.

FIG. 11. Regression relationships for mean temperature for the previous month or week and mean discharge for the previous month or week with mean mass of 53–106 μm (solid squares) and 106–212 μm (open triangles) size fractions of zooplankton for the (a) Ovens River at Warby Range Road and (b) Goulburn River for Northwood Road, during the 2006–2007 spawning season. Equations are given only for significant regressions.

2004, Todd et al. 2005, Sponaugle et al. 2006). Temperature largely determines the size and the quantity of endogenous resources available to a larva at hatch, which in turn affects when exogenous feeding begins and the ability of the larva to feed at this time (Schiemer et al. 2004). It also strongly influences the rate of ontogeny, and can be lethal above and below thresholds, and for this reason has a strong effect on survival during early life history (Kamler 2002). In their typology of environmental variables that group 65 species of western European freshwater fishes, Teletchea et al. (2009) found that temperature during spawning, incubation and larval rearing is a key environmental factor in the life histories of freshwater fishes. Schiemer et al. (2004), for example, showed that there was a temperature band between 10° and 19°C in which mortality of *Chondrostoma nasus* was low. Above or below this band, mortality increased substantially, and related to disparate rates of growth, tissue differentiation, and metabolism. Todd et al. (2005) also found that no Murray cod (*Maccullochella peelii*) larvae reared at temperatures below 13°C survived. This is the temperature common to

the heavily regulated Mitta Mitta River, southern Australia, where the species no longer occurs. Thus, it is likely, despite the potential for local adaptations and different genetic stocks of Australian smelt, that similar factors influence intrinsic mortality across the different regions studied.

While recruitment in response to appropriate temperature ranges is supported by previous research and is logical physiologically, it was also apparent that the majority of Australian smelt recruits in the free-flowing Ovens River in 2006–2007 hatched during the period when the first significant increase in biomass of the two smallest size fractions of zooplankton occurred. By contrast, in the regulated Goulburn River, biomass of the two smallest size fractions of zooplankton showed a completely different pattern from that of the Ovens River: biomass peaked in mid-October, and hatching of recruits peaked between late October and late November. Nevertheless, the biomass of zooplankton in November in both rivers was comparable, and may have been sufficient to provide enough food for externally feeding larvae. A threshold density of

FIG. 12. Comparison of back-calculated hatch date frequency distributions (centered period 3 moving average) of Australian smelt for the entire breeding period (solid line) and for just juvenile recruits collected in February 2007 (dotted line). Numbers above curly brackets show numbers of fish for small values.

appropriate-sized prey is thought to be one of the key drivers in recruitment of fish (Hjort 1914), with the time of first feeding seen as a critical period.

In the case of the free-flowing Ovens River, temperature rose as discharge declined, and was associated with

significant increases in zooplankton biomass. Discharge and temperature for the previous month were the best descriptors of zooplankton biomass because instream production was the likely source of zooplankton in this river. In the regulated Goulburn River, on the other hand, zooplankton biomass was unrelated to temperature and instead showed a quadratic relationship with mean discharge from the previous week: the lowest masses of plankton were at intermediate discharge levels, with the highest masses at the highest discharge levels. The reason for the stronger relationship with discharge from the previous week may have been because the likely source of zooplankton was the warm, shallow Lake Eildon, the storage reservoir for the Goulburn River. Increased discharges from Lake Eildon would have entrained zooplankton; indeed, the peak in zooplankton biomass occurred when discharge rose in mid-September from approximately 23 to almost 70 m³/s in a week and then was maintained at high levels throughout our October sampling visit. Large impoundments are significant sources of zooplankton, and increased releases generally result in increases in advection of zooplankton downstream (Petts 1984), so our results are not new. However, the implications of the timing of those releases for fish recruitment and river regulation are profound.

It is likely that recruitment in the free-flowing Ovens River, and possibly the other rivers studied, was influenced by temperature for the reasons, primarily physiological as discussed above. Indeed, because all rivers showed recruitment peaks late in the breeding season and temperature was similar for each river pair, we hypothesize that temperature, probably related to physiological tolerances and effects on growth, metabolic and tissue differentiation rates, may largely influence the window during which recruitment takes place. But because patterns of timing and magnitude of recruitment were river specific, and based on our observations of plankton in the Ovens and Goulburn rivers, we also hypothesize that prey density, responding to unique interactions between temperature and discharge, plays a role in the timing and magnitude of recruitment of Australian smelt: in effect, a window within a window.

Our results imply that the temperature depression usually experienced by rivers like the Goulburn River (McMahon and Finlayson 1995) could have major effects on the recruitment of fish because of factors related to the physiology of epigenesis. To date, much of the investigation on the effects of temperature depressions in rivers has been on breeding (King 1998, Phillips 2001, Treadwell 2004, O'Connor and Zampatti 2006), whereas our results and some others (e.g., Todd et al. 2005) indicate that there may also be important recruitment effects. Furthermore, because the timing of zooplankton production and its source differ between regulated and free-flowing rivers, it is likely that recruitment of riverine fishes, especially those that breed

for only a short time, may doubly suffer. Thus, while fixing temperature depressions by multi-level offtakes may solve some of the problems with river regulation, there are other, probably more intractable problems associated with source, type, and timing of release of zooplankton from impoundments that need to be addressed also.

Concluding remarks

In conclusion, all hatching events in the rivers in our study did not contribute equally to recruitment of Australian smelt, concordant with predictions from the window-of-opportunity hypothesis. In each case, later breeding events, related to warmer water temperatures, contributed disproportionately to recruitment. This trend was consistent in both regulated and largely free-flowing rivers across the Murray-Darling Basin, although each river showed unique patterns in the timing and magnitude of hatching and recruitment. Results from the free-flowing Ovens and regulated Goulburn rivers suggest that these unique patterns may be because of interactions between local discharge and temperature regimes, coupled with the location of sources of food for the early life stages. While we intentionally studied a protracted spawning species to follow hatching recruitment conditions over an extended period, logical next steps would be to (1) determine whether other protracted spawning species show similar patterns of recruitment, since there is little doubt that temperature tolerances during ontogeny will vary with species; (2) determine if species that breed for only a brief period suffer poor rates of recruitment if hatching occurs outside conditions that are considered optimal; and (3) determine whether annual recruitment is always associated with the same part of the spawning season (the last few months in our case) in protracted spawning species. Further to this is a determination of whether a poor recruitment year is simply a natural phenomenon or one that is created or exacerbated by the effects of river regulation and subsequent alterations to the temperature regime and timing of food availability. A mixture of laboratory and mesocosm experiments, where larvae are exposed to ranges of temperatures and densities of prey at different times during ontogeny, would provide useful results. In addition, a comprehensive description of temporal changes in zooplankton densities, sizes and types in several regulated and free-flowing rivers, as well as determining how far zooplankton entrained in regulated flow releases travel downstream over several years, would tell us much about sources and timing of available food for newly feeding larval fishes.

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