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DYNAMICS OF RIVER FISH POPULATIONS IN RESPONSE TO HYDROLOGICAL CONDITIONS: A SIMULATION STUDY

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ABSTRACT

Increasing multi-sectoral demands on water resources have led to water abstraction and transfer activities, and the construction of dams and embankments that have significantly altered the flood regimes of rivers throughout the world resulting in the loss of fish production and biodiversity. The current emphasis on sustainable development and biodiversity conservation is leading efforts to mitigate these impacts by means of interventions such as the release of artificial floods downstream of dams and the manipulation of water levels within impounded floodplains.

Whilst much work has been done to determine the hydrological requirements for the maintenance of salmonid populations, few equivalent studies are available from which to develop criteria for the management of hydrological regimes for fishes and fisheries in large floodplain–river systems such as the Mekong. The population dynamics of fish in such rivers are believed to respond to hydrological conditions in a density-dependent manner. An age-structured population dynamics model incorporating sub-models describing density-dependent growth, mortality and recruitment was used to explore how hydrological conditions within a theoretical floodplain–river system affect the dynamics of a common floodplain–river fish species.

Graphical summaries of the response of exploitable biomass to a range of different drawdown rates, dry and flood season areas and volumes, and flood season durations are presented under five different model assumptions concerning density-dependent processes. Optimal flooding patterns are also described for the model species and theoretical river system.

The patterns of predictions that emerge from the simulations provide guidelines for managing or manipulating hydrological conditions in river systems for both fixed and variable volume hydrological scenarios. As a general rule of thumb, exploitable biomass is maximized by minimizing the rate of drawdown and maximizing the flood duration and flood and dry season areas or volumes. However, experiences from dam and other hydraulic engineering projects suggest that these predictions should be treated with caution until we better understand the influence of hydrology on spawning behaviour, system primary production, and critical habitat availability. Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS: floodplain fisheries; density dependence; flood control; dam releases

INTRODUCTION

River fisheries are an important source of protein food for many rural communities throughout the tropical world. Fish in unregulated rivers are highly adapted to seasonal changes in the amount of water in the river, and to the changes in the area and types of land flooded (Welcomme and Halls, 2001). The growing pressure on water to satisfy a range of human needs has led to increasing modification of the world's river systems that impact strongly on the quantity and timing of water available. Water abstractions and transfers alter the amount of water in the system. Transversal damming of the channel, construction of longitudinal levees and river training structures, and the poldering of river floodplains change the form and function of the river. The nature and timing of the hydrograph is also influenced by deforestation, land clearances for agriculture and wetland reclamation. These changes

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in hydrology impact on the composition and behaviour of fish populations as well as on community properties such as biomass and production (Welcomme, 2001).

The impacts of changing hydrological regimes are regularly assessed in north temperate rivers using instream flow incremental methodologies and the related Physical Habitat Simulation System (PHABSIM) (Stalnaker *et al.*, 1994; Bovee *et al.*, 1998). Instream flow methodologies have been used in many temperate zone countries to determine legal discharge requirements for the protection of fish and invertebrate faunas of salmonid rivers as well as large streams (for example Lamouroux and Souchon, 2002). Other methodologies have been developed to assess the impacts on fish of changing hydrological regimes in Australia (Arthington *et al.*, in press). The application of these methods, has been, with few exceptions, restricted to examining instream or main channel processes with little regard to the impacts of changes in flooding conditions upon the floodplains.

Natural resource managers and conservationists are equally concerned about retaining the sustainable production and biodiversity of tropical floodplain systems. Recently, attempts have been made to link the productivity of larger floodplain rivers to their flow characteristics through value-based systems such as the DRIFT methodology used in South Africa and Australia (King *et al.*, 2003). These methods do not, however, examine the dynamics of individual elements of the fauna to any degree and tend to give qualitative rather than quantitative answers. A more detailed analysis through simulation is needed to understand the processes resulting from hydrological changes and to predict outcomes of such changes through scenario-based determination of ecological flows. For example, the increasing withdrawal of water from aquatic systems and impoundment of water behind large dams is accompanied by a reliance on artificial releases and flood regimes to mitigate for the impacts of such schemes.

Age-structured population dynamics models of floodplain fisheries were first developed in 1977 to answer questions about the dynamics of fish populations under fluctuating water regimes (Welcomme and Hagborg, 1977). The original model has been adapted by various authors, to fluctuating systems such as the lakes of Madagascar (Moreau, 1980), the Central Delta of the Niger (Morand and Bousquet, 1994) and the dynamics of the spotfin swamp barb *Puntius sophore* in Bangladesh (Halls, 1998; Halls *et al.*, 2001). The model described by Halls *et al.* (2001) is here further developed and applied to explore optimal strategies for water releases under controlled conditions in floodplain rivers that maximize exploitable biomass. The model continues to be at an intermediate stage of development and there is much scope for further development to more fully address the questions being asked of the interactions between hydrology and fish dynamics.

MATERIALS AND METHODS

The model used in this study simulates the response of a fish population, inhabiting a theoretical floodplain–river system, to a wide range of hydrological (flooding and low flow) conditions. It combines a simple hydrological model with a fish population model.

The hydrological model

The hydrological component can be constructed to model a great variety of situations and even to reflect real systems. The only requirement is that it can generate at least weekly estimates of flooded area and volume as inputs to the population model. For the purpose of this paper the hydrological model comprises a theoretical river channel of minimum width W, and length L. The width of the floodplain is defined by the flooding depth (*FD*) above bankfull and the floodplain slope, θ_2 . Water begins to inundate the floodplain when the water height (*WH*) measured from the bed of the river channel exceeds the water height at bankfull (*WH*_{BF}) up to a maximum water height *WH*_{max} (Figure 1).

If $WH \le WH_{BF}$ then the total volume of water in the system in week w, V_W is given by:

$$V_w = (WL WH_W) + (\tan \theta_1 WH_w^2 L)$$

and the flooded area in week w, A_w is given by:

$$A_w = (WL) + (2\tan\theta_1 WH_w L)$$



Figure 1. The theoretical floodplain river system (see text and Table I for variable names)

If $WH > WH_{BF}$ then:

$$V_w = (WL WH_w) + (\tan\theta_1 WH_w^2 L) + \left(\frac{FD_w^2}{\tan\theta_2} L\right) + (2\tan\theta_1 WH_{BF} FD_w L)$$

and

$$A_{w} = (WL) + (2\tan\theta_{1} WH_{BF} L) + \left(2\frac{FD_{w}}{\tan\theta_{2}}L\right)$$

where

$$FD_w = WH_w - WH_{BF}$$

The selected parameters defining the theoretical floodplain–river system used for the simulations are summarized in Table I. The value of θ_2 was set to 0.172° to give a floodplain width of 1000 m at a maximum floodplain depth of 3 m.

The water height sub-model

The water height in the system during week w, WH_w (for $w = 1, 2, 3 \dots 52$), which determines how water volumes and areas within the theoretical river system change through time (the flooding pattern), is described by a step sine function where:

$$WH_w = a \sin 360 \left(\frac{w}{2T}\right) + WH_{BF}$$
, if $w < T$

Table I. Selected parameters defining the theoretical river system

Parameter	Value
Channel width, W (m) River length, L (m) Floodplain slope θ_2 (degrees) Mainstream bank slope θ_1 (degrees) Water height at bankfull, WH_{BF} (m) Floodplain width (m)	50 10000 0.171887 60 5 1000
Max. floodplain depth, FD_{MAX} (m)	3



Figure 2. Illustration of the three-step sine function parameters, a, b and T, used to generate hydrographs of different forms

and

$$WH_w = b\sin 360\left(\frac{w-T}{2(52-T)}\right) + WH_{BF}, \text{ if } w \ge T$$

where a and b are the flood and dry season amplitudes respectively, and T is the flood season duration in weeks (Figure 2).

By varying, a, b and T, this step sine function provides a very flexible means of simulating changes in water height and therefore different flooding patterns with time in the theoretical floodplain–river system described above. In heavily modified systems, inundation of the floodplain area may be restricted by levees and other hydraulic engineering structures.

Two hydrological scenarios are considered here: the fixed volume scenario and the variable volume scenario.

Fixed volume scenario. In this case it is assumed that a fixed volume of water passes through the system each year, although the rate of discharge can be controlled during the year to generate different flooding conditions. This aims to mimic flooding conditions downstream of dams where often a fixed volume of water must be discharged each year, but where there is some flexibility with respect to how this might be achieved. For example, water may be released to create short but deep floods, or at the other extreme, long but shallow floods, or a range of intermediate combinations.

For this fixed volume scenario, a range of different flooding patterns was simulated by varying the parameters a and T and then solving for the value of b to achieve a *reference* volume of $182.3 \times 10^6 \text{ m}^3$ defined as the sum of the weekly water volumes in the system during a 52 week year:

$$Volume_{ref} = \sum_{w=1}^{w=52} Vol_w$$

corresponding to the river system parameters defined in Table I and the following reference flooding conditions selected to represent median or normal hydrological conditions: a = 1.5 m, b = -2.5 m, T = 15 weeks.

The parameter *a* was then varied from 0.5 m to a maximum of 3 m in 0.5 m increments, whilst the minimum value for *b* was constrained to -4.5 m ensuring a minimum dry season depth of 0.5 m in the main channel. For each value of *a*, the duration of flooding on the floodplain, *T*, was varied from 5 to 40 weeks in 5-week increments to generate a range of different hydrographs (Figure 3) and therefore flooding patterns in the system. The required values of *b* to achieve the reference volume were calculated using the Microsoft[®] EXCEL Solver function.

Three ratio measures were used to describe the different flooding patterns for a given flood season duration T, generated by these hydrographs.

(1) The rate of change in water height between its maximum and minimum values—the drawdown rate, DDR:

$$DDR = \frac{a + |b|}{26}$$



Figure 3. Example hydrographs generated by the step sine function with fixed volume

(2) Flooded area ratio, FAR:

$$FAR = \frac{Minimum \ Flooded \ Area}{Maximum \ Flooded \ Area} \times 100$$

(3) Flooded volume ratio, FVR:

$$FVR = \frac{Dry \ Season \ Water \ Volume}{Flood \ Season \ Water \ Volume} \times 100$$

These ratios effectively encapsulate the important elements of duration and amplitude of the flooding pattern described by Poff *et al.* (1997) and Welcomme and Halls (2001).

Variable volume scenario. In this case, the total volume of water passing through the system can vary by more than a factor of 5 from 97×10^6 m³ a⁻¹ to 560×10^6 m³ a⁻¹ depending upon the selection of values for *a*, *b* and *T*. To generate this range of volumes, values for *a* were varied in the same way as for the fixed volume scenario to generate a range of different flooding conditions. The value of *b* was varied between -0.5 m and -4.5 m in increments of 1 m whilst *T* was varied from 10 to 25 weeks (typical of the flood duration range of most unmodified river systems) in increments of 5 weeks. Combinations of parameter values were constrained only to those that generated flood season volumes that exceed those of the dry season to allow for the effects of evapo-transpiration, abstraction and other losses between the two periods.

This scenario aims to mimic conditions in (i) unmodified systems where natural variations in discharge rates are common, or (ii) modified systems where dry season water volumes cannot exceed flood season volumes due to the seasonality of water availability. These systems would include flood control impoundments on floodplains that receive flood waters from the main river channel, or small rain-fed reservoirs.

The population model

A deterministic age-structured population dynamics model described by Halls *et al.* (2001) was used to examine how the exploitable biomass of a fish population inhabiting the theoretical floodplain–river system would respond to the range of different flooding patterns generated under the two scenarios described above. For reference, the model algorithms are provided in the appendix.

Annual yield or exploitable biomass can be predicted with the model allowing for weekly variations in agedependent growth and mortality rates and inter-annual variations in recruitment strength driven by changes in population density in response to exploitation and/or dynamic hydrological conditions (Figure 4). Here the focus of the investigation is limited to examining the response of an unexploited fish population to different hydrological conditions. Given the potential interactions between exploitation and hydrology on the population dynamics (see Halls *et al.*, 2001), inclusion of both factors would complicate the interpretation and understanding of the results.

The population model was parameterized for the spotfin swamp barb, *Puntius sophore* (Hamilton), a small but abundant cyprinid that inhabits a wide range of different floodplain–river system habitats in Bangladesh and southern Asia. *Puntius sophore* shares very similar characteristics with *Henicorhynchus* species that dominate catches in



Figure 4. Schematic representation of the population model illustrating the processes by which the biomass in week w becomes the biomass in the following week, w + 1. The weekly process is repeated for the 52 weeks of the year, after which recruitment, determined by the surviving spawning stock biomass, is added at the end of week 52. Solid lines indicate direct influences or operations and broken lines indirect influences or occasional operations (adapted from Welcomme and Hagborg, 1977)

the Tonle Sap and Lower Mekong rivers, as indeed with many fishes in highly exploited rivers that rely mainly on individuals belonging to the O+ and 1+ cohorts to supply the fishery. These common characteristics include rapid growth, small size and sexual maturation by the end of their first year. A summary of the parameter values and references to the model parameter estimation methodology are given in the appendix. Exploratory runs of the model with parameters corresponding to larger, slower growing fish with lower mortalities did not change the overall pattern of predictions of the model.

For the fixed volume scenario, exploitable biomass was examined in relation to the three hydrological indices described above (*DDR*, *FAR*, *FVR*). For the variable volume scenario, a greater range of hydrological conditions could be generated allowing exploitable biomass to be examined in relation to combinations of maximum and minimum flood and dry season depths and areas, respectively, and total flood and dry season volumes using contour plots generated with SYSTAT 10.

The model was also used to identify optimal hydrological conditions under the two water volume scenarios by solving for the values of *a*, *b* and *T* (see water height sub-model) that maximize exploitable biomass. Parameter values were constrained as follows: $a \le 3$ m and ≥ 0 m, $b \ge -4.5$ m and ≤ -0.1 m, $T \ge 5$ weeks and ≤ 40 weeks, and total annual water volume = *Volume_{ref}* for the fixed volume scenario.

The hydrological and population models were programmed in two separate MS Excel spreadsheets and then linked dynamically. The model predictions presented below represent equilibrium values of stabilized populations. Stabilized populations are defined here as populations in which inter-annual variations in the population attributes (growth and mortality rates, biomass, recruitment etc.) were less than 0.5% for at least three successive years within a maximum of 20 model years. An initial starting value of 1000 recruits was entered into year 1 of the population model to determine the equilibrium recruitment of the population under the reference hydrological conditions. The population stabilized after just 5 years with an annual recruitment of approximately 8 million juvenile fish. The model was then reseeded in model year 1 with 8 million recruits to begin the simulations.

The population model assumes that growth, mortality and recruitment are all density-dependent, where changes in density are driven by the dynamic interaction of population numbers and biomass, and hydrological conditions (water areas and volumes). Here we examine the relative influence of the three density-dependent processes on our

Model assumption	Growth	Mortality	Recruitment
1	DD	DD	DD
2	DD	DD	CONST
3	DD	CONST	CONST
4	DI	DD	CONST
5	DI	DD	DD

Table II. Combinations of density-dependent effects included in the model simulations for both hydrological scenarios

DD, density-dependent; DI, density-independent; CONST, constant.

model predictions for both hydrological scenarios by repeating the simulations with each possible combination of density-dependent effects in our model (Table II).

RESULTS

Fixed volume scenario

The effect of the drawdown rate (DDR) on exploitable biomass. Under model assumption 1 (all density-dependent processes operating), and for flood season durations (*T*) less than 30 weeks, average annual exploitable biomass is predicted to decline asymptotically with increasing drawdown rate (DDR) (Figure 5) arising from the interaction between higher recruitment and average number of fish in the population, but higher mortality rates and lower cohort mean weight. For values of $T \ge 30$ weeks, this complex interaction actually gave rise to increased biomass at intermediate values of DDR, before eventually declining.

Asymptotic declines in biomass with *DDR* were also found under model assumptions 2–4, but for all values of T examined. The exception to this was under model assumption 5 where growth is modelled to be independent of biomass density. Here, the pattern reflects the interaction between natural mortality and the compensatory stock–recruit relationship. At high values of T, mortality rates are relatively low but increase with increasing *DDR*. This is accompanied by increasing levels of recruitment corresponding to the right-hand limb of the Ricker stock–recruitment relationship. Eventually at intermediate and low values of T, mortality rates increase faster than the rate of recruitment as the drawdown rate increases leading to diminishing exploitable biomass.

The effect of the flooded area ratio (FAR) on exploitable biomass. Except under model assumption 5, exploitable biomass increases asymptotically with increasing FAR for all values of T (except T = 40 under model assumption 1) towards an apparently common asymptote corresponding to a FAR of between 10 and 15% depending on the model assumptions (Figure 5).

Under model assumption 5, complex interactions between compensatory recruitment and density-dependent natural mortality occur. Above *FAR* values of approximately 5%, exploitable biomass declines with increasing *FAR*. Higher biomasses are achievable for the same *FAR* by decreasing *T*. Below *FAR* values of approximately 5%, the converse in true.

The effect of the flooded volume ratio (FVR) on exploitable biomass. Except under model assumption 5, exploitable biomass also appears to increase asymptotically with increasing FVR for all values of T (except T = 40 under model assumption 1). In most cases, the same biomass is achievable across a range of FVR values by varying T.

Under model assumption 5, a complex interaction between compensatory recruitment and natural mortality, similar to that described above, occurs. For $T \ge 30$ weeks, biomass declines with increasing *FVR*. For T < 30 weeks, biomass is maximized at some intermediate *FVR* value which increases with decreasing *T*.

The optimal flooding pattern. Under the assumption of constant recruitment (model assumptions 2–4) and for the parameter constraints set, exploitable biomass is maximized by simultaneously maximizing the dry and flood season depth and flood season duration whilst minimizing the drawdown rate (Figure 6).



Figure 5. The response of exploitable biomass to (a) *DDR*, (b) *FAR* and (c) *FVR* for different flood season durations (FSD) under the five different model assumptions (Table II) for the fixed volume scenario



Figure 6. Flooding conditions for a fixed volume of water that maximizes exploitable biomass under model assumption 1 (dashed line), assumptions 2–4 (solid line) and assumption 5 (dotted line) in relation to bankfull height (solid horizontal line)

Under model assumption 5 where only density-dependent mortality and (compensatory) recruitment are assumed to be operating, a significant drawdown rate is required to raise natural mortality rates in order to counter the compensatory effect of the recruitment on the number of individuals in the population. Under assumption 1, this required drawdown is less pronounced since density-dependent growth is also operating, which counters the compensatory recruitment effect by lowering the fecundity of individuals. Under these two assumptions, long floods that are as deep as possible, are also required to maximize biomass since these conditions maximize the mean weight of individuals in the population.

Variable volume scenario

The relationships between exploitable biomass and the three combinations of hydrological variables considered all exhibited very similar patterns across the range of flood season durations examined, although biomass tended to increase with *T*. For the sake of brevity, we therefore present results only for T = 25 weeks for which the greatest number of combinations of values for *a* and *b* could be examined. Except under model assumption 5, this pattern was also very consistent under all four remaining model assumptions. Biomass is predicted to increase to a maximum as the flood and dry season variables examined increase simultaneously (Figure 7). In other words, biomass is maximized when both flood and dry season depths or areas or volumes (and flood season duration) are simultaneously maximized.

These predictions imply that when flood season depth, area and volume approach maximum values, exploitable biomass is determined almost exclusively by their dry season equivalents and vice versa. In other words, losses in biomass arising from reductions in depth, area or volume during the flood season can be compensated by increasing their magnitudes during the dry season or vice versa.

Under model assumption 5, a more complex picture emerges where maximum biomass corresponds to the maximum values for depth, flood area and volume during the flood season flood, but followed by a relatively short period of low dry season depths, areas and volumes (Figure 7). This reflects the effects of the compensatory nature of the stock recruitment relationship underlying this assumption as described above. Exploitable biomass was also predicted to increase with increasing flood season duration (not illustrated).

The optimal flooding pattern. Under model assumptions 1–4, exploitable biomass is maximized by simultaneously maximizing the dry and flood season depth and flood season duration, whilst minimizing the drawdown rate (Figure 8). Similar to the fixed volume scenario, when growth is assumed to be independent of biomass density, a significant drawdown is required to raise natural mortality rates in order to counter the compensatory effect of recruitment on the number of individuals in the population (see dotted line in Figure 8).

DISCUSSION

The population model assumes that growth, mortality and recruitment are all density-dependent. Beyond that described for *P. sophore*, empirical evidence of these processes in populations inhabiting large river systems is



Figure 7. Response of exploitable biomass to minimum dry season and maximum flood season (a) depths and (b) areas, and (c) total flood and dry season volumes, for the variable volume scenario under the five different model assumptions and a flood season duration, *T*, of 25 weeks

largely anecdotal or only implicit within the positive correlations found between catches or cohort mean length and various indices of flood strength and duration (see Welcomme (1985, 1995) for reviews). It is uncertain whether these correlations reflect diminished competition as available food and shelter per individual increase with flooded area and volume (density-dependent effects) or whether changes in primary production per unit flooded area or volume are also important (density-independent effects). Of course, in the case of catches, these correlations could also reflect changes in fishing effort and gear efficiency, but both effort and gear efficiency might be expected to



Figure 8. Flooding conditions for the variable volume scenario (subject to the constraints defined above) that maximizes exploitable biomass under model assumptions 1–4 (solid line) and assumption 5 (dotted line)

decrease, not increase, with more extensive flooding as fish densities are lowered and fishing operations become disrupted.

However, what is apparent from these empirical relationships is that if competition (density-dependent) effects are not important (i.e. if food and shelter are not limiting), then increased primary production would not lead to improved fish growth and catches. In other words, these empirical relationships must, at least partially, reflect the effects of density-dependent processes on the population. Density-independent effects are simply likely to exaggerate or diminish them depending on whether the effect of flooding on primary production per unit flooded area or volume is positive or negative, respectively.

Greater uncertainty surrounds the relative importance of density-dependent effects on the three main population regulation processes (growth, mortality and recruitment). Le Cren (1958), Kapetsky (1974), Backiel and Le Cren (1978) and Welcomme (1985) all report evidence of density-dependent growth, although Bayley (1988) found evidence of this process only among certain types of Amazonian species, possibly reflecting the special conditions of the Amazon where fish densities never reach levels where the process becomes important.

However, the model predictions presented here appear largely robust to the density-dependent assumptions underlying the model. That is, similar response patterns emerge regardless of where the density-dependent processes are assumed to be operating in the model. The major exception to this is when growth is modelled to be density-independent and both recruitment and mortality are modelled to be density-dependent (model assumption 5). The complex patterns that emerged from this combination reflect the compensatory Ricker stock–recruitment relationship used in the population model. This relationship predicts that at low spawning stock densities, recruitment increases with spawning stock density (corresponding to the left-hand limb of the curve) up to a certain point, and then declines with further increases in stock size (the right-hand limb of the stock–recruitment in most exploited fish populations typically corresponds to the almost linear left-hand limb of the stock–recruitment curve, so these complex compensatory recruitment effects would generally not be expected. Density-dependent growth produces a similar effect by effectively moving the population to this left-hand limb by reducing individual fecundity.

The patterns that emerge from these simulations provide some general guidelines for managing or manipulating hydrological conditions in floodplain–river systems.

For downstream fixed volume releases from dams (fixed volume scenario):

- Exploitable biomass is maximized by minimizing drawdown rates (*DDR*). If the drawdown rate is constrained, exploitable biomass may be increased by increasing the flood season duration, *T*.
- Exploitable biomass is maximized by maximizing the dry to flood season area ratio (*FAR*). Generally speaking, higher *FAR* values are achievable for longer flood season durations, *T*, when water release volumes are fixed.
- For a given value of *T*, exploitable biomass can be increased by increasing the dry to flood season volume ratio (*FVR*), but biomass is maximized at high values of *T*, which generally give rise to low values of *FVR* (high flood season volumes) when water release volumes are fixed.
- As a general rule, exploitable biomass tends towards some maximum as the *DDR* is minimized whilst simultaneously maximizing the flood season duration, *T*, the *FAR* and the flood season volume. The optimal

combination of parameter values that maximizes biomass will be unique to the system and its inhabitant fish populations and can only be identified using non-linear search techniques with models of these type.

For the variable volume scenario:

- Exploitable biomass is maximized by simultaneously maximizing flood and dry season depths, areas or volumes and flood season duration, *T*.
- As flood season depths, areas and volumes approach their maximum, exploitable biomass is determined almost exclusively by their dry season equivalents and vice versa. Therefore, losses in biomass arising from reductions in depth, area or volume during the flood season can be compensated by increasing their magnitudes during the dry season and vice versa.

For both scenarios:

• If (i) the population(s) is unexploited, (ii) recruitment is compensatory in nature, and (iii) growth, in particular, is density-independent, the optimal flooding pattern may need to include a period of low dry season water levels to reduce the spawning stock size to a level that maximizes recruitment. A preceding long deep flood season will help to maximize the mean weight of these recruits.

However, the general message that emerges here is that exploitable biomass is predicted to be maximized by simultaneously maximizing flood and dry season depths, areas or volumes and flood season duration to create a long, competition-free growing season and a short but deeply flooded dry season that minimizes the effects of density-dependent mortality. Indeed, without constraints placed upon the values of the hydrological model parameters a, b and T, the model predicts that biomass is maximized by inundating the floodplain throughout the year to a maximum depth with no drawdown phase or dry season period.

Competing demands from the agricultural sector for the highly fertile floodplain land during the dry season period usually make this permanent floodplain inundation scenario undesirable and even impossible on a large scale. The exception may be upstream of dams where river-lakes or reservoirs have been created for irrigation or hydroelectric generation, or within floodplain impoundments. However, experience from dam projects around the world indicates that the shift from pulse-regulated to more stable system dynamics upstream of the dam can bring about changes in community structure and overall production both upstream and downstream (World Commission on Dams, 2000). The most widely reported causes for these changes upstream (not including the interruption of migratory pathways by dam walls or levees) are the disruption of flow or thermal-based spawning cues, and changes to primary production and critical habitat diversity and availability arising from the modified hydrological conditions. Even natural lakes tend to be less productive than rivers. Bayley (1991) quotes yields of up to 125 kg ha⁻¹ a⁻¹ in rivers as opposed to 97 kg ha⁻¹ a⁻¹ in lakes in Africa that may reflect 'dynamic edge effects' (Junk *et al.*, 1989) on overall system productivity.

When viewed against practical knowledge of the fish and their behaviour in natural systems, this model forms a powerful and flexible tool for exploring the effect of varying hydrological conditions on fish populations and provides a means to develop scenarios upon which environmental flows can be assessed. (Assessment of environmental flows addresses how much and which elements of the original flow regime of a river should continue to flow down it and onto its floodplains in order to maintain specified, valued features of the ecosystem; Arthington and Pusey, 1993.) The present analysis does not remove fish by fishing, although provision is made in the general model to do so where gear catchability (efficiency) is modelled to vary as a function of biomass density.

The simulations presented here have been based upon a hypothetical river channel with floodplains subject to inundation. In heavily modified systems, inundation of this floodplain area may be restricted by levees and other hydraulic engineering structures. The effects of such modifications require further investigation. The model is currently being developed to include behavioural guilds of fish with interaction, critical habitat and spawning success components.

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APPENDIX

The population model and algorithms (from Halls et al., 2001)

The yield, *Y* in year *k* is given by:

$$Y_{k} = \sum_{i=0}^{i=t_{l}} \sum_{w=1}^{w=52} \left(\left[\frac{F_{k,i,w}}{F_{k,i,w} + M'_{k,w}} \right] \left[1 - \exp(-(F_{k,i,w} + M'_{k,w})) \right] N_{k,i,w} \overline{W}_{k,i,w} \right)$$

where t_i is the species longevity, integer years (1, 2, 3...); w is the week number (1, 2, 3...52); i is the age of fish in integer years (0, 1, 2, ...); $F_{k,i,w}$ is the weekly instantaneous fishing mortality rate during week w of year k on age i fish; $M'_{k,w}$ is the weekly instantaneous density-dependent natural mortality rate during week w of year k; $N_{k,i,w}$ is the number of age i individuals at the start of week w in year k; and $\overline{W}_{k,i,w}$ is the mean weight in week w of year k for age i fish.

If R_k is the number of recruits in year k, recruiting at age 0 at the beginning of week 1, then the numbers of age i fish at the start of week w in year k is given by:

$$N_{k,0,1} = R_k$$
 for $i = 0, w = 1$

$$N_{k,i,w} = R_{k-i} \exp\left[-\sum_{x=k-i}^{x=k-1} \sum_{y=0}^{y=i-1} \sum_{z=1}^{z=52} (F_{x,y,z} + M'_{x,z})\right] \exp\left[-\sum_{z=1}^{z=w-1} (F_{k,i,z} + M'_{k,z})\right] \quad \text{if } i \ge 1$$

and

$$N_{k,0,w} = R_k \exp\left[\sum_{z=1}^{z=w-1} (F_{k,0,z} + M'_{k,z})\right] \text{ for } i = 0, w > 1$$

The number of recruits in year k is determined by floodplain system fertility measured in terms of nitrate concentration (N), flooded area (A) and the density of eggs (S) produced by the spawning stock in the last week (week 52) of the previous year. The relationship is described by an extended form of the Ricker stock-recruitment model:

$$R_k = (\alpha S_{k-1,52} e^{-\beta S_{k-1,52} + cN_{k-1,52}}) A_{WH52}$$

where α , β and *c* are parameters of the extended Ricker stock-recruitment model; $N_{k,52}$ is the nitrate concentration (mg/100 litres) in week 52 of year *k*; A_{WH52} is the flooded area for water height (*WH*) at week 52; and $S_{k,52}$ is the number of eggs per square metre produced by the spawning stock in week 52 of year *k*.

The density of eggs produced in week 52 is a combination of the numbers of spawning individuals and their mean fecundity:

$$S_{k,52} = \frac{\sum_{i=t_m}^{i=t_l} N_{k,i,52} \overline{F}_{k,i,52}}{A_{WH52}}$$

where t_m is the age at maturity, integer years (0, 1, 2, ...) and $\overline{F}_{k,i,52}$ is the mean fecundity of age *i* fish in week 52 of year *k*.

The mean fecundity is given by:

$$\overline{F}_{k,i,w} = d(\overline{L}_{k,i,w})^e$$

where *e*, *d* are parameters of the length–fecundity relationship, and $\overline{L}_{k,i,w}$ is the mean length of age *i* fish in week *w* of year *k*. The relationship is described by the seasonally oscillating von Bertalanffy growth function (Pitcher and Macdonald, 1973). The asymptotic length is dependent upon biomass density after Lorenzen (1996):

$$\overline{L}_{k,i,w} = L_{\infty B,k,w} \left(1 - e^{-K \left[(i + \frac{w}{52} - t_0) + \frac{C \sin\left(2\pi (i + \frac{W}{52} - t_w)\right)}{2\pi} \right]} \right)$$

where *K* is the von Bertalanffy growth parameter, t_0 is the age at length zero, *C* is the amplitude of seasonal growth oscillation in growth rate (0–1), t_{ω} is the starting (winter) point of growth oscillation, and $L_{\infty B,k,w}$ is the asymptotic length in week *w* of year *k*.

This asymptotic length is dependent upon the biomass density B in the previous week given by:

$$L_{\infty B,k,w} = L_{\infty L} - g B_{k,w-1}$$
 for w = 2, 3, ... 52

$$L_{\infty B,k,w} = L_{\infty L} - g B_{k-1,52}$$
 for w = 1

where $L_{\infty L}$ is the limiting asymptotic length, g is the competition coefficient, and $B_{k,w}$ is the biomass density in week w of year k. Biomass density is described by:

$$B_{k,w} = \frac{\sum_{i=0}^{i=t_l} N_{k,i,w} \overline{W}_{k,i,w}}{V_{k,w}}$$

where $V_{k,w}$ is the volume of water upon the floodplain in week w of year k. The mean weight, \overline{W} , of age i fish in week w of year k, is given by:

$$\overline{W}_{k,i,w} = a(\overline{L}_{k,i,w})^b$$

where *a* and *b* are parameters of the length–weight relationship.

The weekly instantaneous density-dependent natural mortality rate $M'_{k,w}$ during week w of year k is a function of the numerical density ρ (N m⁻³) in the previous week given by:

$$M'_{k,1} = \gamma + \delta \rho_{k-1,52} \quad \text{for } w = 1$$

$$M'_{k,w} = \gamma + \delta \rho_{k,w-1}$$
 for $w = 2, 3, \dots 52$

where γ and δ are parameters of the mortality–density relationship.

The numerical density $\rho_{k,w}$, is defined by:

$$\rho_{k,w} = \frac{\sum_{i=0}^{i=t_l} N_{k,i,w}}{V_{k,w}}$$

The weekly instantaneous fishing mortality rate on age i fish during week w of year k is given by:

$$F_{k,i,w} = f_{k,w} q_{k,i,w}$$

where $f_{k,w}$ is the fishing effort during week w of year k, and $q_{k,i,w}$ is the catchability coefficient for age i fish during week w of year k defined as:

$$q_{k,i,w} = bB_{k,w}$$

where *b* is the slope coefficient.

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Sub-model	Parameter	Estimate	Reference(s)
DD Natural mortality	γ	0.000576	Halls (1998)
	$\delta (a^{-1} \text{ N}^{-1} \text{ m}^{-3})$	0.002	Halls (1998)
Stock-recruitment	α	0.000976	Halls (1998); Halls et al. (2000)
	β	-0.00018	Halls (1998); Halls et al. (2000)
	с	0.0292	Halls (1998); Halls et al. (2000)
	N $(mg l^{-1})$	1	Horne and Goldman (1994)
Length-fecundity	\overline{d}	4.5e-09	Halls et al. (1999)
	е	6.195	Halls et al. (1999)
DD growth	$L_{\infty L}$ (mm)	80	Halls et al. (2001)
	$g (\mathrm{mm kg^{-1} m^{-2}})$	0.016	Halls (1998)
VBGF	$K(a^{-1})$	2.15	Halls (1998)
	С	1	Halls (1998)

0.04

-0.08

8.14e-06

3.21

Halls (1998)

Halls (1998)

Halls et al. (1999)

Halls et al. (1999)

Table A1. The population model parameter estimates

ts

 t_0

а b Length-weight