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Riverscape recruitment: a conceptual synthesis of drivers of fish recruitment in rivers

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1 **Riverscape recruitment: a conceptual synthesis of drivers of fish**

2 **recruitment in rivers**

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5

6 **Abstract**: Most fish recruitment models consider only one or a few drivers in isolation, rarely include

7 species' traits and have limited relevance to riverine environments. Despite their diversity, riverine

8 fishes share sufficient characteristics that should enable predictions of recruitment. Here we

9 synthesize the essential components of fish recruitment hypotheses and the key features of rivers to

10 develop a model that predicts relative recruitment strength, for all fishes, in rivers under all flow

11 conditions. The model proposes that: *interactions between flow and physical complexity will create*

12 *locations in rivers, at meso-scales, where energy and nutrients are enriched, the resultant production*

13 *of small prey concentrated, and prey and fish larvae located (through dispersal or retention) so that*

14 *the larvae can feed, grow and recruit.* Our synthesis provides a rationale for how flow and physical

15 complexity affect fish recruitment, and provides a conceptual basis to better conserve and manage

16 riverine fishes globally.

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Introduction

Understanding what drives fluctuations in the sizes of fish populations has been one of the dominant pursuits of fisheries scientists for more than a century (Hjort 1914; Houde and Hoyt 1987; Matthews 1998). This is largely because of the desire to manage stocks for sustainable commercial and recreational harvesting in highly variable, unpredictable and complex environments (Lewin et al. 2006; Ricker 1954). Despite some progress, the general consensus is that this goal has not been realized, and most exploited marine fish stocks are degraded and sustainable fisheries overall are still remarkably rare (Caddy and Seijo 2005). The status of non-exploited fishes is no less dire (Hilborn et al. 2003; Jelks 2008). Knowledge of fish population dynamics in freshwaters generally lags far behind that in marine environments (Schlosser and Angermeier 1995; Ziv et al. 2012; Lintermans 2013; Cohen et al. 2016; McIntyre et al. 2016); the exception being recreational freshwater sport fisheries (Lewin et al. 2006).

The increasing imperilment of freshwater fishes worldwide (Jelks 2008; Froese and Pauly 2018) emphasizes the need for understanding the fundamental processes influencing the size and composition of fish populations. Knowledge of what drives fish recruitment is a key piece of the population dynamics puzzle, but is poorly understood (Chambers and Trippel 2012). Recruitment can be broadly defined as the number of individuals entering the population at some well-defined age- or stage-class in any given year (e.g. Caley et al. 1996; Maceina & Pereira 2007; King et al. 2013). We define recruitment as the number of 0+ individuals entering the population each year, as measured at a time following hatching, such that individuals have passed through the period when the majority of larval mortality has occurred (see King et al. 2013). This definition applies well to fishes of contrasting life histories and is quantitative.

It is axiomatic that recruitment is higher when the early life stages of a fish coincide with conditions favorable for survival (Houde and Hoyt 1987; Houde 1989a; Cushing 1990). However, what constitutes favorable recruitment conditions is the subject of much debate (see Chambers and

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63 Trippel 2012; King et al. 2013). The huge diversity of fish traits (e.g. morphology, life history,

64 physiology, behavior) also makes generalizations concerning recruitment problematic (Winemiller

65 and Rose 1993; Wootton 1998). Despite this diversity of traits and environments in which fishes live,

66 the majority of fishes share enough characteristics to suggest the potential for some common

67 drivers that influence recruitment strength (Chambers and Trippel 2012). The profusion of fish

68 recruitment hypotheses and models and the doggedness of fisheries scientists are testament to this

69 potential (Table 1).

70   For a young fish to develop, survive and therefore recruit successfully, it has to be located in

71 an area of suitable water quality, find enough food of the appropriate size and type that meets its

72 nutritional requirements and avoid being eaten. Importantly, the traits of the progeny of different

73 species (e.g. egg and larval size, number and dispersal capability) will influence interactions with

74 these drivers (Winemiller and Rose 1993). Most recruitment hypotheses have their origins in marine

75 systems (Table 1, Chambers and Trippel 2012), however, and because many marine bony fishes are

76 broadcast spawning, 'periodic' species, (*sensu* Winemiller and Rose 1992), comparative studies of

77 recruitment drivers of species of different life history strategies are relatively rare (Winemiller 2005).

78   The physical, chemical and biological characteristics of rivers are quite unlike those of

79 marine ecosystems, and furthermore, riverine fishes from all life history strategies (opportunistic,

80 periodic and equilibrium) are common (Winemiller 1989; Winemiller and Rose 1992; Humphries et

81 al. 1999; Mims and Olden 2012). Thus, even though the same requirements of all young fish have to

82 be met for them to recruit, the manner in which riverine fish accomplish this is necessarily

83 ecosystem- and life history strategy-dependent (see Hoagstrom and Turner 2015). Several fish

84 recruitment hypotheses, mostly from marine environments, have attempted to explain how young

85 riverine fish coincide with appropriate conditions for recruitment in space and time (Humphries et

86 al. 1999; Humphries et al. 2013; Hoagstrom and Turner 2015). These hypotheses, however, tend to

87 be limited geographically, climatically or phylogenetically: to date, there has been no integrated

88   model that predicts recruitment for all types of fishes, in rivers under all flow conditions.

89   Furthermore, despite the contribution that River ecosystem concepts have played in shaping our

90   current understanding of riverine patterns and processes (Vannote et al. 1980; Poff et al. 1997; Junk

91   et al. 1989; Walker et al. 1995), they are rarely invoked when attempts have been made to

92   understand recruitment processes in riverine fish (but see Zeug and Winemiller 2008; Falke et al.

93   2010).

94   We propose that to understand the drivers of fish recruitment in rivers, we need to consider

95   how species traits during the early life stage interact with the physical, chemical and biological

96   features of rivers, and how these in turn are affected by flow and climate. We develop the

97   Riverscape Recruitment Synthesis Model (RRSM) to describe how flow and physical complexity of

98   rivers affect fish recruitment, and to provide a conceptual basis to generate predictions relevant and

99   useful for management and research. This paper aims to:

100   1)   Assess which existing fish recruitment hypotheses are most relevant to riverine fishes;

101   2)   Determine how flow mediates macro- and meso-scale processes in rivers that are

102   relevant to fish recruitment;

103   3)   Describe how life history and other species traits influence interactions of species with

104   riverine patterns and processes relevant to recruitment, such as temperature, feeding

105   and predation;

106   4)   Describe how processes associated with the Fundamental Triad (Bakun 1998) – the

107   recruitment model that we consider best encapsulates the spatial and temporal factors

108   responsible for fish recruitment – likely operate in rivers; and

109   5)   Propose the RRSM that conceptualizes our understanding of what drives recruitment in

110   rivers

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112

113   Table 1 about here

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Fish recruitment hypotheses

117   Fish recruitment hypotheses can be broadly grouped as those that: (i) are associated with

118   matching fish larvae with a suitable prey environment, (ii) emphasize growth-mediated predator

119   avoidance, or (iii) highlight the importance of movement to, or retention in, nursery areas (see Table

120   1 and references therein). Most hypotheses assume high densities of appropriately-sized prey as

121   being a necessary requirement for successful recruitment, and some suggest that high levels of

122   predation can be avoided by growing fast (e.g. 'bigger is better'), or by dispersing to relatively benign

123   nursery areas ('coast conveyer-belt'). Recruitment hypotheses can also be grouped as those

124   suggesting the interaction between larvae and environmental factors (largely food and predators)

125   are spatially-related (e.g. 'plankton contact') or those that are temporally-related (e.g. 'window-of-

126   opportunity'). Most food- and predator-related hypotheses consider temporal coincidence of larvae

127   with prey. A more limited sub-set of hypotheses (e.g. 'aberrant drift') consider spatial coincidence of

128   larvae with prey; with movement a central theme in several of these.

129   We contend that Bakun's Fundamental Triad hypothesis (Bakun 1996, 1998, 2010) is the

130   most comprehensive in both its inclusion of several drivers (food, predator-avoidance,

131   movement/retention) thought to influence recruitment variability, and that it considers the

132   influence of these drivers spatially and temporally across different environments. The Fundamental

133   Triad arose in an attempt to describe the drivers of recruitment for broadcast-spawning pelagic

134   marine fishes (Bakun 1996, 1998, 2010). It incorporates three physical processes that are likely to

135   enhance recruitment: nutrient enrichment, food concentration, and processes that result in larvae

136   and their food being retained in, or moved to, suitable habitat. It also connects these processes to

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137　their sources and at the scales at which they operate. For example, macro-scale patterns (e.g.

138　climate) influence the overall amounts of available energy (i.e. carbon) and nutrients (e.g. nitrogen

139　and phosphorus) while, meso-scale patterns (e.g. water movement) influence where energy and

140　nutrients are incorporated into primary and secondary production, and in turn how this translates

141　into food for young fish. Hoagstrom and Turner (2015) extended the concept into freshwaters,

142　illustrating the potential relevance of the Fundamental Triad for braided lowland rivers of the North

143　American Great Plains, where broadcast-spawning fishes breed during floods, and recruitment is

144　enhanced through the nutrient enrichment and concentration, and propagule retention, that occur

145　associated with flood recession and slackwater habitats. Indeed, we propose that, with some

146　modifications, Bakun's Fundamental Triad can be further developed into a more generic riverine fish

147　recruitment model suitable for most river types and flow conditions (termed the 'Riverscape

148　Recruitment Synthesis Model' [RRSM], see below). But first, we explore the macro-scale patterns

149　that drive production in rivers, the meso-scale patterns in rivers that provide the template on which

150　fish recruitment acts, and the overriding role of flow in linking these two. We also consider other key

151　drivers of fish recruitment in rivers that are rarely incorporated into previous models (species traits,

152　temperature, nutrient and food retention and dispersal), before presenting the new model.

153

Flow-mediated macro- and meso-scale patterns and fish recruitment in rivers

155　　　　**Macro-scale patterns.** Rivers comprise a dendritic network of channels connected by

156　downstream flow, which in some rivers connect to a much larger floodplain during flooding. Climate

157　and geology largely govern the predictability, variation, and shape of the flow regimes (Figure 1).

158　Flow in turn influences the physical (e.g. temperature) and chemical (e.g. salinity) characteristics of

159　rivers, the sources, storage, transformation and transport of energy and nutrients, and the transport

160　of sediment, amongst other processes (Vannote et al. 1980; Junk et al. 1989; Walker et al. 1995;

161　Thorp et al. 2008; Humphries et al. 2014). At macro-scales (i.e. within a river catchment), carbon

162   (energy) and nutrient inputs are majorly influenced by flow and can be derived from headwaters

163   (Vannote et al. 1980), the floodplain (Junk et al. 1989) or locally within the river channel (Thorp and

164   Delong 1994), as a result of natural or anthropogenic processes (Kobayashi et al. 2009; Binckley et al.

165   2010; Hale et al. 2015). Regardless of the source of carbon, it is the magnitude, duration and

166   recurrence interval of flow events and the overall flow regime – interacting with the geology and

167   geomorphology of rivers – that determine the magnitude, timing and location of energy and nutrient

168   inputs (Humphries et al. 2014). These basal resources drive primary and secondary production, and

169   ultimately, fish recruitment.

170   Figure 1 here

171   **Interactions between macro-scale and meso-scale patterns.** Flow regimes and flow events

172   may be conceived as waves progressing from upstream to downstream, which interact with

173   geomorphic, and other types of structure in rivers to create a diversity of flow-retention zones (such

174   as eddies, slackwaters and confluences, Figure 1), influencing the transport and retention of energy

175   and nutrients in rivers derived at macro-spatial scales (Thorp et al. 2008; Humphries et al. 2014). For

176   example, at the extreme trough of a wave, when a river ceases to flow: there is very limited

177   transport, resulting in high retention of energy and nutrients along small scales within the river; the

178   vast majority of energy inputs and production occur locally; and flow-retention zones are in effect

179   disconnected lentic pools. At the other extreme, at the crest of a wave, during overbank flooding:

180   there tends to be substantial transport of energy and nutrients longitudinally and laterally; for those

181   rivers with substantial floodplains, flooding has a major input to river ecosystem metabolism; and

182   there is typically a diversity and large extent of floodplain flow-retention zones. For these rivers,

183   during and post-flooding, the floodplain will act as the zone of greatest retention. At intermediate

184   positions on the river wave (e.g. within channel flows), longitudinal transport will tend to

185   predominate over lateral transport of energy and nutrients, and there will be an intermediate

186   diversity of flow-retention zones.

187   It is these flow-retention zones – whose type, features and spatial location and distribution

188   will change as flow changes – that we propose are equivalent to Bakun's meso-scale (1 – 100 m^2)

189   habitats within which recruitment processes of many riverine fishes takes place. They are therefore

190   a key component in our RRSM.

191   **Meso-scale patterns.** Larval fish interact with their prey, predators and the physico-chemical

192   characteristics of their environment at the meso-scale (Figure 1; Winemiller and Rose 1993;

193   Schiemer et al. 2001; Fausch et al. 2002; King 2004b; Bakun 2010). This is unsurprisingly, also the

194   scale in rivers at which nutrients, algae and zooplankton production are related (Reynolds and

195   Descey 1996; Reynolds 2000; Ning et al. 2010). The more physically complex (structural [e.g. woody

196   debris, vegetation], geomorphic and hydraulic) a reach (O'Neill and Thorp 2011), the longer the

197   water residence time, and the more eddies, dead zones and slackwaters that exist (Reynolds 2000,

198   Schiemer et al. 2001; Vietz et al. 2013). This, in turn leads to greater accumulation of inorganic and

199   organic matter (Pringle et al. 1988; Sheldon and Thoms 2006), storage and transformation of

200   nutrients (Newbold 1992; Hein et al. 2005). It also leads to greater production of phytoplankton and

201   zooplankton (Reckendorfer et al. 1999; Reynolds 2000) and finally resulting in an increased potential

202   for young fish to find enough food. Zones of high water residence time, also allow relatively poorly-

203   swimming young fish an opportunity to be retained in this relatively benign rearing environment or

204   find faster currents for dispersal, if avoiding predators is necessary (Humphries et al. 1999; Schiemer

205   et al. 2001; Schludermann et al. 2012; Lechner et al. 2013; Lechner et al. 2017). Further discussion of

206   the role of physical complexity in retaining nutrients, and other basal resources, phytoplankton and

207   algae, the prey of fish larvae, and the fish larvae themselves is presented below.

208   These high retention zones are fundamental to the survival of those larval fish that have

209   little yolk reserve at hatch, and must begin feeding exogenously within hours-days (Figure 2, Table 2;

210   Schiemer et al. 2001). High concentrations of prey may be less important for others that have large

211   stores of yolk at hatch, thereby having their own intrinsic source of nutrient enrichment (Winemiller

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212   and Rose 1993; King 2005; Kaminskas and Humphries 2009), and therefore effectively bypass the

213   larval stage (*sensu* Balon 1999). Thus, because fishes differ enormously in their life history and other

214   species traits, the nature of, and requirements associated with, enrichment, concentration and

215   retention/dispersal processes will vary among species. To appreciate the implications of this for

216   recruitment, we need to take a short detour and consider patterns in life history and other species

217   traits.

218   Figure 2 here

219   **Species traits and recruitment**

220   Winemiller and Rose (1992) developed a triangular life history model, elaborating on

221   Pianka's *r-* and *K*-selection continuum (Pianka 1970), that seeks to explain how traits, such as

222   longevity, age at maturity, fecundity and size of offspring, interact with environmental conditions to

223   ensure the best chance for the survival of young. This model applies widely to marine and

224   freshwater fishes (Winemiller 1989; Humphries et al. 1999; Winemiller 2005; King et al. 2013; Mims

225   and Olden 2013). Winemiller and Rose's model proposes three conceptual endpoints or groups of

226   fishes: opportunistic, periodic and equilibrium (Table 2). The larvae of opportunistic and periodic

227   species typically have small amounts of yolk (consumed within hours-days) are small, undeveloped

228   and tend to swim poorly when first feeding exogenously (Wolter and Arlinghaus 2004; Kopf et al.

229   2014). For example, the early-stage 5-6 mm larvae of silver perch, *Bidyanus bidyanus*, a periodic

230   species, have critical swimming speeds less than 2 cm s^{-1} when they first start feeding at only 1-2

231   days-old (Kopf et al. 2014). Larvae of opportunistic species (e.g. Australian smelt, *Retropinna*

232   *semoni*, and Murray River rainbowfish, *Melanotaenia fluviatilis*), often occupy shallow habitats (King

233   2004b), and rely on dense zooplankton or meiofauna (e.g. rotifers, micro-crustaceans) to get them

234   through the transition phase from endogenous to exogenous feeding (King 2005; McCasker 2009).

235   Larvae of periodic species, such as golden perch, *Macquaria ambigua*, feed on tiny zooplankton prey

236   (e.g. planktonic rotifers and micro-crustaceans), because they are themselves planktonic and are

237   broadcast into the water column, typically in one batch (Arumugam and Geddes 1987). By contrast,

238   the larvae of equilibrium species typically have large amounts of yolk, which they consume over

239   many days, and are large, well-developed and swim well when first feeding exogenously. The larvae

240   of Murray cod, *Maccullochella peelii*, for example, are 8-10 mm and typically 7-10 days-old when

241   first feeding (Kaminskas and Humphries 2009) and have critical swimming speeds at this time of 15-

242   30 cm s^{-1} (Kopf et al. 2014). First-feeding equilibrium species typically feed on larger meiofauna and

243   early instars of insects, such as benthic cladocerans and chironomids (King 2005; Kaminskas and

244   Humphries 2009; Sauvanet et al. 2013).

245   Table 2 here

246   For the early life stages of fishes in rivers, movement and the capacity to disperse cannot be

247   divorced from their life history and other species traits. This is because traits, such as development

248   of fins, body size and the amount of yolk, will affect the capacity of a species to move to, and/or

249   maintain its position in, a preferred location (Kopf et al. 2014), and to find food that may be patchily

250   distributed (Winemiller and Rose 1993; Nishimura and Hoshino 2009; Jorgensen et al. 2014). There is

251   also variation within life history strategies in the amount and type of movement of the early life

252   stages (Wolter and Arlinghaus 2003). Most broadcast spawners are periodic species (Winemiller and

253   Rose 1992), and so drift of eggs and larvae of these species in river currents is the norm (Lechner et

254   al. 2016). But the larvae of only a subset of opportunistic and equilibrium species drift (Humphries

255   and King 2004; Lechner et al. 2016). This, together with the importance of dispersal and retention

256   processes as part of the Fundamental Triad, means that our RRSM needs to include an axis of life

257   history strategy, but also of movement and dispersal during early life.

258

259   **Temperature**

260   Temperature can have a strong influence on all processes affecting the dynamics of fish

261   populations, but it exerts a particularly strong effect on recruitment. The breadth of a fish species'

262   fundamental thermal niche (*sensu* Allen-Ankins and Stoffels 2017) is generally narrower during early

263   life history than at the juvenile stage and early adulthood (Fuiman and Werner 2002; Portner and

264   Farrell 2008). Furthermore, the relatively poor swimming capacity of larval fish leaves them less able

265   to regulate body temperatures through active selection of thermal habitats (Wolter and Arlinghaus

266   2004). Indeed, of all physical variables, temperature is thought to have the greatest effect on

267   survival of the early life stages of fishes (Houde 1989). There exists significant interspecific variation

268   in the fundamental thermal niche of riverine fishes within the same assemblage, including the larval

269   stages of those fishes. For example, the eggs, alevins, parr and smolt of arctic charr (*Salvelinus*

270   *alpinus*) have both a narrower and 'cooler' thermal niche than that of the brown trout, *Salmo trutta*

271   (Elliott and Elliott 2010; Turschwell et al. 2017). Within the Danube River, the fundamental thermal

272   niches for embryogenesis and larval development differ among brown trout, nase (*Chondrostoma*

273   *nasus*) and roach (*Rutilus rutilus*), resulting in them recruiting in river segments with different

274   thermal regimes (Schiemer et al. 2004). It follows, therefore, that spatial and temporal variation in

275   the thermal properties of the riverscape will likely have an effect on (a) intraspecific recruitment,

276   hence population dynamics, and (b) determining interspecific variation in recruitment, hence

277   dynamics at the community level .

278   The temperature of aquatic habitat varies at multiple spatial and temporal scales in

279   riverscapes (Caissie 2006). Variation in geomorphology, topography, solar radiation, streambed

280   composition, groundwater exchange and hydraulics — among other factors — causes spatial

281   heterogeneity in temperature along both the lateral and longitudinal dimensions of the riverscape.

282   Laterally, thermal regimes of habitats vary among the lotic (flowing channels) and lentic (e.g. oxbow

283   lakes) habitats of the riverscape (Tonolla et al. 2010); among lentic waterbodies on a floodplain

284   (Tonolla et al. 2010; Stoffels et al. 2017); and among habitats within the channel itself, even on a

285   scale of metres (Wawrzyniak et al. 2013; Dugdale et al. 2015; Baldock et al. 2016). Longitudinally,

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286   strong thermal gradients occur on a scale of kilometres within rivers (Caissie 2006; Fullerton et al.

287   2015; Stoffels et al. 2016; Allen-Ankins and Stoffels 2017). At yet larger spatial scales, variation in

288   geomorphology, orientation — hence solar radiation — and the influence of snowmelt and

289   groundwater generates spatial heterogeneity in thermal regimes across rivers within catchments

290   (Lisi et al. 2015; Snyder et al. 2015; Eschbach et al. 2017). Variation in climatic conditions among

291   seasons and years also generates temporal variation in the thermal states of aquatic habitats (Caissie

292   2006; Vatland et al. 2015). Temporal variation in river flows within and across years further alters

293   the thermal properties of the riverscape. Temporal changes in flow can cause changes in

294   hydrological connectivity, as well as the thermal mass of the waterbodies in, and hydraulics of, the

295   riverscape, which in turn alters the thermal dynamics of that riverscape (Caissie 2006; van Vliet et al.

296   2011).

297   Thus the riverscape is a dynamic mosaic of thermal habitats, which should interact with the

298   narrow, species-specific thermal niches of larval fish to influence spatial and temporal variation in

299   recruitment. It follows that any conceptual synthesis of riverine fish recruitment must include the

300   effects of temperature.

301

302   **Enrichment, concentration and retention processes in rivers**

303   Bakun's Fundamental Triad identifies three physical processes that are likely to enhance

304   recruitment: nutrient enrichment, nutrient and food concentration, and processes that result in

305   larvae and their food being retained in, or dispersed to, the same location (Bakun 1996, 1998, 2010).

306   The concept and related processes were developed for fishes in the marine environment, however,

307   below we describe how, when and where these processes may be applicable to the riverine

308   environment, for inclusion in the RRSM.

309   *Nutrient enrichment*. Potential sources of nutrient enrichment in rivers are unlike those in

310   marine systems, and include: flood-induced releases of soil nutrients (Baldwin and Mitchell 2000)

311   and vegetation decomposition (Naiman and and Decamps 1997; Watkins et al. 2011), runoff from

312   snowmelt (Townsendsmall et al. 2011), seasonal litter-fall (Vannote et al. 1980), deposition of fish

313   carcasses (Johnston et al. 2004; Verspoor et al. 2011; Swain and Reynolds 2015), mass-spawning of

314   vertebrate and invertebrate eggs (Näslund et al. 2015), terrestrial runoff (Hale et al. 2015), point-

315   source nutrient-enriched wastewater effluent (Aratani et al. 2007) and groundwater intrusions

316   (Briody et al. 2016; Table 2; Figure 2). For opportunistic and periodic species that are small and need

317   to feed soon after hatch , these sources of enrichment would provide enhanced primary production

318   which would in turn enhance the production of benthic and pelagic zooplankton (e.g. rotifers,

319   copepods, cladocerans), their principal food (King 2005; Pease et al. 2006; Nunn et al. 2007). For

320   equilibrium species, we contend that the nutrient enrichment process has largely been supplied to

321   the young fish by their mother through the provision of a relatively large yolk sac. Of course, if the

322   yolk is consumed before reaching the juvenile stage, then the same potential sources of nutrient

323   enrichment, mentioned above, may also be important for equilibrium species.

324   *Concentration*. Nutrient and larval fish food concentration can occur in a range of riverine

325   meso-scale hydrogeomorphic patches and also as yolk for some species (Figure 2, Table 2), but life

326   history strategy will influence the significance of each of these as a potential site of concentration.

327   For opportunistic fish species, that may spawn over extended periods, and that need to find dense

328   aggregations of small prey in which to start feeding in the first few days of life, some of the most

329   significant sites for nursery rearing or recruitment include: summer slackwaters, hyporheic or

330   groundwater upwellings (Humphries et al. 1999; King 2004a; Thorp et al. 2006), retentive mid-

331   channel (Reynolds and Descey 1996) or edge habitats (Schiemer et al. 2001), especially when

332   associated with eddies, floodplain habitats, such as disconnected oxbow lakes (Zeug and Winemiller

333   2008), and isolated in-channel water holes (Kerezsy et al. 2011). All these habitats occur where

334   currents are slowed or still, living and non-living organic material is deposited, and water

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335   temperatures are warm. For periodic species, which typically spawn over a shorter period than

336   opportunistic species, and often in response to rises in flow (King et al. 2003; Hoagstrom and Turner

337   2015), floodplains and off-channel habitats are probably the most likely locations for successful

338   rearing, due to the higher concentrations of nutrients and food in these habitats (Lake 1967;

339   Winemiller and Jepsen 1998; De Lima and Araujo-Lima 2004; Feyrer et al. 2006). But this would

340   depend on the longevity of both water in floodplain habitats and connection (or re-connection) with

341   the main river channel, to facilitate later dispersal. Slackwaters may also concentrate prey and

342   provide good conditions for feeding, growth and survival for periodic species in specific situations,

343   such as following flood recession (Hoagstrom and Turner 2015). Although larvae of both life history

344   strategies need small prey, opportunistic species tend to disperse more actively over short distances

345   to find food, whereas periodic species typically disperse more passively in the drift (Humphries et al.

346   1999; Kopf et al. 2014). Based on Winemiller and Rose's (1993) model, largely passive-dispersing tiny

347   larvae of periodic species would require relatively denser and larger patches of food than

348   opportunistic species for successful feeding. As suggested above, recently inundated floodplains,

349   even when food is patchily distributed, would meet this requirement in many cases. For equilibrium

350   species, their mothers have largely performed the concentration process for them: relatively large

351   yolk reserves, which are typical of such species, may be able to sustain fish for many days after

352   hatch. It will only be once the yolk is used up that suitable concentrations of prey will be required.

353   But by then, many of the food-related challenges associated with recruitment have been overcome,

354   and the comparatively large juveniles, with wide mouth gapes, have access to a large range of

355   invertebrates as prey (King 2005; Kaminskas and Humphries 2009). For these species, mortality may

356   be highest at the juvenile stage, when other demands, such as finding a territory, competition for

357   resources and predator avoidance become critical (Houde 1994).

358   *Retention/dispersal.* Fish larvae being retained in, or dispersing to, prey-rich, meso-scale

359   areas, are also likely to be critical for successful recruitment in rivers (Figure 2, Table 2). Poor-

360   swimming fish larvae and their zooplankton prey will be affected by similar physical forces in rivers

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361   as they are in oceans. More specifically, the more retentive a river reach (defined as approximately

362   two meander bends or about 20 times the width of the channel [Gordon et al. 2004]), the greater

363   the opportunity for zooplankton prey to feed, grow and reproduce and the greater the opportunity

364   for young fish to feed on this concentration of prey (Reynolds et al. 1991; Humphries et al. 1999;

365   Reckendorfer et al. 1999; Schiemer et al. 2001). If food is concentrated where fish hatch, then, all

366   other things being equal, there will be an advantage in those young fish being retained locally (King

367   2004a, b); this would be especially advantageous for opportunistic species. Alternatively, if food is

368   concentrated at some distance from where fish hatch, there will be an advantage in dispersing to

369   these more prey-rich locations and remaining there (Zeug and Winemiller 2008); this would be

370   especially advantageous for periodic species. This does not mean that all types of highly retentive

371   reaches are conducive for recruitment (Mallen-Cooper and Zampatti 2018): weir pools, for example,

372   create other problems, such as a uniformity of depth and velocity, while also providing good

373   conditions for the predators of young fish (Bice et al. 2017). In free-flowing rivers, retentiveness of

374   reaches is a function of the interaction between discharge and physical complexity and is relevant to

375   all river types (Reynolds et al. 1991; Reckendorfer et al. 1999; Schiemer et al. 2001; Vietz et al. 2013).

376   For example, a river with multiple channels may have high overall physical complexity during

377   moderate – high within channel flows, because the multiple channels create a diversity of hydraulic

378   and structural conditions. But this may be lost when the river recedes to only one channel as flows

379   decline. Determining the relationship between discharge and physical complexity of a reach is critical

380   in an assessment of reach retentiveness. This relationship will also affect the extent and behaviour

381   of hyporheic zones, and so nutrient concentration and transformation. As a consequence of this

382   retentiveness, the more physically complex a reach is, the greater the hydraulic diversity, instream

383   production, retardation and accumulation of organic and inorganic particles, enrichment and

384   concentration of nutrients, and the shorter the nutrient spiral length, all which contribute to

385   enhanced conditions for fish recruitment (Pringle et al. 1988; Reynolds et al. 1991; Newbold 1992;

386   Vranovsky 1995; King 2004b; Sheldon and Thoms 2006). If the larvae of opportunistic species are

387   retained in summer slackwaters and the larvae of periodic species can disperse on to floodplains,

388   where high concentrations of prey and slow or still currents occur, little energy needs to be

389   expended to maintain position and find food. For equilibrium species that have a high concentration

390   of food already available as yolk that will last for many days, dispersing downstream or upstream to

391   suitable juvenile rearing habitats, while avoiding concentrations of conspecifics and predators, may

392   instead, be paramount.

393   We predict that the influence of physical complexity on the three processes of enrichment,

394   concentration and retention in rivers is likely to be least at extreme low and high flows, and greatest

395   at intermediate flows. At extreme low flows, and cease-to-flow conditions, regardless of the

396   physical complexity, nutrient enrichment and concentration of potential prey can be enhanced

397   through shrinking water volumes (Ning et al. 2010). During flooding, when water moves out on to

398   previously dry floodplain, nutrient enrichment and concentration processes can be enhanced

399   through breakdown of vegetation and ponding, regardless of physical complexity (Naiman and

400   Decamps 1997; Watkins et al. 2011). At intermediate flows in a free-flowing river, the greatest

401   contrast in retentiveness would likely be between physically complex and simple reaches. Conditions

402   comprising a diversity of hydraulic habitat, high nutrient enrichment and concentration, high

403   retention of prey and fish larvae, are ideal conditions for fish recruitment, assuming predator density

404   does not overwhelm everything else.

405   The Fundamental Triad (Bakun 2010) does not directly address the effects of predation on

406   fish recruitment, although there is much literature to suggest predation is a significant factor (see

407   Houde 2009). It does, however, add a caveat or 'loophole strategy', which allows for good

408   recruitment under relatively poor feeding conditions if predators are few or absent; or alternatively,

409   allows for poor recruitment under good feeding conditions if predators are abundant (also see Gido

410   and Propst 2012). We therefore recognise the need to include predation as a factor in our RRSM.

411

412   **The Riverscape Recruitment Synthesis Model**

413   We have synthesized previous thinking about fish recruitment drivers (largely from marine

414   systems), riverine productivity and riverscape scaling considerations, and concepts related to life

415   history and other species traits for fish, and developed the Riverscape Recruitment Synthesis Model

416   (RRSM). The RRSM can be used to predict relative recruitment strength under various conditions for

417   fish from the three life history strategies (Figure 3, reading horizontally through the model). Climate

418   and flow are assumed to be the most influential drivers of many of the processes that lead to fish

419   recruitment; leading the RRSM to describe how, where and when these processes might take place

420   in riverscapes and how the different species traits (particularly life history) interact with these

421   processes to predict recruitment strength through the flow wave (reading vertically in the model).

422   The main hypothesis of the RSSM proposes that: *interactions between flow and physical complexity*

423   *will create locations in rivers, at meso-scales, where energy and nutrients are enriched, the resultant*

424   *production of small prey concentrated, and prey and fish larvae located (either through dispersal or*

425   *retention) so that the larvae can feed, grow and recruit.*

426   The RRSM includes as predictors of relative recruitment strength: a) flow-related amount

427   and sources of energy; b) processes associated with the Fundamental Triad and how they are

428   influenced by flow and physical complexity; c) flow-related movement and dispersal of the young

429   stages of fish from different life history strategies; and d) temperature, food and predation (Figure

430   3). Predictions are made for equilibrium, periodic and opportunistic life history strategies.

431   Descriptions of the inputs are brief, as they have previously been discussed.

432   The model includes:

433   a) *Amount and sources of energy* (Figure 3a). As discharge increases from base levels to overbank

434   flooding, sources and amounts of energy inputs to rivers are likely to change: at low flow, sources

435   may be local, whereas as discharge increases, sources of energy from upstream and from low-

436   lying floodplain habitats, such as benches and anabranches, may increase in importance (see

437   Humphries et al. 2014). As discharge increases, the amount of energy in perennial river systems

438   increases, as a greater area of a river is inundated and so more carbon becomes available, and

439   more material is transported longitudinally through the system (Vannote et al. 1980; Junk et al.

440   1989). Once discharge is overbank, the floodplain proper will contribute a large percentage of the

441   energy into rivers (Junk et al. 1989). In ephemeral systems, the amount of energy may be high at

442   low discharge, moderate at moderate discharge and high again at high discharge, depending on

443   antecedent conditions, sources of carbon, and the amount of shading and turbidity (Pringle et al.

444   1988).

445   b) *The Fundamental Triad processes and physical complexity* (Figure 3b). Nutrient enrichment,

446   concentration of nutrients and the prey of larval fish, and the retention of same will vary with

447   flow and reach physical complexity: being greatest at low and flood flows and intermediate at

448   within-channel discharge. Reach physical complexity will mediate the effects of discharge on

449   these processes, because it has a substantial influence on hydraulics, instream production,

450   retardation of organic and inorganic particles and nutrient spiral length.

451   c) *Movement/dispersal* (Figure 3c). For some riverine fishes, adults move to locations conducive to

452   the rearing of their young (De Lima and Araujo-Lima 2004), whereas for others, adults spawn in

453   one location and the eggs and/or larvae disperse, presumably to increase their chances of

454   encountering good conditions for recruitment (Lechner et al. 2016). Both types of movement will

455   be mediated by flow: low flow limits dispersal for species of all life history strategies, whereas

456   high flows and flooding provides the opportunity for larger-scale dispersal. The scale of

457   movement will thus be influenced by the life history and life stage of the species, but also by how

458   that movement is facilitated or impeded by the prevailing hydrologic environment (Lechner et al.

459   2017).

460   d) *Temperature, food and predation* (Figure 3d). Ideal recruitment conditions should occur when

461   temperatures are optimal for egg and larval development and growth, food is abundant and

462   predation is low. Because of the size, ability to move and how much parental care they receive,

463   the relative importance of biotic and abiotic factors in influencing recruitment of species from the

464   three life history strategies will differ. Thus, we give separate predictions of recruitment strength

465   based on hypothesized temperature, food and predation conditions for each life history strategy.

466   The types and densities of food available, will also be influenced by temperature and flow (Ning

467   et al. 2010). We also differentiate between reaches with low and high physical complexity

468   because of the substantial influence we suggest that this has on the Fundamental Triad

469   processes.

470   *e) Relative recruitment strength* (Figure 3e). Using our understanding of the key processes

471   influencing recruitment during different river flow conditions, we make predictions of the relative

472   recruitment strength of fish species from the three life-history strategies under three broad flows

473   and for reaches with low (solid color fish) and high (hatched fish) physical complexity.

474 Our model predictions assume that:

475   *i.*   at extreme low flows and extreme high flows, physical complexity will have little effect on

476   the components of the Fundamental Triad, although available energy would likely be lower

477   in reaches with low complexity, because of less potential decomposable material and less

478   surface area for primary and secondary production;

479   *ii.* at low flows, dispersal is limited, whereas dispersal becomes increasingly easier as flows

480   increase;

481   *iii.* recruitment strength is maximized when temperature is optimal for a particular species for

482   the eggs and larvae to grow and develop;

483   *iv.* recruitment strength is maximized when larvae coincide in time and space with high food

484   density and low predator density;

485   *v.*   based on the definitions of opportunistic, periodic and equilibrium end-point life history

486   strategies, we assume that populations of opportunistic and periodic species will vary

487   annually more than equilibrium species, and that populations of the first two will rarely be

488   limited by the carrying capacity of the environment, whereas populations of the last will be

489   limited by, and often at, the carrying capacity of the environment (Winemiller 2005).

490

491   Figure 3 here

492   The RRSM allows the relative recruitment strength of fish species of the three life history

493   strategies to be predicted, regardless of climate and river type (e.g. temperate stochastic, temperate

494   seasonal, tropical seasonal, arid stochastic), although how low flows or flooding are coupled with

495   temperatures conducive for enhanced productivity needs to be taken into account (Winemiller

496   2004). Antecedent conditions of flow and climate are also known to influence fish recruitment

497   strength (Stewart-Koster et al. 2011; Balcombe et al. 2012; Beesley et al. 2014), but are not explicitly

498   included in the RRSM. We acknowledge that longer-term flow and more general climatic conditions,

499   such as multi-year drought, are likely to be important influences on recruitment dynamics, but this

500   level of complexity is beyond the scope of the current model and should be developed as the model

501   is tested and refined. Nevertheless, we propose that the RRSM predictions are generalizable,

502   because they are based on processes and conditions associated with levels of flow (and interactions

503   with physical complexity of the river), and do not relate to particular flow regimes, or return times of

504   floods or low flows. Reliance or focus on flow regime has, in our opinion, allowed development of

505   ecological concepts in rivers (e.g. Vannote et al. 1980; Junk et al. 1989), but also ultimately limited

506   their generalizability. This is discussed further below in relation to predictions with the three broad-

507   flow levels considered in the RRSM.

508   **Low flow predictions** (lower arrow, Figure 3): In Mediterranean and wet-dry tropical and

509   arid-zone rivers, low-flow conditions are typically coupled with warmer temperatures conducive for

510   food production and optimal fish growth (Humphries et al. 1999; Balcombe et al. 2012; King et al.

511   2015). Irrespective of physical complexity of reaches, the amount of available energy to fuel

512   production is likely to be high during low flows, as nutrients are being concentrated by shrinking

21

513　habitats. This will result in enhanced growth rates of planktonic algae, and in turn rapid growth and

514　turnover of zooplankton and so increasing concentration of food for fish larvae. Low flows and the

515　abundance of shallow slackwaters, isolated water holes and highly retentive habitats more

516　generally, will mean that the movement of larger fish will be more restricted than under higher flow

517　conditions, but concentration of all organisms will increase as rivers contract, and so predation

518　should be moderate – high. Under these conditions, we predict that recruitment strength of

519　equilibrium and opportunistic species would be moderate because many of the conditions (i.e.

520　optimal temperatures, high food) are conducive for larval survival (Figure 3e). Predation intensity

521　should, however, be lower for equilibrium species, as parental care should provide a degree of

522　protection. The presence of predators at moderate – high densities, density-dependent competition

523　or water quality issues other than temperature would reduce survival. Structural refuge from

524　predation may also influence recruitment strength during low-flow conditions. Under the same

525　conditions, we predict that recruitment strength of periodic species would be zero – low, because: in

526　many cases, these species will not breed under such conditions (e.g. King et al. 2009, 2010; Zampatti

527　and Leigh 2013); but if fish do breed, the lentic or low-flow conditions would mean that eggs and

528　larvae, which normally disperse either wholly or largely passively, would tend to remain mostly near

529　where they were spawned and so likely end up in a narrower range of habitats than if dispersed

530　widely. Combining this with a poor swimming ability and small size – and therefore a need to find

531　lots of food quickly – may create conditions that make survival extremely uncertain for the larvae of

532　periodic species. For all life history strategies, the ability to disperse to new locations, will be limited

533　(Figure 3c).

534　　　　**Intermediate flow predictions** (middle arrow, Figure 3)**:** Under intermediate, within channel

535　flows, quite different conditions for recruitment strength are likely to prevail in river reaches with

536　low versus high physical complexity (Figure 3b). The coupling (e.g. tropical rivers) or otherwise (e.g.

537　Mediterranean rivers) of intermediate flows with warm temperatures will likely be an important

538　factor driving relative recruitment strength among the three exemplar river types. In all river types,

22

539   reaches with low complexity and therefore low retentive capacity may have high energy and

540   nutrient loads, but there would be few places where enrichment can take place naturally, except

541   perhaps during initial rises in flow. The poor retention of water, energy and nutrients would also

542   translate to poor production, growth and retention of fish larvae and their food. Under these

543   conditions, we predict that there would be relatively poor recruitment for periodic and opportunistic

544   species (Figure 3e). However, those equilibrium species that have parental care, and those with

545   larvae that are relatively large and swim well, may be buffered against the overall relatively poor

546   conditions, and so may experience moderate recruitment.

547   In contrast, in reaches with high complexity, recruitment strength should be proportionally

548   greater than in structurally simple reaches for fish of all life history strategies. This is because greater

549   complexity should: increase the potential for nutrient enrichment through downstream transport of

550   nutrients from areas higher in the catchment, runoff from previously dry areas, and increased

551   upwellings of groundwater and hyporheic water; and equally, if not more importantly, create a

552   greater number and diversity of hydrogeomoprhic zones (e.g. slackwaters, eddies and dead zones),

553   that would act as sites of concentration and retention of water, nutrients, fish larvae and their food.

554   Of the three life history strategies, recruitment should be lowest for periodic species at intermediate

555   flows, because, although they may spawn during these conditions, unless there are downstream

556   lentic areas where small, poorly swimming larvae passively find dense aggregations of appropriately-

557   sized prey, the likelihood is that mortality will be very high. In the case of intermediate flows,

558   opportunities for predators to move will be greater, and so predation may play a significant role in

559   affecting relative recruitment strength. But, such conditions also provide the potential for dispersal

560   of actively-swimming larval fish to avoid predators and competitors and to recruit to alternative

561   locations (Figure 3c). Recruitment conditions at intermediate flows for the early stages of fishes will

562   vary depending on whether the river is rising or whether it is falling and the rate of change. Free-

563   flowing rivers will generally rise rapidly but fall more slowly and spend relatively little time at any

564   one intermediate flow, whereas regulated rivers may remain for considerable periods at an

565   intermediate flow.

566   **Flood flow predictions** (upper arrow, Figure 3)**:** During flooding in reaches of both low and

567   high physical complexity for all river types, drifting eggs and larvae will be dispersed downstream

568   and laterally. On floodplains, enrichment through decomposition of terrestrial plants and other

569   organic matter and release of soil nutrients will occur, which will fuel the production of zooplankton

570   (Watkins et al. 2011). Concentration of nutrients and zooplankton, as floodplain water bodies

571   contract after flooding, enhances feeding conditions for larval fish (Lake 1967; Winemiller and

572   Jepsen 1998; De Lima and Araujo-Lima 2004; Feyrer et al. 2006). Flooding in tropical rivers

573   predictably occurs coupled with warmer temperatures optimal for the spawning, growth and

574   development of the early life stages (King et al. 2013); however, this coupling is less predictable in

575   Mediterranean rivers (where flooding commonly occurs from late winter – early summer) or arid-

576   zone rivers (where flooding occurs stochastically, but can occur throughout the year depending on

577   prevailing weather conditions). Assuming there is a coupling of high flows and warm temperatures,

578   we predict that periodic species would have the strongest relative recruitment strength of all life

579   history strategies under these conditions (Figure 3e); as large numbers of small eggs and larvae

580   would be dispersed widely among a diversity of environments, a subset of which would comprise

581   ideal conditions for survival and growth (McGinley et al. 1987; Winemiller and Rose 1993). Flood

582   flow conditions will affect the recruitment of equilibrium species quite differently from periodic

583   species, as many equilibrium species tend to breed predictably in the main channel, regardless of

584   flow (Humphries 2005). Eggs and larvae of those species receiving parental care generally require

585   flowing water or active intervention by the guarding male to provide enough oxygen; conditions that

586   are more challenging on floodplains than in the main channel. Recruitment of equilibrium species

587   may also be lower than during low flows because of the greater risk of predation and high current

588   speeds in the main channel increasing the risk of premature washout from nests or disruption to

589   other male guarding practices (e.g. mouth brooding). Under flood flow conditions, we predict that

590   recruitment strength for opportunistic species will be relatively high, for similar reasons as for

591   periodic species. The differences in relative recruitment strength would probably lie in the lower

592   fecundity of opportunistic species, which increases the risk of larvae ending up in unfavorable

593   conditions. Flooding does not typically cue opportunists to spawn (King et al. 2003), but it does allow

594   dispersal of larvae amongst floodplain wetlands (Tonkin et al. 2008), which is favorable for

595   recruitment overall.

596

Use of the RSSM for Conservation and Management of Riverine Fishes

598   Our synthesis highlights some key factors and processes that will not only contribute to

599   understanding flow-ecology relationships, but we hope will also assist in the conservation and

600   management of riverine fishes. In recent decades, environmental flows of various types have been

601   proposed to enhance or preserve riverine fish populations, particularly in flow-altered rivers

602   (Arthington 2012). Although flow is a key driver for recruitment, our model integrates other

603   important factors, such as temperature, physical complexity, movement, predation and species

604   traits that interact with flow to influence fish recruitment strength. The model can therefore be used

605   to explore elements of a river (e.g. temperature, physical complexity, flow) that are potentially able

606   to be manipulated or ameliorated by managers in regulated rivers, or protected in at-risk rivers.

607   Predictions can readily be made and tested about which species, based on life history and

608   knowledge of the physical complexity of river reaches, would benefit and which could be impaired

609   by flow alteration.

610   Our synthesis also proposes the likely zones in rivers that are critical for producing food for

611   fish larvae, and suggests flow-related mechanisms and pathways that are responsible for the growth

612   and survival of young fishes. It highlights the importance of physical complexity (hydraulic,

613   geomorphic and structural) in rivers and its role in the retentive capacity of reaches, which we

614   predict will have major influences on recruitment, especially at intermediate, in-channel flows. It

615   must be emphasized, however, that higher retention alone is insufficient to guarantee successful

616   recruitment, because of other mitigating factors, such as predation, lack of sheltering habitat and

617   hydraulic diversity and the presence of alien species. We conclude – as many others have before us –

618   that there is a need for a diversity of flows, from low-flows to flooding (Poff et al. 1997), and a

619   diversity of hydraulic and physical complexity, to promote recruitment for riverine fish assemblages.

620   Our synthesis now provides a solid rationale for why physical complexity is important for the earliest

621   stages of fishes' lives, whereas previously the focus of adding woody debris, for example, to rivers

622   for fish has been on providing adult habitat.

623   We embarked on this synthesis hoping to evaluate the significance of factors affecting

624   recruitment by drawing on multi-year and multi-species studies of riverine fishes. To our surprise,

625   there were no studies that we could find that simultaneously considered the relationship between

626   recruitment, life history and other traits of multiple fish species, and reach physical complexity over

627   a number of years under a range of flows. Such studies are desperately needed if we are to progress

628   our understanding of riverine fish recruitment, and in particular enable informed decisions about

629   environmental watering to improve fish populations. To reiterate our observation from the

630   Introduction, fish recruitment research in freshwater lags behind that in marine environments.

631   Furthermore, most freshwater fish recruitment research has focused on single recreational species,

632   rather than fish assemblages. Although solid foundations have been laid for understanding flow-fish

633   population dynamics relationships (see e.g. Schlosser 1985; Schlosser and Angermeier 1995) and

634   some promising developments have followed (e.g. Falke et al. 2010; Kerezsy et al. 2011; Balcombe et

635   al. 2012; Hoagstrom and Turner 2015), there seems a reluctance by researchers to posit recruitment

636   models in rivers and then to test them. Marrying the key principles of the riverscape concept (Fausch

637   et al. 2002) and river ecosystem models (Vannote et al. 1980; Junk et al. 1989; Thorp and Delong

638   1994) with the drivers of fish recruitment would seem to be a logical way forward.

639

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647

648   **References**

649   Allen-Ankins, S., and Stoffels, R.J. 2017. Contrasting fundamental and realized niches: two fishes with

650   similar thermal performance curves occupy different thermal habitats. Freshwater Science

651   **36**(3): 635-652.

652   Aratani, Y., Tajima, A., and Minamiyama, M. 2007. Relationship of nutrient and residual chlorine

653   concentration in treated wastewater with periphytic algae grown in a stream receiving treated

654   wastewater. *In* Water Science and Technology. pp. 375-386.

655   Arthington, A.H. 2012. Environmental flows: saving rivers in the third millennium. University of

656   California Press, Berkeley, California.

657   Arumugam, P.T., and Geddes, M.C. 1987. Feeding and growth of golden perch larvae and fry

658   (*Macquaria ambigua* Richardson). Trans. R. Soc. S. Aust. **111**(1): 59-65.

659   Bakun, A. 1996. Patterns in the ocean. California Sea Grant, in cooperation with Centro de

660   Investigaciones Biologicas del Noroeste, La Paz, Mexico.

661   Bakun, A. 1998. Ocean triads and radical interdecadal variation: bane and boon to scientific fisheries

662   management. *In* Reinventing fisheries management. Springer. pp. 331-358.

663 Bakun, A. 2010. Linking climate to population variability in marine ecosystems characterized by non-

664 simple dynamics: conceptual templates and schematic constructs. Journal of Marine Systems

665 **79**(3): 361-373.

666 Balcombe, S.R., Lobegeiger, J.S., Marshall, S.M., Marshall, J.C., Ly, D., and Jones, D.N. 2012. Fish body

667 condition and recruitment success reflect antecedent flows in an Australian dryland river.

668 Fisheries Science **78**(4): 841-847.

669 Baldock, J.R., Armstrong, J.B., Schindler, D.E., and Carter, J.L. 2016. Juvenile coho salmon track a

670 seasonally shifting thermal mosaic across a river floodplain. Freshwater Biology **61**(9): 1454-

671 1465.

672 Baldwin, D.S., and Mitchell, A. 2000. The effects of drying and re-flooding on the sediment and soil

673 nutrient dynamics of lowland river–floodplain systems: a synthesis. River Research and

674 Applications **16**(5): 457-467.

675 Balon, E.K. 1999. Alternative ways to become a juvenile or a definitive phenotype (and on some

676 persisting linguistic offenses). Environmental Biology of Fishes **56**: 17-38.

677 Beesley, L.S., Gwinn, D.C., Price, A., King, A.J., Gawne, B., Koehn, J.D., and Nielsen, D.L. 2014. Juvenile

678 fish response to wetland inundation: how antecedent conditions can inform environmental

679 flow policies for native fish. Journal of Applied Ecology **51**(6): 1613-1621.

680 Bice, C. M., Gibbs, M. S., Kilsby, N. N., Mallen-Cooper, M., and Zampatti, B. P. 2017. Putting the

681 "river" back into the Lower River Murray: quantifying the hydraulic impact of river regulation

682 to guide ecological restoration. Transactions of the Royal Society of South Australia, **141**(2):

683 108-131.

684 Binckley, C.A., Wipfli, M.S., Medhurst, R.B., Polivka, K., Hessburg, P., Brion Salter, R., and Kill, J.Y.

685 2010. Ecoregion and land-use influence invertebrate and detritus transport from headwater

686 streams. Freshwater Biology **55**(6): 1205-1218.

687   Briody, A.C., Cardenas, M.B., Shuai, P., Knappett, P.S.K., and Bennett, P.C. 2016. Groundwater flow,

688   nutrient, and stable isotope dynamics in the parafluvial-hyporheic zone of the regulated Lower

689   Colorado River (Texas, USA) over the course of a small flood. Hydrogeology Journal: 1-13.

690   Caddy, J.F., and Seijo, J.C. 2005. This is more difficult than we thought! The responsibility of

691   scientists, managers and stakeholders to mitigate the unsustainability of marine fisheries.

692   Philosophical Transactions of the Royal Society B: Biological Sciences **360**(1453): 59-75.

693   Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater biology **51**(8): 1389-1406.

694   Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., and Menge, B.A. 1996. Recruitment

695   and the local dynamics of open marine populations. Annual Review of Ecology and

696   Systematics **27**: 477-500.

697   Chambers, R.C. 1997. Environmental influences on egg and propagule sizes in marine fishes. *In* Early

698   life history and recruitment in fish populations. Springer. pp. 63-102.

699   Chambers, R.C., Leggett, W.C., and Brown, J.A. 1989. Egg size, female effects, and the correlations

700   between early life history traits of capelin, *Mallotus villosus*: An appraisal at the individual

701   level. Fishery Bulletin **87**(3): 515-523.

702   Chambers, R.C., and Trippel, E. 2012. Early life history and recruitment in fish populations. Springer

703   Science & Business Media.

704   Cohen, A.S., Gergurich, E.L., Kraemer, B.M., McGlue, M.M., McIntyre, P.B., Russell, J.M., Simmons,

705   J.D., and Swarzenski, P.W. 2016. Climate warming reduces fish production and benthic habitat

706   in Lake Tanganyika, one of the most biodiverse freshwater ecosystems. Proceedings of the

707   National Academy of Sciences **113**(34): 9563-9568.

708   Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press Archive, Cambridge.

709   Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of

710   the match/mismatch hypothesis. Advances in Marine Biology **26**: 250-293.

711   De Lima, Ã.C., and Araujo-Lima, C.A.R.M. 2004. The distributions of larval and juvenile fishes in

712   Amazonian rivers of different nutrient status. Freshwater Biology **49**(6): 787-800.

713   Dugdale, S.J., Bergeron, N.E., and St-Hilaire, A. 2015. Spatial distribution of thermal refuges analysed

714   in relation to riverscape hydromorphology using airborne thermal infrared imagery. Remote

715   Sensing of Environment **160**: 43-55.

716   Elliott, J.M., and Elliott, J.A. 2010. Temperature requirements of Atlantic salmon Salmo salar, brown

717   trout Salmo trutta and Arctic charr Salvelinus alpinus: predicting the effects of climate change.

718   Journal of Fish Biology **77**(8): 1793-1817.

719   Eschbach, D., Piasny, G., Schmitt, L., Pfister, L., Grussenmeyer, P., Koehl, M., Skupinski, G., and

720   Serradj, A. 2017. Thermal-infrared remote sensing of surface water-groundwater exchanges in

721   a restored anastomosing channel (Upper Rhine River, France). Hydrological Processes **31**(5):

722   1113-1124.

723   Falke, J.A., Bestgen, K.R., and Fausch, K.D. 2010. Streamflow reductions and habitat drying affect

724   growth, survival, and recruitment of brassy minnow across a Great Plains riverscape.

725   Transactions of the American Fisheries Society **139**(5): 1566-1583.

726   Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to riverscapes: Bridging the

727   gap between research and conservation of stream fishes. BioScience **52**(6): 483-498.

728   Feyrer, F., Sommer, T., and Harrell, W. 2006. Managing floodplain inundation for native fish:

729   Production dynamics of age-0 splittail (*Pogonichthys macrolepidotus*) in California's Yolo

730   Bypass. Hydrobiologia **573**(1): 213-226.

731   Francis, M.P. 1994. Duration of larval and spawning periods inPagrus auratus (Sparidae) determined

732   from otolith daily increments. Environmental biology of fishes **39**(2): 137-152.

733   Froese, R., and Pauly, D. Editors. 2018. FishBase. World Wide Web electronic publication.

734   www.fishbase.org, version (02/2018).

735   Fuiman, L.A., and Werner, R.G. 2002. Fishery science: the unique contributions of early life stages.

736   Blackwell, Oxford.

737 Fullerton, A.H., Torgersen, C.E., Lawler, J.J., Faux, R.N., Steel, E.A., Beechie, T.J., Ebersole, J.L., and

738   Leibowitz, S.G. 2015. Rethinking the longitudinal stream temperature paradigm: region-wide

739   comparison of thermal infrared imagery reveals unexpected complexity of river temperatures.

740   Hydrological Processes **29**(22): 4719-4737.

741 Gido K.B., and Propst D.L. 2012. Long-term dynamics of native and nonnative fishes in the San Juan

742   River, New Mexico and Utah, under a partially managed flow regime. Transactions of the

743   American Fisheries Society **141**(3):645-659.

744 Gordon, N.D., McMahon, T.A., and Finlayson, B.L. 2004. Stream hydrology: an introduction for

745   ecologists. John Wiley and Sons.

746 Hale, R.L., Grimm, N.B., Vörösmarty, C.J., and Fekete, B. 2015. Nitrogen and phosphorus fluxes from

747   watersheds of the northeast U.S. from 1930 to 2000: Role of anthropogenic nutrient inputs,

748   infrastructure, and runoff. Global Biogeochemical Cycles **29**(3): 341-356.

749 Hansen, M.J., Bozek, M.A., Newby, J.R., Newman, S.P., and Staggs, M.D. 1998. Factors affecting

750   recruitment of walleyes in Escanaba Lake, Wisconsin, 1958–1996. North American Journal of

751   Fisheries Management **18**(4): 764-774.

752 Harris, J.H., and Gehrke, P.C. 1994. Development of predictive models linking fish population

753   recruitment with streamflow. Proceedings of the Australian Society for Fish Biology Workshop.

754   *In* Population Dynamics for Fisheries Management. *Edited by* D.A. Hancock. Bureau of Rural

755   Resources Proceedings, Canberra. pp. 195-199.

756 Hein, T., Reckendorfer, W., Thorp, J.H., and Schiemer, F. 2005. The role of slackwater areas for

757   biogeochemical processes in rehabilitated river corridors: examples from the Danube. Arch.

758   Fur Hydrobiol. Suppl. Large Rivers **15**: 425-442.

759 Hilborn, R., Branch, T.A., Ernst, B., Magnussson, A., Minte-Vera, C.V., Scheuerell, M.D., and Valero,

760   J.L. 2003. State of the world's fisheries. *In* Annual Review of Environment and Resources. pp.

761   359-399.

762   Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapport du Conseil

763   d'Exploration de Mer **20**: 1-228.

764   Hoagstrom, C.W., and Turner, T.F. 2015. Recruitment ecology of pelagic-broadcast spawning

765   minnows: Paradigms from the ocean advance science and conservation of an imperilled

766   freshwater fauna. Fish and Fisheries **16**(2): 282-299.

767   Houde, E.D. 1989a. Subtleties and episodes in the early life of fishes. Journal of Fish Biology **35**(sA):

768   29-38.

769   Houde, E.D. 1989b. Comparative growth, mortality, and energetics of marine fish larvae:

770   temperature and implied latitudinal effects. Fishery Bulletin **87**(3): 471-495.

771   Houde, E.D. 1994. Differences between marine and freshwater fish larvae: implications for

772   recruitment. ICES Journal of Marine Science: Journal du Conseil **51**(1): 91-97.

773   Houde, E.D., and Hoyt, R. 1987. Fish early life dynamics and recruitment variability. Transactions of

774   the American Fisheries Society.

775   Houde, E.D. 2009. Recruitment variability. *In* Fish Reproductive Biology: Implications for Assessment

776   and Management. *Edited by* M.J. Fogarty, T.M. Jakobsen, and B.A. Megrey. Wiley, New York.

777   pp. 91-171.

778   Humphries, P. 2005. Spawning time and early life history of Murray cod, *Maccullochella peelii peelii*

779   (Mitchell) in an Australian river. Environmental Biology of Fishes **72**(4): 393-407.

780   Humphries, P., Keckeis, H., and Finlayson, B. 2014. The River Wave Concept: Integrating River

781   Ecosystem Models. BioScience **64**(10): 870-882.

782   Humphries, P., and King, A.J. 2004. Drifting fish larvae in Murray-Darling Basin rivers: composition,

783   spatial and temporal patterns and distance drifted. *In* Downstream movement of fish in the

784   Murray-Darling Basin. Statement, recommendations and supporting papers from a workshop

785   held in Canberra 3-4 June 2003. *Edited by* M. Lintermans and B. Phillips. Murray-Darling Basin

786   Commission, Canberra. pp. 51-58.

787   Humphries, P., King, A.J., and Koehn, J.D. 1999. Fish, Flows and Flood Plains: Links between

788   Freshwater Fishes and their Environment in the Murray-Darling River System, Australia.

789   Environmental Biology of Fishes **56**(1): 129-151.

790   Humphries, P., Richardson, A., Wilson, G., and Ellison, T. 2013. River regulation and recruitment in a

791   protracted-spawning riverine fish. Ecological Applications **23**(1): 208-225.

792   Iles, T., and Sinclair, M. 1982. Atlantic herring: stock discreteness and abundance. Science **215**(4533):

793   627-633.

794   Jelks, H.L.e.a. 2008. Conservation status of imperiled North American freshwater and diadromous

795   fishes. Fisheries **33**: 372-407.

796   Johnston, N., MacIsaac, E., Tschaplinski, P., and Hall, K. 2004. Effects of the abundance of spawning

797   sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams.

798   Canadian Journal of Fisheries and Aquatic Sciences **61**(3): 384-403.

799   Jorgensen, C., Opdal, A.F., and Fiksen, O. 2014. Can behavioural ecology unite hypotheses for fish

800   recruitment? ICES Journal of Marine Science **71**(4): 909-917.

801   Junk, W.J., Bayley, P.B., and Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems.

802   Can. Spec. Publ. Fish. Aquat. Sci. **106**: 110-127.

803   Kaminskas, S., and Humphries, P. 2009. Diet of Murray cod (*Maccullochella peelii peelii*)(Mitchell)

804   larvae in an Australian lowland river in low flow and high flow years. Hydrobiologia 636(1):

805   449.

806   Keckeis, H., Kamler, E., Bauer-Nemeschkal, E., and Schneeweiss, K. 2001. Survival, development and

807   food energy partitioning of nase larvae and early juveniles at different temperatures. Journal

808   of Fish Biology **59**(1): 45-61.

809   Kerezsy, A., Balcombe, S.R., Arthington, A.H., and Bunn, S.E. 2011. Continuous recruitment underpins

810   fish persistence in the arid rivers of far-western Queensland, Australia. Marine and Freshwater

811   Research **62**(10): 1178-1190.

812 Kerr, S.R., and Dickie, L.M. 2001. The biomass spectrum: a predator-prey theory of aquatic

813   production. Columbia University Press, Cambridge.

814 King, A.J. 2004a. Density and distribution of potential prey for larval fish in the main channel of a

815   floodplain river: Pelagic versus epibenthic meiofauna. River Research and Applications **20**(8):

816   883-897.

817 King, A.J. 2004b. Ontogenetic patterns of habitat use by fishes within the main channel of an

818   Australian floodplain river. Journal of Fish Biology **65**(6): 1582-1603.

819 King, A.J. 2005. Ontogenetic dietary shifts of fishes in an Australian floodplain river. Marine and

820   Freshwater Research **56**(2): 215-225.

821 King, A.J., Humphries, P., and Lake, P.S. 2003. Fish recruitment on floodplains: The roles of patterns

822   of flooding and life history characteristics. Canadian Journal of Fisheries and Aquatic Sciences

823   **60**(7): 773-786.

824 King, A.J., Humphries, P., and McCasker, N.G. 2013. Reproduction and early life history. *In* Ecology of

825   Australian Freshwater Fishes. *Edited by* P. Humphries and K.F. Walker. CSIRO Publishing,

826   Collingwood. pp. 159-192.

827 King, A.J., Townsend, S.A., Douglas, M.M., and Kennard, M.J. 2015. Implications of water extraction

828   on the low-flow hydrology and ecology of tropical savannah rivers: an appraisal for northern

829   Australia. Freshwater Science **34**(2): 741-758.

830 Kobayashi, Y., Kim, C., Yoshimizu, C., Kohzu, A., Tayasu, I., and Nagata, T. 2009. Longitudinal changes

831   in bacterial community composition in river epilithic biofilms: Influence of nutrients and

832   organic matter. Aquatic Microbial Ecology **54**(2): 135-152.

833 Kopf, S., Humphries, P., and Watts, R. 2014. Ontogeny of critical and prolonged swimming

834   performance for the larvae of six Australian freshwater fish species. Journal of Fish Biology.

835   **84**(6): 1820-1841.

836 Lake, J.S. 1967. Rearing experiments with five species of Australian freshwater fishes. I. Inducement

837   to spawning. Australian Journal of Marine and Freshwater Research **18**(2): 137-154.

838   Lasker, R. 1978. Factors contributing to the variable recruitment of the northern anchovy (Engraulis

839   mordax) in the Californian current: contrasting years 1975-1978. Rapports et Porcčs-Verbaux

840   des Réunions, Conseil International pour l'Exploration de la Mer **178**: 375-388.

841   Lechner, A., Keckeis, H., Glas, M., Tritthart, M., Habersack, H., Andorfer, L., and Humphries, P. 2017.

842   The influence of discharge, current speed and development on the downstream dispersal of

843   larval nase (Chondrostoma nasus) in the River Danube. Canadian Journal of Fisheries and

844   Aquatic Sciences **75**(2): 247-259.

845   Lechner, A., Keckeis, H., and Humphries, P. 2016. Patterns and processes in the drift of early

846   developmental stages of fish in rivers: a review. Reviews in Fish Biology and Fisheries **26**(3):

847   471-489.

848   Lechner, A., Keckeis, H., Schludermann, E., Loisl, F., Humphries, P., Glas, M., Tritthart, M., and

849   Habersack, H. 2013. Shoreline configurations affect dispersal patterns of fish larvae in a large

850   river. ICES Journal of Marine Science **71**(4), 930-942.

851   Lewin, W.-C., Arlinghaus, R., and Mehner, T. 2006. Documented and Potential Biological Impacts of

852   Recreational Fishing: Insights for Management and Conservation. Reviews in Fisheries Science,

853   **14**(4): 305-367.

854   Lintermans, M. 2013. Conservation and management. *In* Ecology of Australian freshwater fishes.

855   *Edited by* P. Humphries and K. Walker. CSIRO Publishing, Collingwood. pp. 282-316.

856   Lisi, P.J., Schindler, D.E., Cline, T.J., Scheuerell, M.D., and Walsh, P.B. 2015. Watershed

857   geomorphology and snowmelt control stream thermal sensitivity to air temperature.

858   Geophysical Research Letters **42**(9): 3380-3388.

859   Maceina, M., and Pereira, D.L. 2007. Recruitment. *In* Analysis and Interpretation of Freshwater

860   Fisheries Data. *Edited by* C.S. Guy and M.L. Brown. American Fisheries Society, Bethesda,

861   Maryland. pp. 121-185.

862   Mallen-Cooper, M., & Zampatti, B. P. (2018). History, hydrology and hydraulics: Rethinking the

863   ecological management of large rivers. Ecohydrology **11**(5): e1965.

864 Matthews, W.J. 1998. Patterns in Freshwater Fish Ecology. Kluwer Academic Publishers, Norewll,

865   Massachusetts.

866 McGinley, M.A., Temme, D.H., and Geber, M.A. 1987. Parental investment in offspring in variable

867   environments: theoretical and empirical considerations. The American Naturalist **130**(3): 370-

868   398.

869 McIntyre, P.B., Liermann, C.A.R., and Revenga, C. 2016. Linking freshwater fishery management to

870   global food security and biodiversity conservation. Proceedings of the National Academy of

871   Sciences **113**(45): 12880-12885.

872 Mims, M.C., and Olden, J.D. 2012. Life history theory predicts fish assemblage response to

873   hydrologic regimes. Ecology **93**(1): 35-45.

874 Mims, M.C., and Olden, J.D. 2013. Fish assemblages respond to altered flow regimes via ecological

875   filtering of life history strategies. Freshwater Biology **58**(1): 50-62.

876 Naiman and, R.J., and Decamps, H. 1997. The ecology of interfaces: riparian zones. Annual review of

877   Ecology and Systematics **28**(1): 621-658.

878 Näslund, J., Aldvén, D., and Závorka, L. 2015. Eggs from anadromous adults provide marine-derived

879   nutrients to Atlantic salmon and brown trout parr in late autumn – observations from a

880   Swedish coastal stream. Environmental Biology of Fishes **98**(12): 2305-2313.

881 Newbold, J.D. 1992. Cycles and spirals of nutrients. *In* The rivers handbook. Vol. 1. *Edited by* P.

882   Callow, and G. Petts. Blackwell Publising, Oxford. pp. 379-408.

883 Ning, N.S.P., Nielsen, D.L., Paul, W.L., Hillman, T.J., and Suter, P.J. 2010. Microinvertebrate dynamics

884   in riverine slackwater and mid-channel habitats in relation to physico-chemical parameters

885   and food availability. River Research and Applications **26**(3): 279-296.

886 Nishimura, K., and Hoshino, N. 2009. The evolutionary pattern of early life history in water currents.

887   Evolutionary Ecology **23**(2): 207-221.

888   Nunn, A., Harvey, J., and Cowx, I. 2007. The food and feeding relationships of larval and 0+ year

889   juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic shifts and

890   interspecific diet similarity. Journal of Fish Biology **70**(3): 726-742.

891   O'Neill, B.J., and Thorp, J.H. 2011. A simple channel complexity metric for analyzing river ecosystem

892   responses. River Systems **19**(4): 327-335.

893   Otterlei, E., Nyhammer, G., Folkvord, A., and Stefansson, S.O. 1999. Temperature-and size-

894   dependent growth of larval and early juvenile Atlantic cod (Gadus morhua): a comparative

895   study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal of Fisheries and

896   Aquatic Sciences **56**(11): 2099-2111.

897   Pease, A.A., Davis, J.J., Edwards, M.S., and Turner, T.F. 2006. Habitat and resource use by larval and

898   juvenile fishes in an arid-land river (Rio Grande, New Mexico). Freshwater Biology **51**(3): 475-

899   486.

900   Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., and

901   Stromberg, J.C. 1997. The natural flow regime: a paradigm for river conservation and

902   restoration. BioScience **47**(11): 769-784.

903   Pörtner, H.O., and Farrell, A.P. 2008. Physiology and climate change. Science: 690-692.

904   Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welocmme, R.L.,

905   and Winterbourne, M.J. 1988. Patch dynamics in lotic ecosystems: the stream as a mosaic.

906   Journal of the North American Benthological Society **7**(4): 503-524.

907   Rayner, T.S., Pusey, B.J., and Pearson, R.G. 2008. Seasonal flooding, instream habitat structure and

908   fish assemblages in the Mulgrave River, north-east Queensland: towards a new conceptual

909   framework for understanding fish-habitat dynamics in small tropical rivers. Marine and

910   Freshwater Research **59**(2): 97-116.

911   Reckendorfer, W., Keckeis, H., Winkler, G., and Schiemer, F. 1999. Zooplankton abundance in the

912   River Danube, Austria: the significance of inshore retention. Freshwater Biology **41**(3): 583-

913   591.

914   Reynolds, C.S. 2000. Hydroecology of river plankton the role of variability in channel flow.

915   Hydrological Processes **14**(16-17): 3119-3132.

916   Reynolds, C.S., Carling, P., and Beven, K. 1991. Flow in river channels: new insights into hydraulic

917   retention. Archiv fur Hydrobiologie **121**(2): 171-179.

918   Reynolds, C.S., and Descey, J.P. 1996. The production, biomass and structure of phytoplankton in

919   large rivers. Archiv fur Hydrobiologie Supplement **113**: 161-187.

920   Ricker, W.E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada **11**(5):

921   559-623.

922   Sauvanet, J., Bourdier, G., Jouve, L., Bec, A., and Desvilettes, C. 2013. Feeding of pike larvae (*Esox*

923   *lucius* L.) in an alluvial river backwater: fatty acid as markers of two organic matter flows.

924   Fundamental and Applied Limnology/Archiv für Hydrobiologie **183**(4): 337-350.

925   Schiemer, F., Keckeis, H., Reckendorfer, W., and Winkler, G. 2001. The "inshore retention concept"

926   and its significance for large rivers. Archive fur Hydrobiologie, Supplement **135**: 509-516.

927   Schiemer, F., Keckeis, H., Nemeschkal, H., Schludermann, E., Winkler, G., and Zweimuler, I. 2004.

928   Ontogenetic patterns in thermal adaptation of fish vs. long-term temperature trends in large

929   rivers. *In* International Congress Series. Elsevier, London. pp. 209-217.

930   Schlosser, I.J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes.

931   Ecology **66**(5): 1484-1490.

932   Schlosser, I.J., and Angermeier, P.L. 1995. Spatial variability in demographic processes in lotic fishes:

933   conceptual models, empirical evidence and implications for conservation. American Fisheries

934   Society Symposium **17**: 360-370.

935   Schludermann, E., Tritthart, M., Humphries, P., and Keckeis, H. 2012. Dispersal and retention of

936   larval fish in a potential nursery habitat of a large temperate river: an experimental study.

937   Canadian Journal of Fisheries and Aquatic Sciences **69**(8): 1302-1315.

938   Sheldon, F., and Thoms, M. 2006. In-channel geomorphic complexity: The key to the dynamics of

939   organic matter in large dryland rivers? Geomorphology **77**(3): 270-285.

940   Sinclair, M., and Iles, T.D. 1988. Population richness of marine fish species. Aquatic Living Resources

941   **1**(1): 71-83.

942   Snyder, C.D., Hitt, N.P., and Young, J.A. 2015. Accounting for groundwater in stream fish thermal

943   habitat responses to climate change. Ecological Applications **25**(5): 1397-1419.

944   Stewart-Koster, B., Olden, J. D., Kennard, M. J., Pusey, B. J., Boone, E. L., Douglas, M. and Jackson, S.

945   (2011). Fish response to the temporal hierarchy of the natural flow regime in the Daly River,

946   northern Australia. Journal of Fish Biology **79**(6): 1525-1544.

947   Stoffels, R., Weatherman, K., and Allen-Ankins, S. 2017. Heat and hypoxia give a global invader,

948   Gambusia holbrooki, the edge over a threatened endemic fish on Australian floodplains.

949   Biological Invasions **19**(8): 2477-2489.

950   Stoffels, R.J., Richardson, A.J., Vogel, M.T., Coates, S.P., and Muller, W.J. 2016. What do metabolic

951   rates tell us about thermal niches? Mechanisms driving crayfish distributions along an

952   altitudinal gradient. Oecologia **180**(1): 45-54.

953   Swain, N.R., and Reynolds, J.D. 2015. Effects of salmon-derived nutrients and habitat characteristics

954   on population densities of stream-resident sculpins. PLoS ONE **10**(6).

955   Thorp, J.H., and Delong, M.D. 1994. The riverine productivity model: an heuristic view of carbon

956   sources and organic processing in large river ecosystems. Oikos **70**(2): 305-308.

957   Thorp, J.H., Thoms, M.C., and Delong, M.D. 2006. The riverine ecosystem synthesis: Biocomplexity in

958   river networks across space and time. River Research and Applications **22**(2): 123-147.

959   Thorp, J.H., Thoms, M.C., and Delong, M.D. 2008. The Riverine Ecosystem Synthesis. Elsevier,

960   London.

961   Tonkin, Z.D., King, A.J., and Mahoney, J. 2008. Effects of flooding on recruitment and dispersal of the

962   Southern Pygmy Perch (*Nannoperca australis*) at a Murray River floodplain wetland. Ecological

963   Management and Restoration **9**(3): 196-201.

964   Tonolla, D., Acuna, V., Uehlinger, U., Frank, T., and Tockner, K. 2010. Thermal Heterogeneity in River

965   Floodplains. Ecosystems **13**(5): 727-740.

966   Townsendsmall, A., McClelland, J.W., Holmes, R.M., and Peterson, B.J. 2011. Seasonal and hydrologic

967   drivers of dissolved organic matter and nutrients in the upper Kuparuk River, Alaskan Arctic.

968   Biogeochemistry **103**(1): 109-124.

969   Turschwell, M.P., Balcombe, S.R., Steel, E.A., Sheldon, F., and Peterson, E.E. 2017. Thermal habitat

970   restricts patterns of occurrence in multiple life-stages of a headwater fish. Freshwater Science

971   **36**(2): 402-414.

972   Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river

973   continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**: 130-137.

974   van Vliet, M.T.H., Ludwig, F., Zwolsman, J.J.G., Weedon, G.P., and Kabat, P. 2011. Global river

975   temperatures and sensitivity to atmospheric warming and changes in river flow. Water

976   Resources Research **47**: 19.

977   Vatland, S.J., Gresswell, R.E., and Poole, G.C. 2015. Quantifying stream thermal regimes at multiple

978   scales: Combining thermal infrared imagery and stationary stream temperature data in a

979   novel modeling framework. Water Resources Research **51**(1): 31-46.

980   Verspoor, J.J., Braun, D.C., Stubbs, M.M., and Reynolds, J.D. 2011. Persistent ecological effects of a

981   salmon-derived nutrient pulse on stream invertebrate communities. Ecosphere **2**(2): 1-17.

982   Vietz, G.J., Sammonds, M.J., and Stewardson, M.J. 2013. Impacts of flow regulation on slackwaters in

983   river channels. Water Resources Research **49**(4): 1797-1811.

984   Vranovsky, M. 1995. The effect of current velocity upon the biomass of zooplankton in the River

985   Danube side arms. Biologia **50**(5): 461-464.

986   Walker, K.F., Sheldon, F., and Puckridge, J.T. 1995. Perspective on dryland river ecosystems.

987   Regulated Rivers: Research & Management **11**(1): 85-104.

988   Watkins, S.C., Nielsen, D., Quinn, G.P., and Gawne, B. 2011. The influence of leaf litter on

989   zooplankton in floodplain wetlands: changes resulting from river regulation. Freshwater

990   Biology **56**(12): 2432-2447.

991   Wawrzyniak, V., Piegay, H., Allemand, P., Vaudor, L., and Grandjean, P. 2013. Prediction of water

992   temperature heterogeneity of braided rivers using very high resolution thermal infrared (TIR)

993   images. International Journal of Remote Sensing **34**(13): 4812-4831.

994   Winemiller, K.O. 1989. Patterns of variation in life history among South American fishes in seasonal

995   environments. Oecologia **81**(2): 225-241.

996   Winemiller, K.O. 2004. Floodplain river food webs: generalizations and implications for fisheries

997   management. RAP Publication 2004/17, FAO Regional Office for Asia and the Pacific Bangkok,

998   Thailand, pp. 285-309.

999   Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries

1000   management. Canadian Journal of Fisheries and Aquatic Sciences **62**(4): 872-885.

1001   Winemiller, K.O., and Jepsen, D.B. 1998. Effects of seasonality and fish movement on tropical river

1002   food webs. Journal of Fish Biology **53**(SUPPL. A): 267-296.

1003   Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American

1004   fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic

1005   Sciences **49**(10): 2196-2218.

1006   Winemiller, K.O., and Rose, K.A. 1993. Why do most fish produce so many tiny offspring? American

1007   Naturalist **142**(4): 585-603.

1008   Wolter, C., and Arlinghaus, R. 2003. Navigation impacts on freshwater fish assemblages: The

1009   ecological relevance of swimming performance. Reviews in Fish Biology and Fisheries **13**(1):

1010   63-89.

1011   Wolter, C., and Arlinghaus, R. 2004. Burst and critical swimming speeds of fish and their ecological

1012   relevance in waterways. Berichte des IGB **20**: 77-93.

41

1013   Wootton, R.J. 1998. Ecology of Teleost Fishes. Kluwer Academic Publishers, Dordrecht, The

1014   Netherlands.

1015   Zampatti, B. P., and Leigh, S. J. 2013. Within-channel flows promote spawning and recruitment of

1016   golden perch, *Macquaria ambigua ambigua* – implications for environmental flow

1017   management in the River Murray, Australia. Marine and Freshwater Research **64**(7): 618–630.

1018   Zeug, S.C., and Winemiller, K.O. 2008. Relationships between hydrology, spatial heterogeneity, and

1019   fish recruitment dynamics in a temperate floodplain river. River Research and Applications

1020   **24**(1): 90-102.

1021   Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I., and Levin, S.A. 2012. Trading-off fish biodiversity,

1022   food security, and hydropower in the Mekong River Basin. Proceedings of the National

1023   Academy of Sciences **109**(15): 5609-14.

1024

1025

1026   **Tables**

1027   Table 1. How the major fish recruitment hypotheses are aligned with the key factors influencing

1028   survival, and whether the interaction between the early stages of fish and these factors are spatially

1029   or temporally related.

	Matching suitable prey environment with critical early life stages	Size and growth-mediated predator avoidance	Movement (dispersal & retention)
Temporal	Match-mismatch[1]	Bigger is better[10]	
	Critical period[2]	Stage-duration[11]	
	Flood recruitment model[3]	Growth-selection predation[12]	
	Stable ocean[4]	Growth-predation[13]	
	Parental condition[5]	Loophole strategies[14]	
	Low flow recruitment[6]		
	Window-of-opportunity[7]		
	Fundamental triad[8]		
Spatial	Plankton contact[9]	Growth-mortality[15]	Coast conveyer-belt[16]
	Fundamental triad[8]		Aberrant drift[17]
			Member-vagrant[18]
			Fundamental triad[8]

1030   [1] (Cushing 1990) [2](Hjort 1914) [3](Harris and Gehrke 1994) [4](Lasker 1978) 5 [6](Humphries et al. 1999) [7](Humphries

1031   et al. 2013) [8] (Bakun 1998), [9] [10] (Kerr and Dickie 2001) [11] (Francis 1994) [12] [13] [14] (Bakun 1998) [15] [16] [17](Cushing 1975)

1032   [18] (Iles and Sinclair 1982, Sinclair and Iles 1988)

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1034 Table 2. Species traits and the most significant potential sources and location of processes

1035 associated with the Fundamental Triad relevant for fish recruitment in rivers.

	Life history strategy		
	Opportunistic	Periodic	Equilibrium
Species traits			
Size at maturity	Small	Moderate-large	Moderate-large
Fecundity	Low	Very high	Low
Parental care	Possibly	None	Often
Size at hatch	Tiny	Small	Large
Yolk size	Small	Small	Large
Time from hatch to first feeding	Hours-days	Hours-days	Days-weeks
Size at first feeding	Tiny	Small	Large
Swimming ability	Poor	Very poor	Good
Fundamental Triad processes			
Nutrient enrichment	Flooding (soil nutrients), vegetation decomposition; snow melt; litter-fall; fish carcasses; eggs; terrestrial runoff; point-sources; groundwater	Flooding (soil nutrients), vegetation decomposition; snow melt; litter-fall; fish carcasses; eggs; terrestrial runoff; point-sources; groundwater	Maternal sources/yolk
Concentration of nutrients and food	Summer slackwaters; hyporheic upwellings; retentive mid-channel and edge habitats; eddies; floodplains habitats; isolated in-channel water holes; downstream of dams; macrophyte beds; debris dams	Floodplains; slackwaters during flood recession	Yolk
Retention/dispersal of food and fish larvae	Remain or disperse among slackwaters; disperse on to floodplains	Disperse on to floodplains; disperse to slackwaters during flood recession	Disperse downstream to various locations

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Recruitment of riverine fishes

Captions to figures

Figure 1. Macro-scale and meso-scale environmental patterns and interactions between the two, how they are filtered by life history and other species traits, influence individual or population processes and are mediated by dispersal/retention to create fish recruitment in rivers.

Figure 2. Examples in rivers of sources of nutrient enrichment; locations for concentration of food; and habitats likely to enhance retention of food and propagules. All the senior author's photographs and drawings, except: fish larvae (Tim Kaminskas) salmon carcass (By Peter Sircom Bromley, CC BY-SA 4.0; https://creativecommons.org/licenses/by-sa/4.0)], via Wikimedia Commons).

Figure 3. Riverscape recruitment synthesis model. The relationship between flow and: a) the amount & sources of energy in rivers; b) the Fundamental Triad of nutrient enrichment and the concentration and retention of young fish and their food mediated by physical complexity of the river reach; c) the potential for movement and dispersal of eggs & young fish (note: no periodic species are included during low flow because of the uncertainty of spawning under these conditions); and how this combines with d) hypothesized relative levels of temperature (Temp. & T), food (F) and predation (Pr) considered relevant for fish from opportunistic (O, blue), periodic (P, green) and equilibrium (E, orange) life history strategies; to predict e) relative recruitment strength for fish in low complexity (solid fish) and high complexity (hatched fish) reaches. For b), solid line = low physical complexity, dashed line = high physical complexity. ? = uncertainty of breeding.
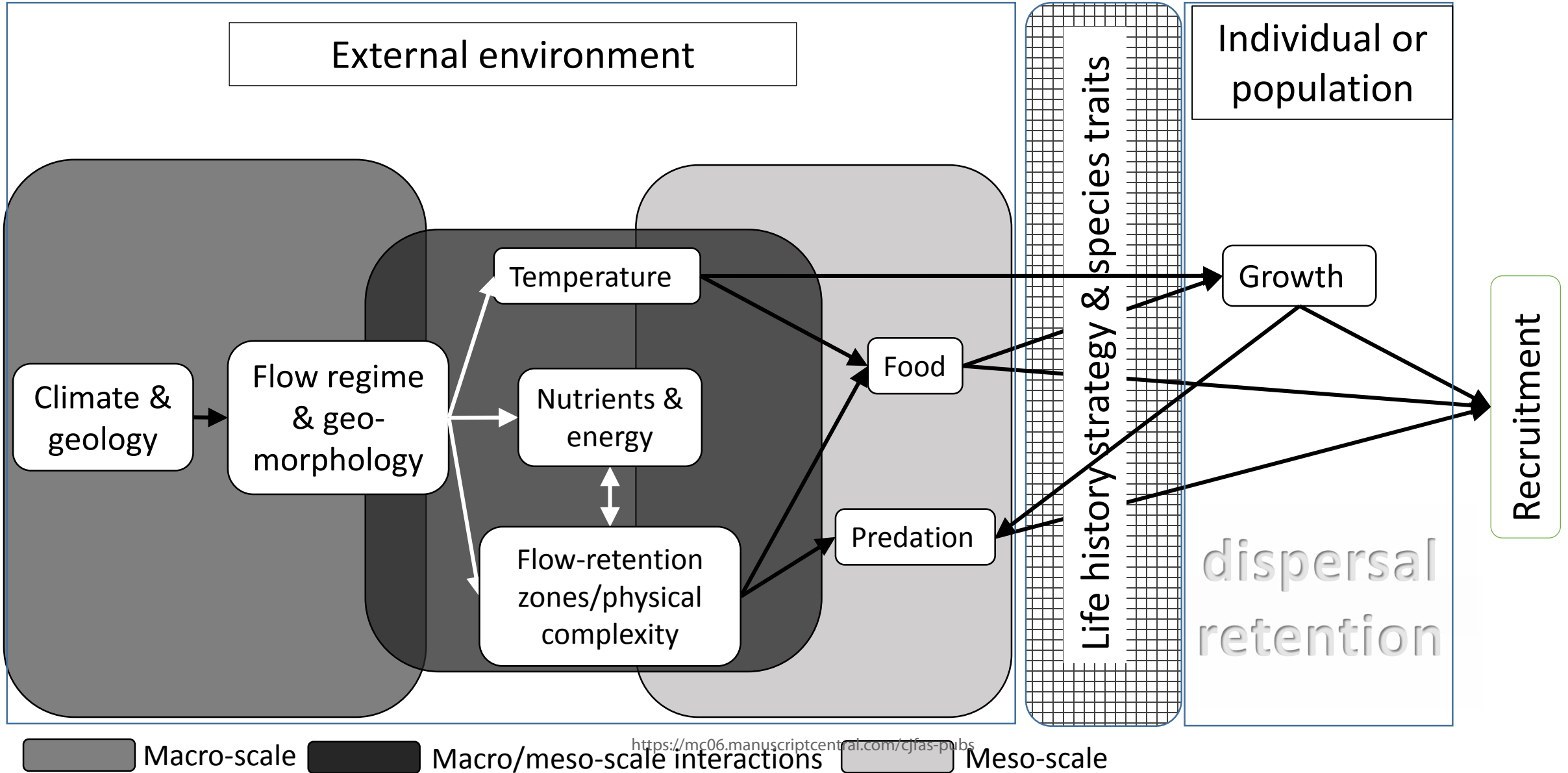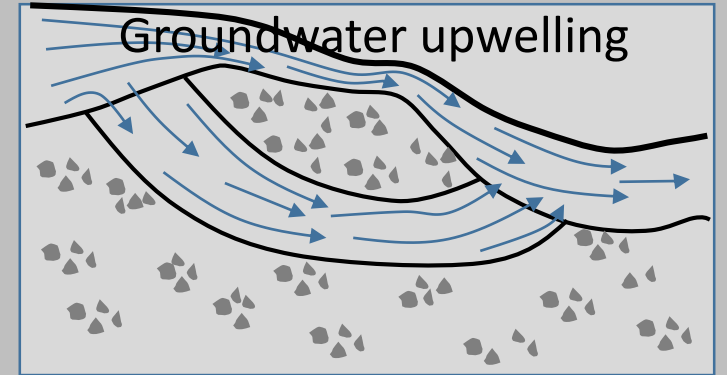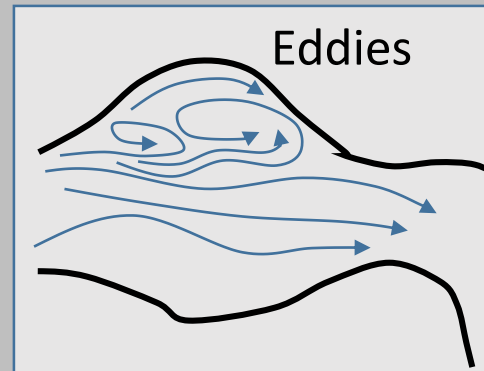
Recruitment of riverine fishes

Figure 1

Figure 2

1. Enrichment
   - Flooding
   - Salmon carcasses
   - Groundwater upwelling

2. Concentration
   - Yolk sacs
   - Eddies
   - Drying floodplain

3. Retention
   - Woody debris
   - Eddies
   - Slackwaters

Figure 3