Natural England Research Report NERR035

An evidence base for setting flow targets to protect river habitat

www.naturalengland.org.uk

Natural England Research Report NERR035

An evidence base for setting flow targets to protect river habitat

C P Mainstone

Natural England

Published on 10 January 2011

ISSN 1754-1956

Publications

Natural England

3rd Floor, Touthill Close, City Road

Peterborough

PE1 1XN

Tel: 0845 600 3078

Fax: 01733 455103

Email: enquiries@naturalengland.org.uk

Project details

A summary of the findings covered by this report, as well as Natural England's views on this research, can be found within Natural England Research Information Note RIN035 – An evidence base for setting flow targets to protect river habitat.

This report should be cited as:

MAINSTONE, C.P. 2010. An evidence base for setting flow targets to protect river habitat. *Natural England Research Reports, Number 035*. Natural England, Sheffield.

Project manager

Chris Mainstone
Evidence Team
Natural England
3rd Floor, Touthill Close
City Road
Peterborough
PE1 1XN
Tel: 0300 060 0956
Chris.Mainstone@naturalengland.org.uk

Acknowledgements

Thanks are due to Mike Dunbar (CEH), Patrick Armitage (FBA), Paul Wood (Loughborough University), Judy England, Mark Warren and Juliette Hall of the Environment Agency, and Dan Cadman (independent ecologist) for helpful feedback and information. Thanks also to Barry Gray of Natural England Information Services for assistance with obtaining scientific papers.

I am grateful to the following publishers for their permission to use tables and figures from their journals free of charge:

- North American Benthological Society (Tables 2 and 3 and Figures 2 and 3), **Journal of the Society of the North American Benthological Society**;
- John Wiley and Sons (Figures 5, 8, 9 and 14), **River Research and Applications - Wiley Online Library**, and **Freshwater Biology**;
- American Fisheries Society (Figure 6 and 7), **AFS Online Journals - American Fisheries Society**;
- Ecological Society of America (Figure 4), **ESA Online Journals - Ecological Applications**; and
- American Institute of Biological Sciences (Table 1, from Bioscience), **Bioscience**.

Contents

List of tables

List of figures

1 Background

1.1 This document has been produced to underpin decisions about defining appropriate environmental targets to control adverse effects of anthropogenic flow modifications on the characteristic flora and fauna of UK rivers. Whilst its primary aim is to underpin the review of UK Common Standards targets set for rivers with special wildlife designations for their river habitat, the evidence contained within it is also relevant to the control of flow-related impacts on river ecology under the Water Framework Directive and the UK Biodiversity Action Plan (BAP). A supplementary paper is being produced with proposals for how this evidence base should be used to refine existing environmental targets in UK Common Standards guidance on setting conservation objectives for rivers with special wildlife designations for their river habitat.

1.2 This paper seeks to address flow modification impacts on both in-channel and riparian habitats, although as will become evident the majority of available information relates to in-channel habitats. It is important to note that SSSI designations for river habitat include riparian habitats and also adjacent floodplain wetlands that are hydrologically dependent on the river, so these considerations are directly relevant to Common Standards guidance on SSSI river habitat.

1.3 This is an evidence base specifically designed to characterise the effects of flow modifications. This focus does not imply that flow modifications are the only significant anthropogenic problem for riverine wildlife. A range of stresses have to be tackled to secure the ecological integrity of river habitats (Mainstone and Clarke 2008), and this evidence base should be seen as a contribution to this wider work.

2 Characterising ecological impacts of anthropogenic flow modification in rivers

The natural flow regime

2.1 The flow regime of rivers is a fundamental determinant of riverine habitat conditions, upon which most other environmental influences are superimposed. River flows critically determine habitat space (volume and area), substrate types, riparian hydrology, floodplain hydrology, the current velocities organisms experience, and critically influence factors such as water residence time which affects both water and sediment quality (temperature, dissolved oxygen levels).

2.2 The characteristic biological communities of a river are adapted to the natural flow characteristics of that river, exploiting the habitat opportunities that arise from the spatial and temporal variability in flows that the river experiences. The natural flow regime therefore acts as a reference point against which hydrological impacts, and ecological impacts arising from them, can be evaluated. Poff *et al.* (1997) identified five key components of the natural flow regime that are critical to characteristic biological communities of the river and its floodplain: flow magnitude, frequency of occurrence of a given flow magnitude, the duration of a flow condition, its timing or predictability, and the rate of change of flow (or flashiness). Table 1 provides a description of some of the key ecological responses to alterations in these different characteristics of the flow regime.

2.3 At a more detailed level, there have been various attempts to identify a wide range of quantitative indicators of the flow regime in order to help characterise the ecological effects of both natural and anthropogenically impacted flows (Richter *et al.* 1996, Monk *et al.* 2006, 2007, Rosenfeld *et al.* 2007).

2.4 Physical modifications to the river channel and banks modify the way in which river flows shape habitat conditions (Dunbar *et al.* 2010a), both in the river and on the floodplain. The full ecological benefit of a natural flow regime can only be realised in unmodified or physically restored river channels and associated floodplains. Accounting for the physical condition of rivers therefore needs to form an integral part of evaluating modifications to the flow regime.

Characterising ecological responses to flow variation and modification

2.5 Studies that explore links between flow conditions and ecological responses range from those evaluating direct flow/biota relationships, to studies looking at flow/habitat relationships, through to those investigating the complete process of flow variation, abiotic habitat consequences and biological response. Some studies focus on particular components of the biological community, others on single species. In this section the focus is on attempting to describe the nature of ecological changes; attempts to quantify flow/response relationships are dealt with in Section 3.

Table 1 Some ecological responses to alterations in components of the natural flow regime (from Poff *et al.* 1997). For full citations see **Poff *et al.* 1997**

Flow component	Specific alteration	Ecological response	References
Magnitude/ frequency	Increased variation	Wash-out &/or stranding	Cushman 1985, Petts 1984
		Loss of sensitive species	Gehrke *et al*. 1995, Kingsolving and Bain 1993, Travnicheck *et al*. 1995
		Life cycle disruption	Scheidigger and Bain 1995
		Altered energy flow	Valentin *et al*.1995
	Flow stabilisation	Invasion or establishment of exotic species, leading to:	
		local extinction	Kupferberg 1996, Meffe 1984,
		threat to native commercial species	Stanford *et al*. 1996
		altered communities	Busch and Smith 1995, Moyle 1986, Ward and Stamford 1979
		Reduced water to floodplain plant species, causing:	
		seedling dessication	Duncan 1993
		ineffective seed dispersal	Nilsson 1982
		loss of scoured habitat patches and secondary channels needed for plant establishment	Fenner *et al*. 1985, Rood *et al*. 1995, Scott *et al*. 1997, Shankman and Drake 1990
		Encroachment of vegetation into channels	Johnson 1994, Nilsson 1982

Table continued...

Flow component	Specific alteration	Ecological response	References
Timing	Loss of seasonal flow peaks	Disruption of cues for fish:	
		Spawning	Fausch and Bestgen 1997, Montgomery *et al*. 1993, Nesler *et al*. 1988
		egg hatching	Naesje *et al*. 1995
		migration	Williams 1996
		Loss of fish access to wetlands or backwaters	Junk *et al*. 1989, Sparks 1995
		Modification of aquatic food web structure	Power 1992, Wootton *et al*. 1996
		Reduction or elimination of riparian plant recruitment	Fenner *et al*. 1995
		Invasion of exotic riparian plant species	Horton 1977
		Reduced plan growth rates	Reily and Johnson 1982
Duration	Prolonged low flows	Concentration of aquatic organisms	Cushman 1985, Petts 1984
		Reduction or elimination of plant cover	Taylor 1982
		Diminished plant species diversity	Taylor 1982
		Desertification of riparian species composition	Bosch and Smith 1995, Stromberg *et al*. 1996
		Physiological stress leading to reduced plant growth rate, morphological change or mortality	Kondolf and Curry 1986, Perkins *et al*. 1984, Reily and Johnson 1982, Rood *et al*. 1995, Stromberg *et al*. 1992
	Prolonged baseflow ‘spikes’	Downstream loss of floating eggs	Robertson 1997
	Altered inundation duration	Altered plant cover types	Auble *et al*. 1994
	Prolonged inundation	Change in vegetation functional type	Bren 1992, Connor *et al*. 1981
		Tree mortality	Harms *et al*. 1980
		Loss of riffle habitat for aquatic species	Bogan 1993

Table continued...

Flow component	Specific alteration	Ecological response	References
Rate of change	Rapid change in river stage	Wash-out and stranding of aquatic species	Cushman 1985, Petts 1984
	Accelerated flood recession	Failure of seedling establishment	Rood *et al*. 1995

2.6 A considerable number of studies have focused on effects on the benthic macroinvertebrate community, since this is a widely and relatively easily monitored component of riverine communities and has been found to be responsive to flow changes. Studies on individual rivers using multiyear datasets of seasonal biological and daily flow data have typically found that years with lower flows give rise to invertebrate communities that are more lentic (stillwater, limnophilic) in character, with species of lotic (running water, rheophilic) character being reduced in abundance (Bickerton 1995, Boulton and Lake 1992, Wood *et al.* 2001, Rose *et al.* 2008, Extence *et al.* 1999). This loss of lotic character can be caused by a number of mechanisms:

- Reductions in the magnitude and/or frequency of significant hydraulic scouring events, reducing the competitive advantage of adapted lotic species (Jackson *et al.* 2007) and allowing greater accumulation of algal biomass (Lohman *et al.* 1992, Valentin *et al.* 1995, Biggs 2000, Jackson *et al.* 2007, Rose *et al.* 2008)) and silt (Wright and Berrie 1987), creating unsuitable substrate conditions for many lotic species.
- Longer water residence times generating higher temperatures and lower dissolved oxygen levels, leading to inhospitable conditions for lotic species that are generally adapted to cooler, well-oxygenated water (Petts and Bickerton 1994).
- In river types where they occur, loss of habitat associated with rheophilic macrophytes, possibly associated with increased epiphytic cover (Wright and Berrie 1987).

2.7 This response to changes in flow has resulted in the development of macroinvertebrate indices for the detection of flow-related impacts, based on the degree of lotic or lentic character of individual taxa in a community. In the UK, the LIFE Score (Lotic-invertebrate Index for Flow Evaluation) has been developed for this purpose (Extence *et al.* 1999, see Section 3 Flow-biota relationships).

2.8 In addition to changes in habitat and hence biological character, loss of habitat space for different types of meso-scale habitats (for example, riffles, pools, marginal vegetation) can generate large reductions in the abundance of species. This is not necessarily obvious from routine observations of the biota, depending on the sensitivity of monitoring methods to changes in overall habitat space and coverage of different meso-scale habitats. In the UK, macroinvertebrate, fish and macrophyte monitoring is based on the survey of spatially infrequent, small in-channel sites within large river reaches, and data are reported in ways that are independent of changes in habitat space. Such monitoring is therefore not amenable to evaluating loss of habitat space across river reaches (Armitage and Pardo 1995, Armitage and Cannan 1998).

2.9 Loss of habitat space for in-channel fauna initially has the effect of concentrating individuals into the remaining space (Wright and Berrie 1987, Suren and Jowett 2006), increasing population density and apparent abundance. Over time, however, this makes populations more subject to density-dependent mortality and movement (in drift) associated with intra- and inter-.species competition and predation (McIntosh *et al.* 2002, Peckarsky *et al.* 1990). Depending on the timing of observation, therefore, either an increase or decrease in apparent abundance may be observed (Figure 1), which at least partially explains the diverging findings of various studies of flow depletion summarised by Dewson *et al.* (2007) in Tables 2 and 3.

2.10 Species (plants and animals) specialising in marginal wet habitat can be particularly affected by loss of habitat space (Ormerod, *et al.* 1987, Wright 1992, Rose *et al.* 2008) – operational monitoring of these components of river biota in the UK is very limited compared to monitoring of in-channel biota, yet they make a major contribution to the biodiversity of the river corridor as a whole (Armitage 2006). Rose *et al.* (2008) found that, when standard benthic macroinvertebrate biotic scores were generated separately for riffle and edge habitats in Australian streams, riffle scores were far less affected by drought than edge scores. This was because flow-requiring taxa were out-competed in edge habitats by more lentic taxa. In the UK, marginal aquatic habitats are included in integrated 'sweep' samples of the macroinvertebraqte community during routine monitoring, but the values of biotic indices will be sustained during flow stress by rheophilic taxa surviving in remaining riffle habitat.

2.11 Complete drying out of the stream bed has major implications for characteristic flora and fauna. In naturally perennial streams that are subject to artificially induced drying out, the impacts on characteristic biota are dramatic (for example, Ladle and Bass 1981, Wood and Armitage 2004). In streams that naturally dry out, however, the characteristic biota is one that is adapted to a dry phase and the community is maintained by the ephemeral nature of river flow (Wright 1992, Holmes 1996). Holmes (ibid.) found a strong relationship between macrophyte community composition and the length of summer dry period in English winterbournes (Table 4). The overall effect of artificial loss of flow in such streams is to move parts of the winterbourne section to a terrestrial community, shift the winterbourne community downstream into the naturally perennial section, and reduce the length of the perennial section (ie downstream migration of the perennial head of the stream). Species adapted to ephemeral conditions are also found in other sorts of intermittent headwater (for example, Smith *et al.* 2003), and a similar response to artificial flow modifications can be expected.

Table 2 Summary of effects reported for decreased stream flow on invertebrate communities (from Dewson *et al.* 2007). For full citations see **Dewson *et al.* 2007**

Variable	Increase	No Change	Decrease
Density	Gore 1977	Cortes *et al.* 2002	Cowx *et al.* 1984
	Extence 1981	Suren *et al.* 2003a	Hooper and Ottey 1988
	Wright and Berrie 1987		Wood and Petts 1994
	Rader and Belish 1999		Englund and Malmqvist 1996
	Wright and Symes 1999		Malmqvist and Englund 1996
	Dewsen *et al.* 2003		Cazaubon and Giudicelli 1999
	Suren *et al.* 2003a		Rader and Belish 1999
			Wood and Petts 1999
			Wood *et al.* 2000
			McIntosh *et al.* 2002
			Wood and Armitage 2004
			Kinzie *et al*. 2006
Taxonomic richness		Armitage and Petts 1992	Englund and Malmqvist 1996
		Cortes *et al.* 2002	Rader and Belish 1999
		Dewsen *et al.* 2003	Wright and Symes 1999
			Cazaubon and Giudicelli 1999
			Wood and Armitage 1999
			Wood *et al.* 2000
			McIntosh *et al.* 2002
			Wood and Armitage 2004
			Kinzie *et al.* 2006

Table 3 Summary of effects reported for decreased stream flow on invertebrate individuals and populations (from Dewson *et al.* 2007). For full citations see **Dewson *et al.* 2007**

Variable	Increase	No change	Decrease
Drift	Minshall and Winger 1968 Pearson and Franklin 1968 Radford and Hartland-Rowe 1971 Gore 1977 Ruediger 1980 Corrarino and Brusven 1983 Hooper and Ottey 1988 Poff and Ward 1991 Poff *et al.* 1991 Rutledge *et al.* 1992		Poff and Ward 1991 Poff *et al.* 1991 Kinzie *et al.* 2006
Hyporheic use		Gilpin and Brusven 1976 Ruediger 1980 Delucchi 1989	
Predation	Extence 1981 Malmqvist and Sackmann 1996		Zhang *et al.* 1998
Competition	Matczak and Mackay 1990		Zhang *et al.* 1998

2.12 The effect of the frequency of significant hydraulic scouring events on periphyton biomass has been relatively well-studied. Biggs (2000) found a strong relationship between standing algal biomass and the number of days free of significant hydraulic scour, with the effect modified by nutrient concentrations (Figures 2 and 3). Rose *et al.* (2008) noted an increase in autotrophic character of reference streams in response to lower flows, with increased algal biomass and associated grazing invertebrates. This trophic response is perhaps particularly important in watercourses downstream of headwater impoundments or hydropower installations, where natural scouring flows may be lost for significant periods of time due to reservoir-filling phases.

2.13 The magnitude of hydraulic disturbance associated with high flow events has been found to be a major determinant of the character of the plant community more generally. Biggs (1996) developed a conceptual model for plant community succession in rivers: rivers with the highest hydraulic energies and lowest bed stabilities tend to be dominated by periphyton, growing opportunistically between scouring events; at lower hydraulic energies, bryophytes and liverworts are able to establish and dominate; at lower energies still then rooted macrophytes can colonise and dominate. This model has been shown to fit macrophyte distributions in New Zealand streams (Rijs and Biggs 2001) and is broadly consistent with macrophyte patterns in the UK. It follows that anthropogenic alterations to the magnitude and frequency of hydraulic disturbance will alter the balance between these biological states. In particular, flow regulation involving reduced magnitude and frequency of high flows and increased baseflow stability is likely to lead to shifts towards dominance by rooted macrophytes and away from characteristic bryophyte communities.

Table 4 Effect of periodicity of flow on key macrophyte species in headwaters and winterbournes, based on survey of >120 sites in 1992-95 (Holmes 1996)

	Months dry in summer						
Species	**>6**	**4.5-6**	**3-4.5**	**1.5-3**	**0.5-1.5**	**± Perennial**	**Always perennial**
Non-aquatic grasses	5	5	4	3	1		
Non-aquatic herbs	4	3	1	1	1		
Alopecurus geniculatus	4	5	5	2	1		
Stachys palustris	3	3	1				
Mentha aquatica	3	3	2	1			
Myosotis scorpioides	3	3	2	1			
Glyceria fluitans/plicata	1	1	4	5	5	1	1
Apium nodiflorum		1	3	5	5	5	5
Rorippa nasturtium-aquaticum		1	3	5	5	5	5
Rhynchostegium riparioides	2	2	2	2	2	2	2
Fontinalis antipyretica	1	1	1	1	2	2	3
Veronica anagallis-aquatica		1	3	5	5	5	5
Ranunculus peltatus			3	4	4	2	1
Catabrosa aquatica						1	4
Callitriche obtusangula						2	4
Verrucaria spp.						4	5
Hildenbrandia rivularis						3	4
Ranunculus penicillatus. subsp. pseudo.						3	4
Berula erecta						3	4

Key: 5 = expected, 4 = very likely, 3 = typically found, 2 = occasional, 1 = rare on streambed

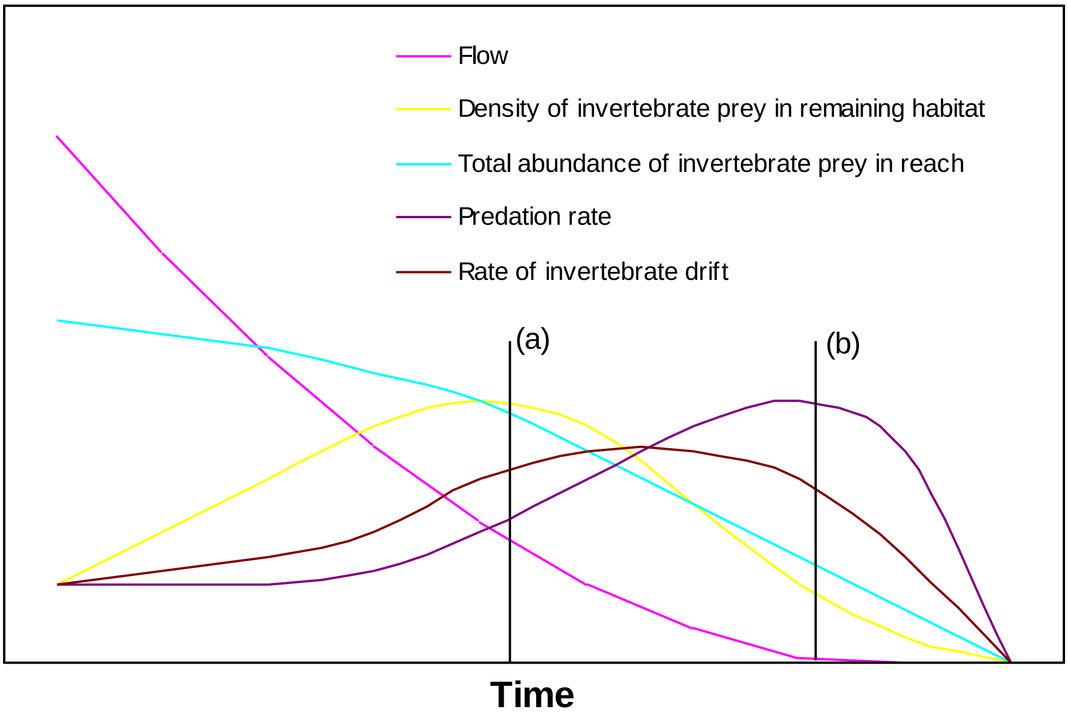
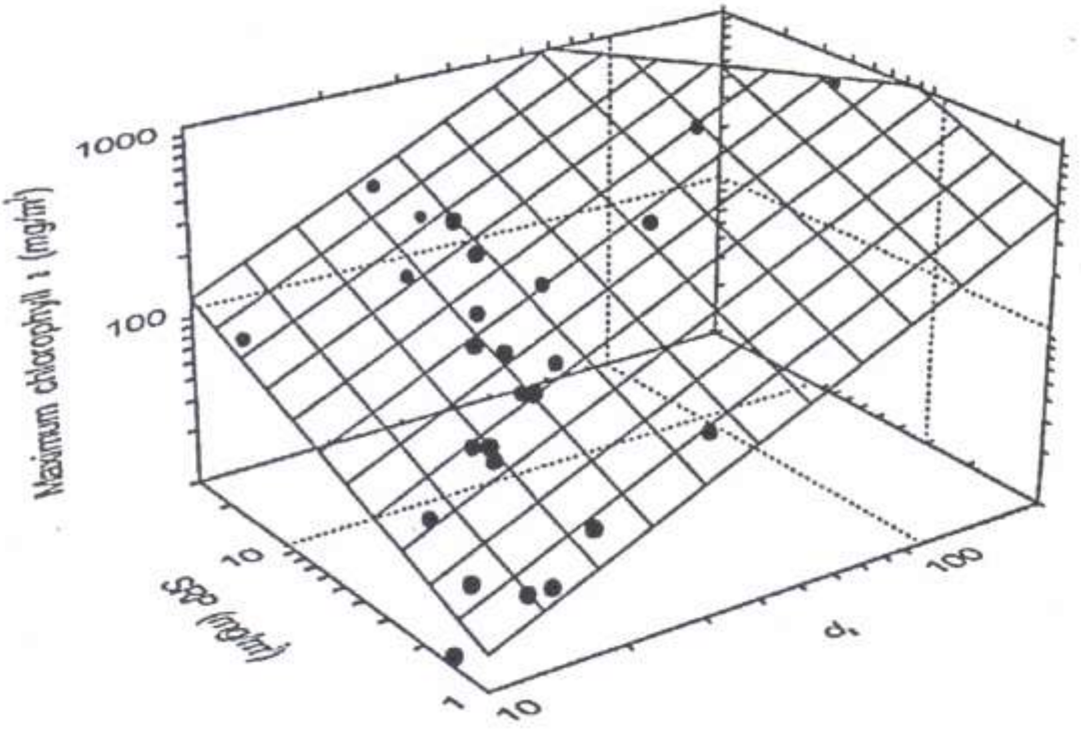
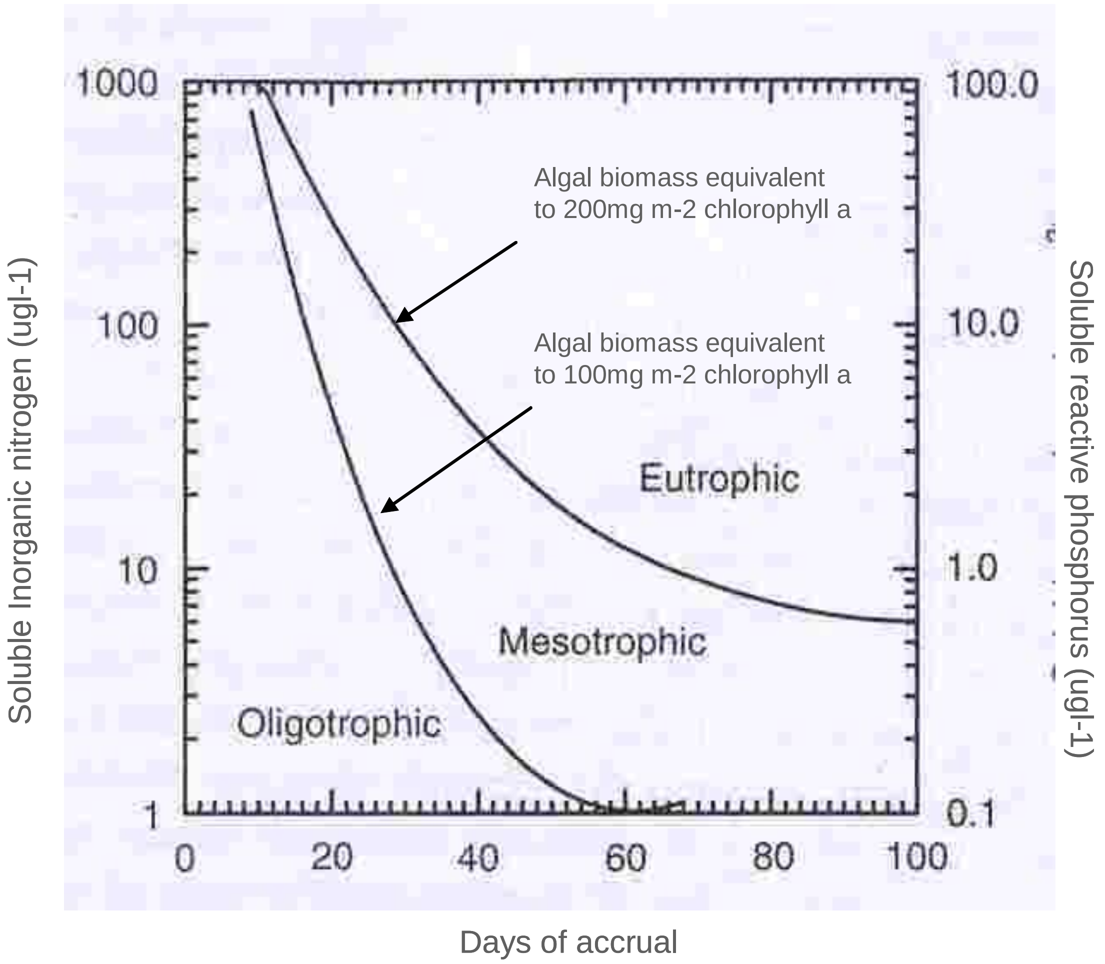


Figure 1 Conceptualised macroinvertebrate responses to summer flow recession during drought. Routine observation at time (a) – high invertebrate prey density, low predation rate; routine observation at time (b) - low prey density, high predation rate



From Biggs 2000

Figure 2 Linear response surface of maximum benthic chlorophyll a concentration as a function of soluble reactive phosphorus (SRP) concentration and days of algal biomass accrual

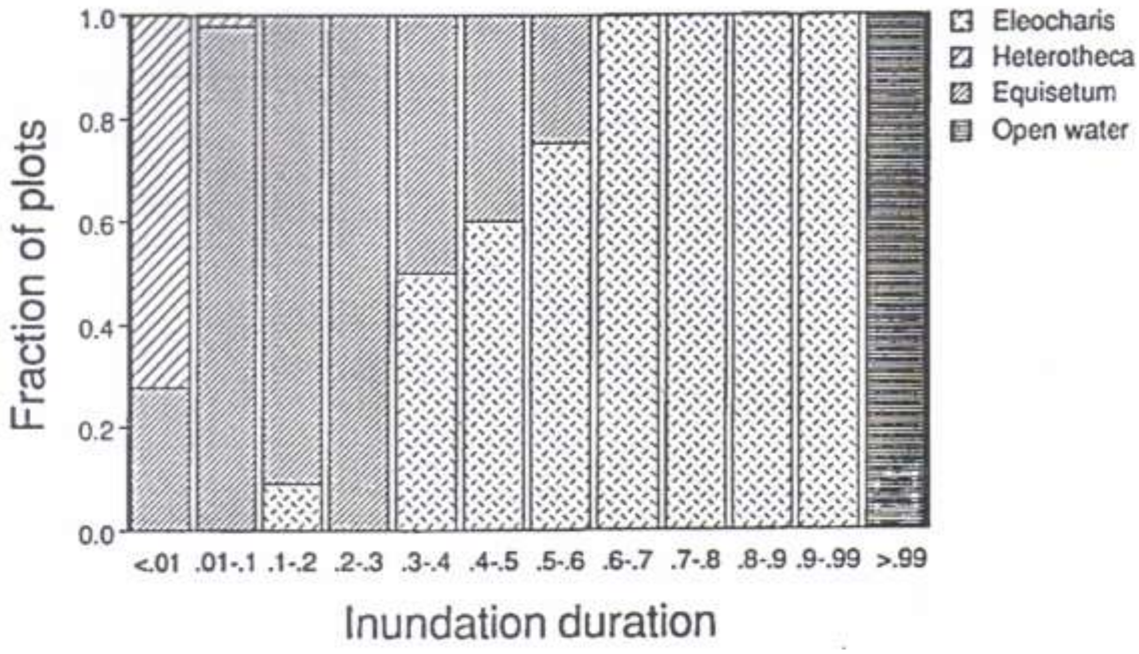


From Biggs 2000

Figure 3 Effect of hydraulic scour frequency and nutrient concentrations on periphyton biomass accrual in New Zealand streams

2.14 Riparian connectivity and variable hydraulic conditions are critically important to the dispersal of riverine plant propagules (Gurnell *et al.* 2008). This flow-related dispersal has also been shown to be critical to structuring riparian plant communities (Nilssen *et al.* 1991), again illustrating the importance of flow variability.

2.15 As has been found in studies of wet grassland vegetation on the floodplain, Auble *et al.* (1994) found the composition of the riparian plant community to be strongly influenced by inundation regime (Figure 4), with a lateral gradient of wetness extending out from the channel associated with shifts in dominance by plant groups adapted to increasingly dry conditions. This pattern mirrors the longitudinal patterns of wetness and macrophyte assemblages observed by Holmes (1996) in winterbourne streams outlined above. Artificially enhanced stability of water levels (which may arise from flow augmentation/ maintenance, or physical impoundment that may or may not be associated with water resource management) leads to a loss of seasonally inundated riparian habitat and therefore space for wetland species (Toner and Keddy 1997). Jansson *et al.* (2000) found that the riparian vegetation of rivers with frequent run-of-river impoundments and stable water levels under baseflow conditions contains fewer species per site and sparser plant cover than free-flowing rivers. Conversely, artificially enhanced rates of draw-down of levels in the riparian zone (arising from abstraction) lead to reduced seasonal wetness and a loss of wetland vegetation character. Artificially high variability (for example, frequent diurnal variation) in flows, as can be experienced below hydropower installations, also leads to an inhospitable riparian environment (Fisher and Lavoy 1972, Gore 1977). This can generate unvegetated zones not only devoid of plant biodiversity but also vulnerable to erosion.



From Auble et al. 1994

Figure 4 Normalised distribution of cover types along a gradient of inundation duration on the banks of the Gunnison River, Colorado

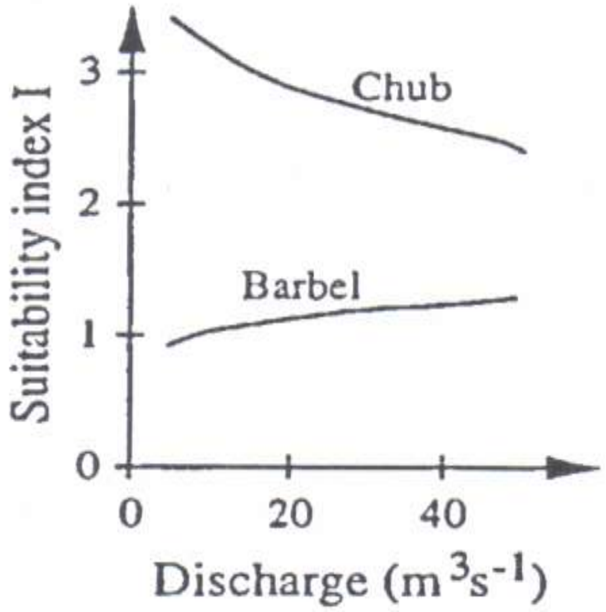
2.16 The invertebrate fauna of exposed riverine sediments, which contains numerous rare species and is therefore of high conservation importance, exploits a similar inundation regime to marginal wetland vegetation and ephemeral headwaters. The fauna is lost as a result of flow augmentation that eliminates the natural summer flow recession, or river impoundment (which may or may not be associated with abstraction) that prevents water levels declining as flows recede (Sadler and Bates 2007). In general, it is clear that the fauna and flora of vegetated and unvegetated, seasonally inundated river habitats require characteristic summer flow and water level recession to provide the ephemeral conditions to which they are optimised.

2.17 Studies of the ecological significance of different components of the flow regime indicate that flows at the time of biological observation are not as important as antecedent flow conditions, which describe the recent history of flow influences on the development phase of observed assemblages . Wood *et al.* (2000) found that high discharges 4-7 months prior to observation of the invertebrate community (ie winter-spring) were most important in describing the late-summer community of chalk streams. Dunbar *et al.* (2006, 2010b) found the previous summer Q95 flow (ie the flow exceeded 95% of the time) to be most effective at explaining the following autumn macroinvertebrate community across 11 sites from the East Midlands located on a range of geologies, although there was also a reasonable correlation with the antecedent Q10 flow (ie the flow exceeded only 10% of the time). Dunbar *et al.* (2006, 2010b, 2010c) found that both antecedent Q95 and Q10 together explained variation in spring and autumn LIFE score. In relation to macrophytes, strong *Ranunculus* growth is related to high river flows in spring, whereas low spring flows are associated with high epiphyte cover and poor *Ranunculus* growth (Wright *et al.* 2002).

2.18 Most studies of flow-related impacts on fish have focused on salmonids and have considered the impact on fish habitat (for example, Beecher 1990, Parasiewicz and Dunbar 2001, Lamouroux and Souchon 2002), due to the practical difficulties of deriving direct flow/biological relationships for fish. Various models have been developed to chart changes in habitat characteristics and usable habitat space with changing flows, which can then be used to evaluate the habitat effects of different abstraction scenarios. The most widely used models link, at the site- (100-500 metre) scale, habitat preference to habitat availability in order to derive a relationship between area-weighted useable habitat (often termed Weighted Useable Area, WUA) to flow volume. Most trace their lineage from the PHABSIM (Physical HABitat SIMulation) model, developed in the USA in the late 1970s. PHABSIM and related models couple a hydraulic model of locations of interest, capable of interpolating and extrapolating hydraulic conditions, with habitat preference models for target species of interest.

2.19 In these models, cross-sections are selected to represent larger waterbodies mapped for mesohabitat types, although in some cases critical or representative reaches may be selected. The general principle is that, while preference for absolute flow volume cannot be transferred between rivers, physical habitat preferences do have some generality. PHABSIM has been used in many UK studies and has generated a wide range of relationships between useable habitat area and flow for different species and age classes, depending on their habitat preferences. The usable area for more lotic species (for example, salmonids) typically declines as flows decline, whilst the usable area for lentic species (for example, deeper bodied cyprinids) increases. Such outputs are difficult to relate to impacts at the level of the fish community or wider biological community, or the reach scale. Although there have been some validation studies which relate weighted usable area to population numbers, such studies in the wider environment are complicated by the multitude of factors affecting fish population size and the mobility of fish species.

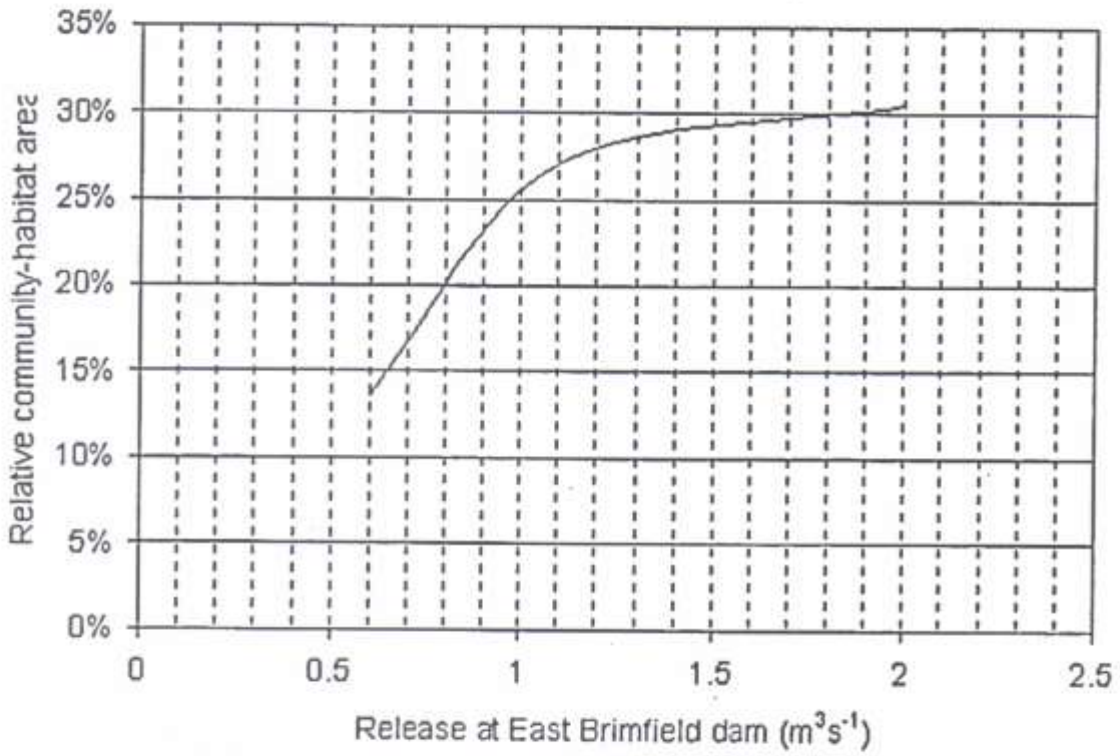
2.20 At a larger scale, Lamouroux *et al.* (1998) have linked hydraulic models to multivariate habitat use models based on detailed observations of fish location in relation to meso-scale physical habitat in French streams and rivers. Based on these data, Figure 5 shows the predicted effect of changes in flow on habitat suitability for chub and barbel in a reach of the Rhone, indicating a decline in suitability for barbel as flows decline due to its more rheophilic nature. Generally, the loss of rheophilic character in the fish community as a result of declining flows is evident from the outputs of such models, and reflects similar observations of the macroinvertebrate community outlined above.



From Lamouroux et al. 1998

Figure 5 Suitability Index as a function of discharge in a reach of the Rhone, France

2.21 Other attempts have been made to step up from the traditional site-scale, single-species focus of fish habitat models to reach-based, community-based procedures. The MesoHABSIM concept (Parasiewicz 2001, 2007) characterises the extent of key flow-based meso-scale habitats (such as runs, pools, riffles, glides) under different flow conditions, as a means of both characterising physical habitat condition and restoration needs as well as evaluating flow-related impacts. Fish habitat preference models, normally constructed using multiple regression (in the case of abundance data), are developed from quantitative electrofishing data with pre-positioned frames, located in a wide variety of habitat types and, if necessary, at different flows. The result is a quantification of physical fish habitat against flow similar to that produced by PHABSIM and derivatives, with the exception that no hydraulic modelling is undertaken (Figure 6). The changes observed in the extent of different mesohabitats with changes in flow (Figure 7) demonstrate how in-channel flow/habitat diversity is highest during the natural summer flow recession, and is 'drowned out' under higher flows, with the picture increasingly dominated by run-type habitat.

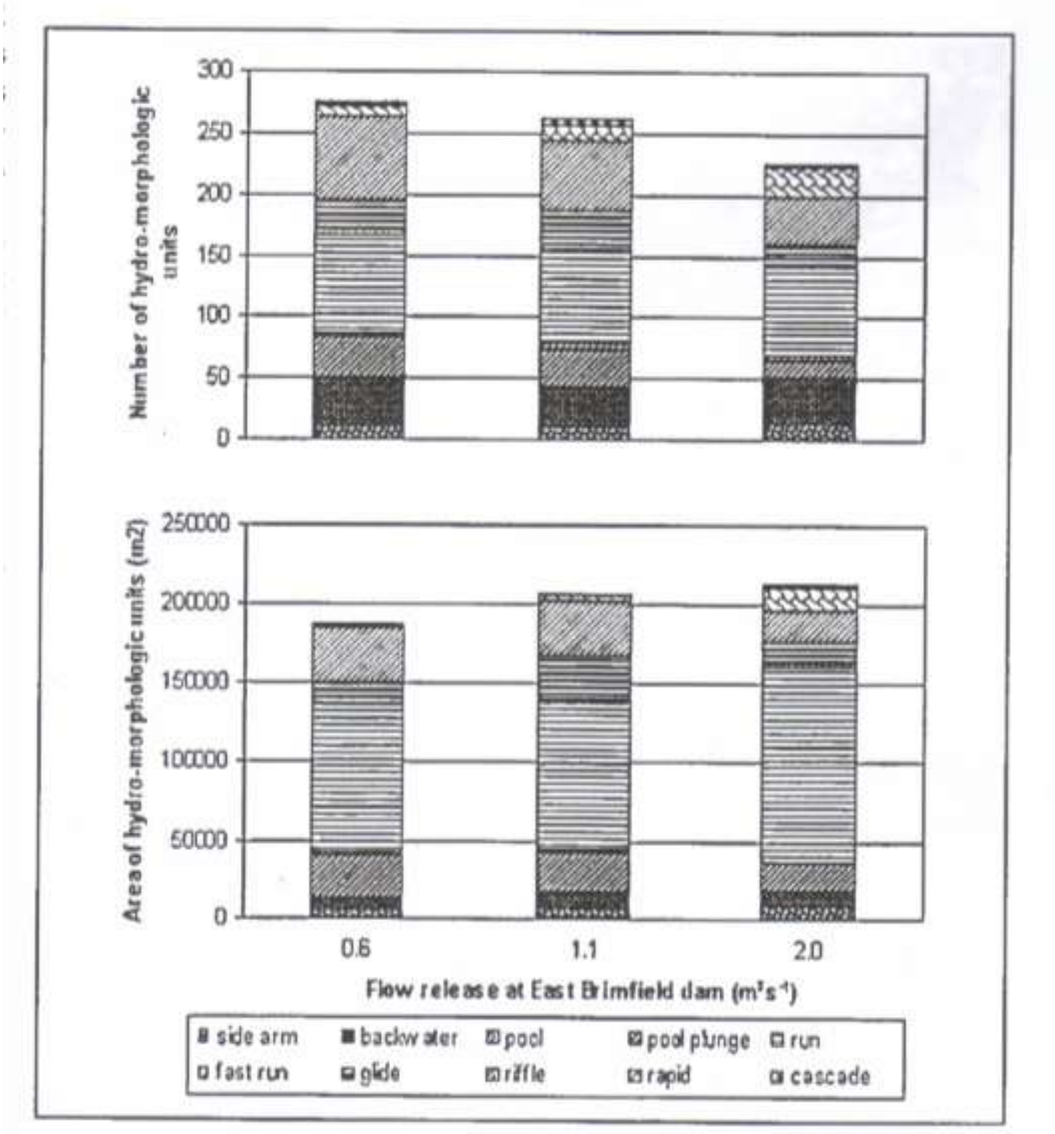


From Parasiewicz 2001

Figure 6 Rating curve of relative fish habitat area versus flow release for a study area on the Quinebaug River, US

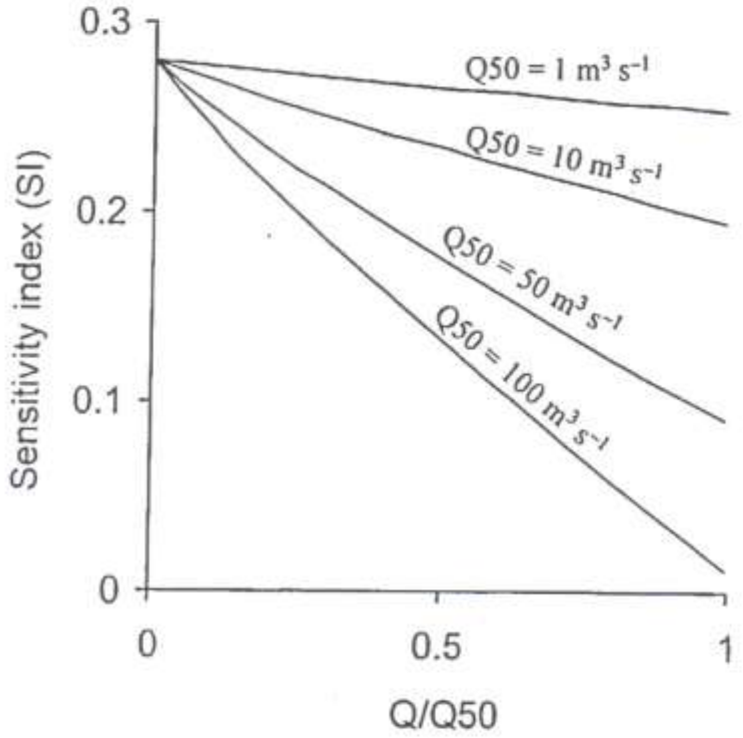
2.22 Lamouroux and Souchon (2002) took a similar reach- and community-based approach to evaluating flow/habitat relationships, providing a basis for simplifying the evaluation of habitat sensitivity to flow changes using generalised equations for flow/channel geometry relationships and the use of certain dimensionless characteristics of stream channels that strongly relate to habitat 'value' (Froude number, essentially a measure of flow intensity, Reynolds number, a measure of flow turbulence, relative roughness and width–to-depth ratio). Using this approach, they derived relationships for a series of habitat-based 'guilds' of fish species (pool, bank, riffle and mid-stream) in French streams that have recognisable counterparts in the UK and elsewhere (Leonard and Orth 1988). Figure 8 shows the results for the midstream guild (species preferring deep and fast-flowing habitats), across a range of value of river sizes (given by median natural daily discharge). This indicates that the rate of change in habitat 'value' (the Sensitivity Index) with flow for this guild is generally higher in smaller streams than larger ones (ie this habitat guild is more sensitive to flow changes in smaller streams than larger ones), and that habitat sensitivity increases as flows decline to their lowest levels across all stream sizes.

2.23 Methods have also been developed to characterise impacts on usable habitat space from an invertebrate perspective. Some approaches have adopted the species-based approach of PHABSIM – for instance, Merigoux *et al*. generated habitat preference curves for a wide range of invertebrates of a large lowland river, and predicted that 27 rheophilic taxa would benefit from flow restoration whilst the habitat space for 12 limnophilic taxa would be shrunk back to backwaters characteristic of the natural river. A more common approach, however,, is the characterisation of more generalised meso-scale habitats, inhabited by species groups with similar preferences. The classification and evaluation of meso-scale habitats is a complicated area, with various classifications developed by different scientific disciplines and research groups: ‘functional habitats’ (Harper *et al.* 1995) and ‘mesohabitats’ (Armitage *et al.* 1995, Pardo and Armitage 1997) are concepts created by invertebrate ecologists through observations of the patchiness of assemblages and their associated habitat conditions. They relate largely to substrate and vegetation components that support discernibly different assemblages. Flow biotopes are readily observable meso-scale flow conditions (such as run, glide, riffle and pool) derived from a geomorphological and hydraulic perspective (Padmore 1998). They were not originally constructed from direct biological observations but have been linked to habitat utilisation (particularly for fish, for example MesoHABSIM). The relationship between flow biotopes and functional habitats/mesohabitats varies with flow conditions, as does the usage made of them by organisms as they strive to stay within their environmental optima or at least tolerance range, forming a complex, dynamic picture of habitat occurrence and habitat use that reflects ecological conditions in rivers.



From Parasiewicz 2001

Figure 7 Quantitative distribution of mesohabitats (numbers in upper graph, area values in lower graph) under 3 flow conditions on a reach of the Quinebaug River, US



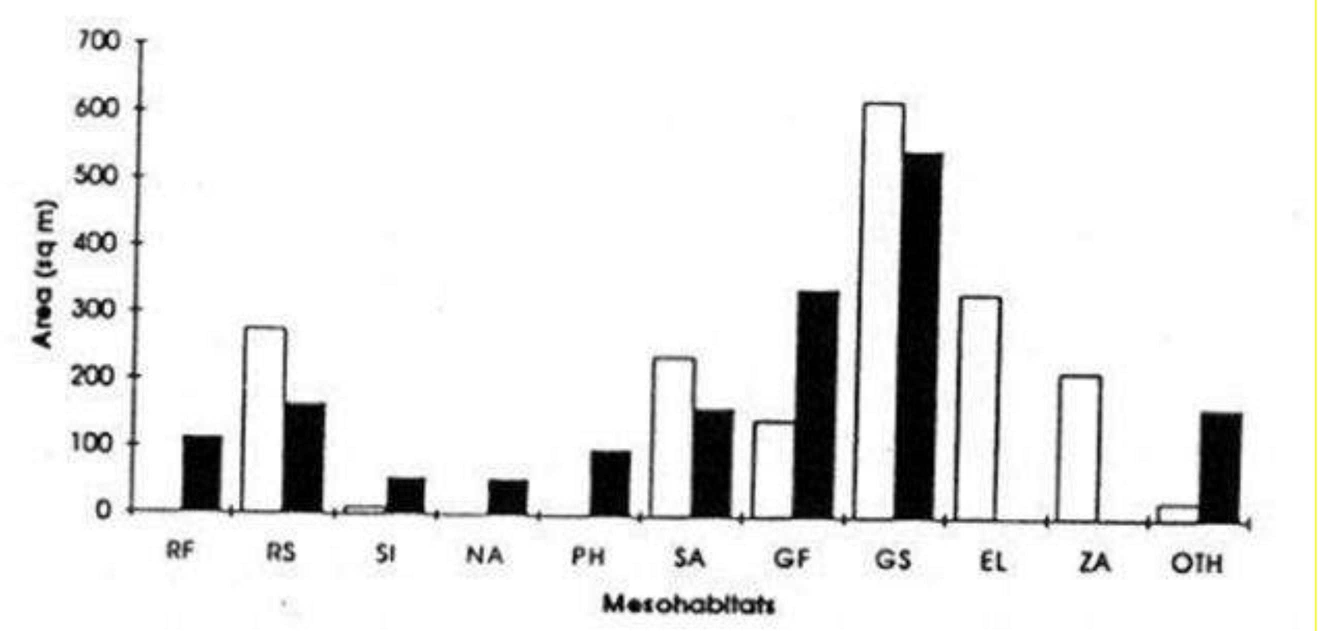
From Lamouroux and Souchon 2002

Figure 8 Relationship between Sensitivity Index (the relative change in Habitat Value) and relative flow/discharge (Q/Q50) for the 'midstream' guild of fish species in French streams and rivers of different sizes (as indicated by their median flow, Q50)

2.24 Armitage and Pardo (1995) demonstrated the effect of run-of-river impoundment by weirs on meso-scale habitats for invertebrates occurring within a chalk river reach (Figure 9), and the same approach can be applied to evaluating artificial changes in flow volumes. Upstream of the weir, the river was characterised by steeper bankslopes, increased depth and flow retention resulting in sedimentation. Mesohabitats characterised by water-cress (*Nasturtium*) and reed (*Phragmites*), which supported a high proportion of taxa in the study river and high density of individuals, were poorly represented in the impounded reach due to the steep banks and lack of natural seasonal recession in water levels. Mesohabitats characterised by Canadian pondweed (*Elodea*) and horned pondweed (*Zannichellia*), and associated with deep and slow-flowing water, dominated the impounded section, whereas mesohabitats characterised by gravel and water-crowfoot (*Ranunculus*), associated with swift-flowing water, were prominent in the free-flowing section downstream. Overall, they found a greater diversity of habitats downstream of the structure than in the impounded section and a severe loss of marginal and lotic habitats in the impounded section. A critical aspect of measures to restore physical riverine habitats and natural riverine processes is the removal of such structures wherever possible - any hydroecological studies of such reaches that fail to take account of the natural character of the river will not provide an informed analysis of the flow requirements of the river.

2.25 Studies of direct relationships between fish populations and flows are largely restricted to river-specific studies on adult salmonid migration. Data on the size of the adult salmonid 'run' up a river provides a spatially integrated picture of population size. Although the factors affecting the adult run are complex and varied, there is considerable scope for useful multivariate analysis. The magnitude and timing of spring and autumn spate flows in any one year is critical to the strength of the adult run of that year (for example, Solomon and Lightfoot In Draft), but more sophisticated analysis of the data can reveal other critical flow conditions for the life cycle. On the Hampshire Avon, for instance, individual cohorts in the adult run have been related back to flow conditions in the catchment in their spawning and nursery years (Solomon and Lightfoot In Draft).

After accounting for other key sources of variation, the strength of the adult cohort was found to be highly sensitive to reductions in summer low flows during their juvenile years (see Section 3 Flow-biota relationships).



RF = *Ranunculus* Fast flow; RS = *Ranunculus* Slow flow; Si = Silt; NA= *Nasturtium*; PH = *Phragmites*; SA = Sand; GF = Gravel Fast flow; GS = Gravel Slow flow; EL = *Elodea*; ZA = *Zannichellia*; OTH = Other

From Armitage and Pardo 1995

Figure 9 Proportions of mesohabitats in upstream regulated (white columns) and downstream unregulated (black columns) sections of the Mill Stream, River Frome, Dorset

2.26 Poff and Allan (1995) undertook a multivariate analysis of fish and hydrological data from a range of sites in midwestern US, of the type more generally associated with macroinvertebrate data. They found a strong association between different types of assemblage and the level of hydrological stability at sites, suggesting the likelihood of community change in instances where the natural level of hydrological disturbance is modified. Supporting this suggestion, some studies of the impacts of upland reservoir impoundments have found that the fish community has shifted towards a more lentic character (Moyle and Light 1996), associated with the loss of scouring flow conditions and the artificial support of low flows. This is consistent with studies cited above concerning shifts towards more limnophilic invertebrate species and rooted macrophytes as the magnitude and frequency of hydraulic disturbance is reduced by anthropogenic activities.

2.27 Biological recovery from flow changes varies widely depending on the nature of the river and its characteristic flora and fauna, and the magnitude, duration and timing of the change. Biological communities are adapted to normal patterns of flow variation, which shape the nature of the community (Maitland 1964), but are likely to be more affected by unseasonal flow changes (Wood *et al.* 2001, Wagner and Schmidt 2004). Recovery from drought seems to take longer than recovery from floods (Boulton 2003), and total abundance of communities recovers more quickly than species richness (Hynes 1961) due to the slow recolonisation rates of a range of species. As might be expected, supra-seasonal drought has greater effects than typical seasonal low flows (Wood and Armitage 2004, Extence *et al.* 1999). Availability of recolonising populations from in situ refugia or upstream and downstream sources also critically dictates recovery time - natural rivers with good habitat diversity and abundant flow refugia and (in cases of complete drying out) high longitudinal connectivity have greater potential to recover more quickly.

Differences in flow modification sensitivity generated by natural differences within and between rivers

2.28 The response of the biological community to flow changes along and between rivers, in accordance with differences in natural environmental conditions and resulting differences in the character of the biological community. It is not a simple matter to characterise these differences, partly due to the large number of mechanisms of flow-related effects and habitat/biological components in riverine systems, and partly due to problems with scale of observation. Differences in response can be expected in habitat and biological character as well as in habitat extent and population/community abundance.

2.29 As might be expected, Monk *et al.* (2006) found macroinvertebrate faunas with significantly different LIFE scores in groups of rivers classified by their characteristic flow regime, based on flow variability. Poff and Allan (1995) found a similar pattern in fish communities. It might be conjectured that those groups of rivers with more rheophilic biological character would be more susceptible to loss of that character resulting from reduced flow volumes or flow variability. In relation to flow volume, the rheophilic character of the biological community can however be maintained by concentration of flow into a smaller channel area of high current velocities, ie habitat character is maintained at the expense of habitat space. Loss of habitat space, with the implications for population size that go with it, is therefore a critical component of flow sensitivity in this situation. In relation to flow variability, the evidence in the previous section would suggest that a loss of flow variability is likely to be most keenly felt by rivers with greater rheophilic character.

2.30 Dunbar *et al.* 2010b noted a distinct difference in the response of macroinvertebrate LIFE score to flow between upland and lowland rivers, with scores from routine monitoring being more affected by low flow conditions in lowland rivers. They conjecture that this may be due to differences in the extent to which residuals flows are concentrated into a smaller habitat area with higher velocities as flows decline, as outlined above. It is unclear whether this observation holds true in instances where lowland rivers have remained more semi-natural in physical character and are therefore more able to focus their remaining flows into natural low-flow channels through vegetation growth or natural channel morphology. The finding also suffers from constraints imposed by the nature of routine macroinvertebrate sampling, which is unable to characterise impacts on individual mesohabitats (see below).

2.31 It is perhaps simpler to consider between-river differences in flow sensitivity generated by differences in river size. Habitat and hydraulic models indicate that smaller streams require a greater proportion of their flow to protect the same amount of habitat (Jowett 1997, Lamouroux and Souchon 2002), suggesting a need to set smaller allowable impacts on naturalised flow in smaller streams. This seems to be the only between-river difference on flow sensitivity around which there is a solid scientific consensus.

2.32 At the meso-scale of habitat and biological evaluation, perspectives on flow sensitivity vary, largely depending on whether habitat character or habitat extent is being considered, which component of the biota is the focus, and what type of flow modification is applied. For the macroinvertebrates of riffles, flow concentration as flows decline tends to maintain habitat and biological character at the expense of habitat extent (as documented above); however, even in this mesohabitat Rose *et al.* (2008) found that more limnophilic species took over riffles at lower flows. For fish, loss of depth over riffles is generally more important than it is for invertebrates, so habitat extent is more impacted by reduced flows. Flora and fauna associated with pool habitat are more limnophilic in nature, and so might be expected to be less sensitive to reduced flow volumes and variability. In fact, the literature indicates that pool-dwelling, limnophilic taxa increase their habitat range under reduced flow conditions (for example, Rose *et al*. 2008), and conversely shrink back to their core habitat under restored flow conditions (for example, Merigoux *et al*. 2009). Glides and runs that that are unable to reduce in spatial extent as flows decline, due for instance to vegetation management, are likely to suffer from loss of current velocity and therefore loss of rheophilic character in the biological community.

2.33 Less contentiously, the vegetation of shallow bank margins is inevitably more affected by flow reductions and reduced flow variability than that of steeper margins due to the extended nature of the hydrological transition zone and the great habitat area subject to impact. Shallow banks have also been shown to support much higher abundances of riverine invertebrate species than steep and artificial banks (Armitage *et al.* 2001), making them doubly sensitive to artificial flow modifications.

2.34 It is important to consider associations between mesohabitats. Riffle habitat is often associated with more extensive ephemeral marginal habitat, which is more susceptible to flow modifications than riffle habitat in various respects (for example, Rose *et al.* 2008). This type of association may be important enough to inform our understanding of between-river sensitivities to flow modification. Energetic rivers can be perceived as composed largely of riffle habitat, and riffle habitat can be perceived as more resilient to flow modifications than other mesohabitats (if only impacts on habitat character and not habitat extent are considered). A broader appreciation of mesohabitat associations in rivers leads to a greater appreciation of the flow sensitivity of such rivers.

Anthropogenic effects confounding ecological relationships with flow

Fine sediment delivery

2.35 Open coarse substrates provide important refugia against reduced flows (Wright and Berrie 1987), providing safe interstices for invertebrates and fish fry. The in-filling of these interstices with silt inhibits the use of the substrate and deeper hyporheos as a form of flow refuge. Enhanced sediment delivery from the catchment, arising from land use and exacerbated bank erosion, increases the siltation effect caused by reduced flows (Wood and Petts 1999) and can therefore increase the impact of flow reductions. Controlling sediment delivery from the catchment and river banks will help to avoid additional stress, but reductions in flows themselves encourage silt deposition and so generate a siltation risk independently of enhanced sediment delivery. There is also an important interaction with physical habitat modification (see below), since oversizing and straightening the river channel, and introducing weirs, also enhances siltation rates.

Effluent loads

2.36 The capacity of the river to dilute effluents declines as flows are reduced, which can compound the stress caused by flow depletions. To avoid additional stress, water quality needs to be managed to ensure the effluent load is ecologically acceptable in the context of the natural flow regime.

Physical habitat modification

2.37 The habitat a riverine organism experiences is generated by the combination of the physical structure of the channel and banks and the flow passing along it, with river flow constantly altering channel and bank form through hydraulic processes. Physical modifications to river habitat, such as impoundment, channel deepening and widening, and bank steepening, affect the nature and extent of the physical and hydraulic habitat and hence the composition and abundance of the biological community. Within the channel, modifications can act to reduce flow and substrate diversity, and move the system towards a more uniform, more lentic character under low-medium flows but a more uniformly hostile hydraulic character under high flows (due to lack of flow refugia). The loss of lotic character generates a community that is less intrinsically sensitive to flow reductions arising from abstraction. In seasonally inundated habitats (riparian areas, exposed riverine sediments, ephemeral headwaters), impoundment reduces the spatial extent of seasonal inundation, which is further reduced by modifications that steepen shallow banks (Pederson *et al.* 2006). In such situations, the community has been shifted away from its natural character and the real sensitivity of the natural river habitat and associated biota can only be revealed by an evaluation against reference physical conditions. An ecologically appropriate flow regime would be one that is compatible with long-term objectives to address the ecological impact of physical modifications.

2.38 Recent studies by Dunbar *et al.* (2006, 2010a,b) and Dunbar and Mould (2008) have suggested that the macroinvertebrate fauna of physically modified rivers are more flow-sensitive than the fauna of natural channels. The exact mechanism for this is unclear, but it may be that the fauna of modified channels is less resilient due to the lack of refugia, particularly under low flows. It ought to follow that such effects should occur under high flows as well (for example, Negishi *et al.* 2002) - increasing flow in more natural channels provides additional niches for many taxa, including those which are associated with slow or still water, whereas in more modified channels, niches with slow flows decrease in extent at higher flows. An alternative explanation relates to water quality issues associated with increased water residence time, although the sites used in the analysis were all screened for known water quality problems.

2.39 The fauna of natural streams and rivers would be expected to benefit from the higher level of habitat refugia available (Lake 2000); however, it is important that this is not taken as an implied insensitivity of natural watercourses to flow reductions. Owing to the limitations of the monitoring methodologies on which the data are based, the analysis of Dunbar *et al.* is not able to take adequate account of the impact of flow reductions on useable habitat area and total population/community abundance, which would be higher in natural streams. Natural watercourses have complex margins that are susceptible to drying out under reduced flows, and shallow cross-sections that are susceptible to small losses of water depth. Wood et al (2001) highlight the difficulties of evaluating ecological relationships without characterisation of meso-scale spatial heterogeneity. The most significant aspect of the observations of Dunbar *et al.* is that the assemblages of physically modified rivers are substantially impacted as a result of those modifications. It should hence follow that physical restoration of the habitat would result in a healthier, more diverse and more resilient macroinvertebrate community. This is subject to the caveats that fauna for recolonisation exist and can move into restored habitats, and that there is sufficient time for them to do so.

2.40 An additional source of complexity in relation to physical habitat modification is the adjustment of river channels that results from an artificial change in the flow regime. The controlling hydraulic effects of flow on channel morphology mean that the channel downsizes in response to artificial reductions in flow, through a combination of sedimentation and vegetation (Petts and Gurnell 2005). This is effectively an artificial channel modification even though it is brought about by natural processes. The resulting channel can function as a river with a different natural flow regime, but the extent and distribution of mesohabitats and associated biota has changed from its natural character. Typically, the spatial extent of low-flow channel habitats is reduced, whilst the spatial extent of the transitional marginal zone may migrate in towards the channel centre and either contract or increase depending on the profile of the bank. Again, these impacts are only apparent if evaluated against reference physical conditions. It follows that restoring a natural flow regime to such river sections, to re-establish habitat extent, will result in a temporary imbalance between flows and channel morphology until the channel readjusts, or unless the channel is restored prior to re-establishing natural flows.

Temperature

2.41 Thermal stress is one of the mechanisms by which artificial flow modifications impact upon biological communities, but this flow-induced stress can be compounded by other causes of temperature stress. Local sources of thermal stress occur (for example, effluents), but climate change is the greatest additional source. The effects of anthropogenic flow reductions can be expected to be more keenly felt by biological communities as water temperatures rise with the changing climate. On the Hampshire Avon, Solomon (2005) warns that the combined effects of anthropogenic stresses driving temperature increases may be leading the river to become marginal for salmon viability. Adaptation strategies for reducing the impact of rising air temperatures on water temperature are becoming increasingly important, such as optimising levels of riparian shading from tree cover.

Climate change effects on the natural flow regime

2.42 Climate change predictions for the UK (Hulme *et al.* 2002) suggest considerable reductions in summer river flows across much of the UK, and significant increases in winter flows, with major implications for biodiversity (Walsh and Kilsby 2007, Johnson *et al.* 2009). This raises questions about what we mean by the natural flow regime and how we frame sensible targets based on it in a changing climate.

2.43 A distinction needs to be made between approaches to defining the natural flow regime based on historical, long-term flow conditions, and approaches based on contemporary rainfall data. Any attempts at defining the natural flow regime using historical rainfall and flow data will rapidly become unworkable if climate changes as predicted, as flow regimes move rapidly away from historical conditions even in the absence of effects from local water resource management. Approaches based on the acceptance of a moving baseline of rainfall patterns, and accepting the flow regime 'received' from the catchment as a contemporary 'natural' (or more appropriately 'naturalised') flow regime, is a workable solution. Flow targets set in terms of acceptable deviations from the contemporary naturalised flow regime (ie the flow regime as modelled in the absence of abstractions and discharges) provide a means of focusing on the containment of local (catchment) management impacts, since the baseline against which hydrological impacts are measured changes on a year-to-year basis as rainfall and other climatic factors change.

2.44 This approach involves an acceptance of the inevitable, that river channels and their biota will adjust to a changing flow regime received from a changing climate, involving the 'natural' downsizing of low-flow channels and potentially greater geomorphological dynamism. These changes will involve a loss of seasonal habitat space at low flows and (in conjunction with other climate change effects, for example, on temperature) changes to habitat and biological character. However, if flow targets are set at ecologically acceptable levels of deviation from today's baseline natural flow regime, then this magnitude of deviation might be seen as a pragmatic Limit of Liability (Mainstone and Clarke 2008) for controlling locally induced hydrological alterations to the changing naturalised flow regime in future years.

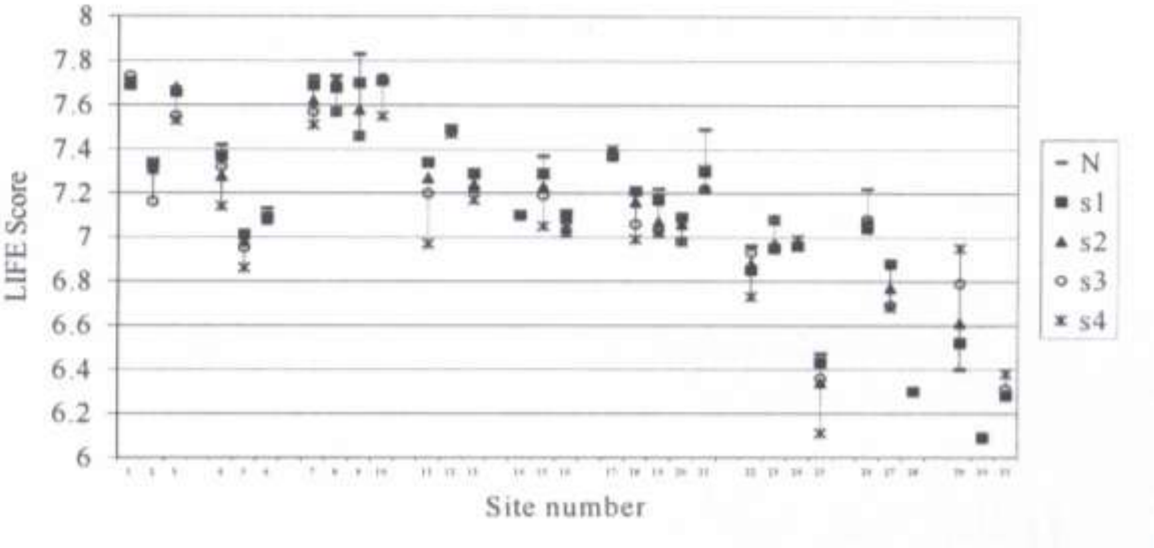
3 Key quantitative evidence for flow targets in the literature

3.1 Attempts are made in this section to capture quantitative information on hydroecological relationships that can be extrapolated to a range of rivers with similar characteristics. Such information can potentially be used to underpin generic flow targets of broad applicability. Given that measurements of absolute flow are specific to a particular river and are not extrapolatable, emphasis is placed on studies that use normalised flow data anchored in the natural flow regime (ie deviations from naturalised flows).

3.2 Much of the hydroecological literature characterises biological changes in response to flow variation, but generally not in a way that easily gives rise to quantitative relationships between biological condition and flow that can be used as the basis to set generic flow targets to protect the natural flow regime. Some key lines of quantitative evidence that help to shed light on the impacts of different numerical levels of flow modification are described below.

Flow-biota relationships

3.3 The LIFE index (Extence *et al.* 1999) is a useful tool for evaluating shifts in the composition of the benthic macroinvertebrate community associated with variations in flow. It has particular potential for setting ecologically relevant flow targets because of the widespread and standardised monitoring of the macroinvertebrate community over extended time periods. However, it is constrained by the lack of spatial and taxonomic resolution in the datasets generated by routine operational monitoring. Clarke *et al.* (2003) simulated the effects of anthropogenic flow reductions on LIFE score across a representative range of sites in the RIVPACS reference database (Figures 10 and 11), selected to cover the 9 major RIVPACS river types (so called 'super-groups'). This showed the potential for LIFE score to predict impacts of flow modifications, although the simulations were restricted by the input variables to the RIVPACS model (discharge category, channel width, depth and substratum category).



N = natural state; S1 to S4 vary in terms of the magnitude of the simulated flow change, with s1 being the least and s4 being the most extreme

Figure 10 Expected LIFE scores at 31 sites in the RIVPACS reference database under 'unimpacted' conditions and 4 simulated conditions involving flow-related changes (Clarke *et al.* 2003)

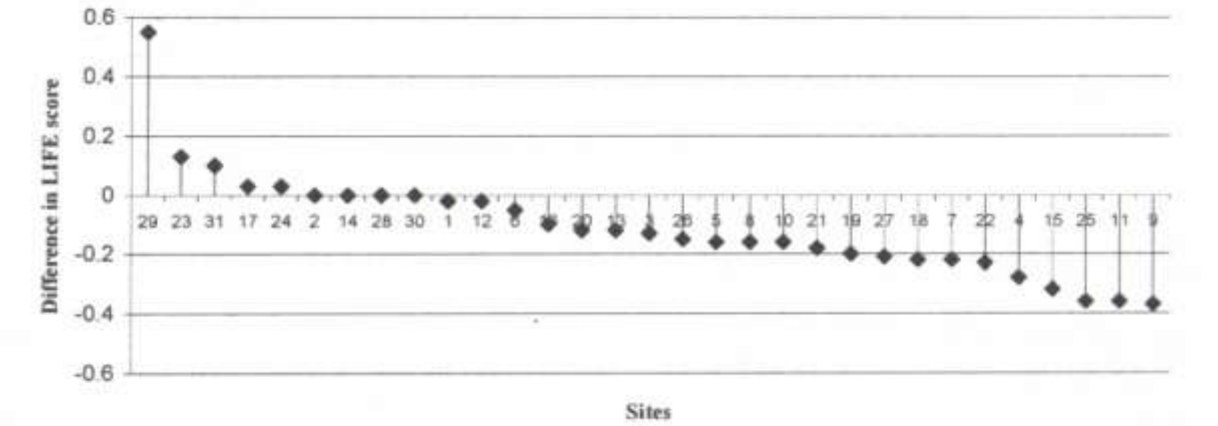


Figure 11 Ranked ranges in expected LIFE score arising from the four flow simulations at the 31 RIVPACS references sites shown in Figure 9 (Clarke *et al.* 2003)

3.4 More complex explanatory models have since been developed, using antecedent flow statistics derived from gauged daily flows. Dunbar and Clarke (2005) generated LIFE/flow regressions for a wide range of (wadeable) sites (Figure 12), using a low-flow (Q95) and a high-flow (Q10) statistic. Relationships varied considerably between sites, probably reflecting between-site differences in local habitat conditions (both natural and anthropogenic). These models have been refined through successive projects (Dried Up 1, 2 and 3, Dunbar *et al.* 2006, Dunbar and Mould 2008, Dunbar *et al.* 2010b - the first two phases are reported in the peer-reviewed literature in Dunbar *et al.* 2010c). Analyses in Dried Up 3 have equated a simulated reduction in autumn LIFE score of 0.1 to flow reductions of between 10 and 30% of mean summer Q95 (which due to most of the sites involved being minimally impacted by flow can be taken as naturalised summer Q95, approximating to an annual Q90) across a range of lowland and upland sites.

3.5 Generalising these relationships for rivers/reaches with similar environmental characteristics is hampered by the large degree of site-level (sub-reach, meso-scale) variation in physical habitat conditions. Whilst some of this variation within the Dried Up database is due to physical habitat modifications, and attempts can be made to factor this out, much of the residual variation is due to the natural habitat variation observed in sites in wadeable streams across England and Wales. Some may also simply be due to sampling variability. There are a number of ways in which this natural variation can be dealt with: 1) the range of variation in relationships within a river/reach type can be reported and management decisions made based upon this variation; 2) a reach-based approach can be taken to habitat evaluation in future, which dampens out the effects of local (site) habitat variation; or 3) flow/response evaluations can be dealt with at a detailed site-scale, involving no generic targets. This problem is inevitably common to the evaluation of flow-habitat relationships, and is discussed further in Section 3 Flow-habitat relationships.

3.6 A further required step in considering this type of LIFE-based analysis is to characterise the ecological meaning of changes in LIFE score. Whilst trends in LIFE score can generally be understood to reflect shifts between lotic and lentic character of the macroinvertebrate community, the acceptability of changes in LIFE score brought about by flow modifications requires consideration of the exact nature of these changes. This type of analysis has not yet been undertaken in a strategic way, and requires characterisation of the loss of abundance/disappearance of rheophilic taxa and increase in/appearance of limnophilic taxa as LIFE score declines. In this way, judgements can be made about the significance of community change, so that limits can be set on acceptable change in a way that allows the derivation of acceptable levels of flow modification from LIFE/flow relationships.

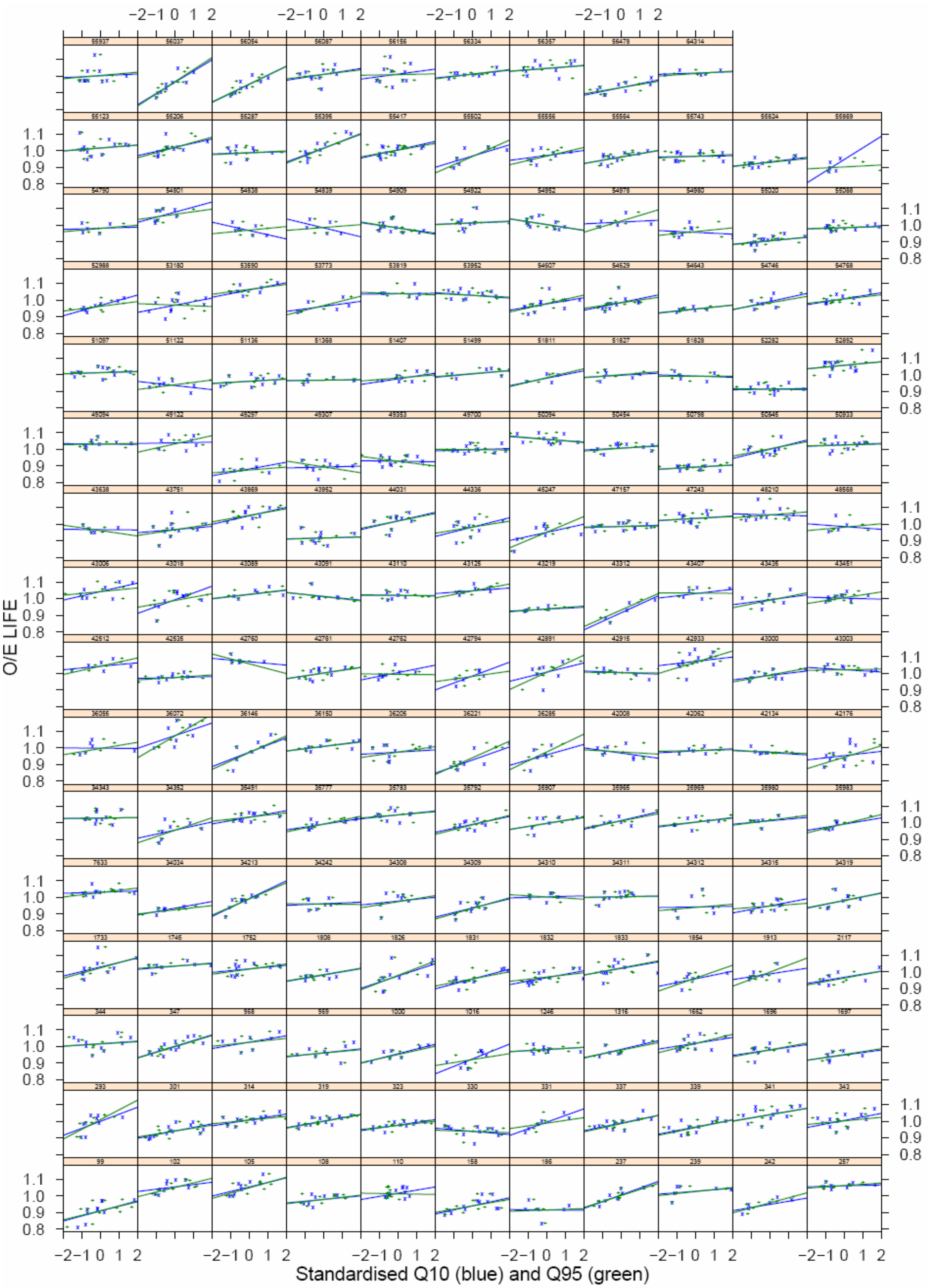


Figure 12 Individual regression lines for autumn observed-to-expected LIFE scores and antecedent flow statistics at a range of sites in the RIVPACS reference database (Dunbar and Clarke 2005)

3.7 Relatively few studies have quantified the influence of inundation patterns on riparian vegetation and the effect that flow modifications have on them, despite such data being readily available from habitat rating curves commonly used in the evaluation of fish habitat (see below) and the ease of collection of riparian vegetation data. Using simple methods, Auble *et al.* (1994) were able to simulate the effects of flow modifications on the distribution of different plant groups in the riparian zone. Similarly, Toner and Keddy (1997) have developed a model for simulating the effects of artificial changes in the flow regime on riparian vegetation. Unfortunately, no data are available to inform the setting of generic targets.

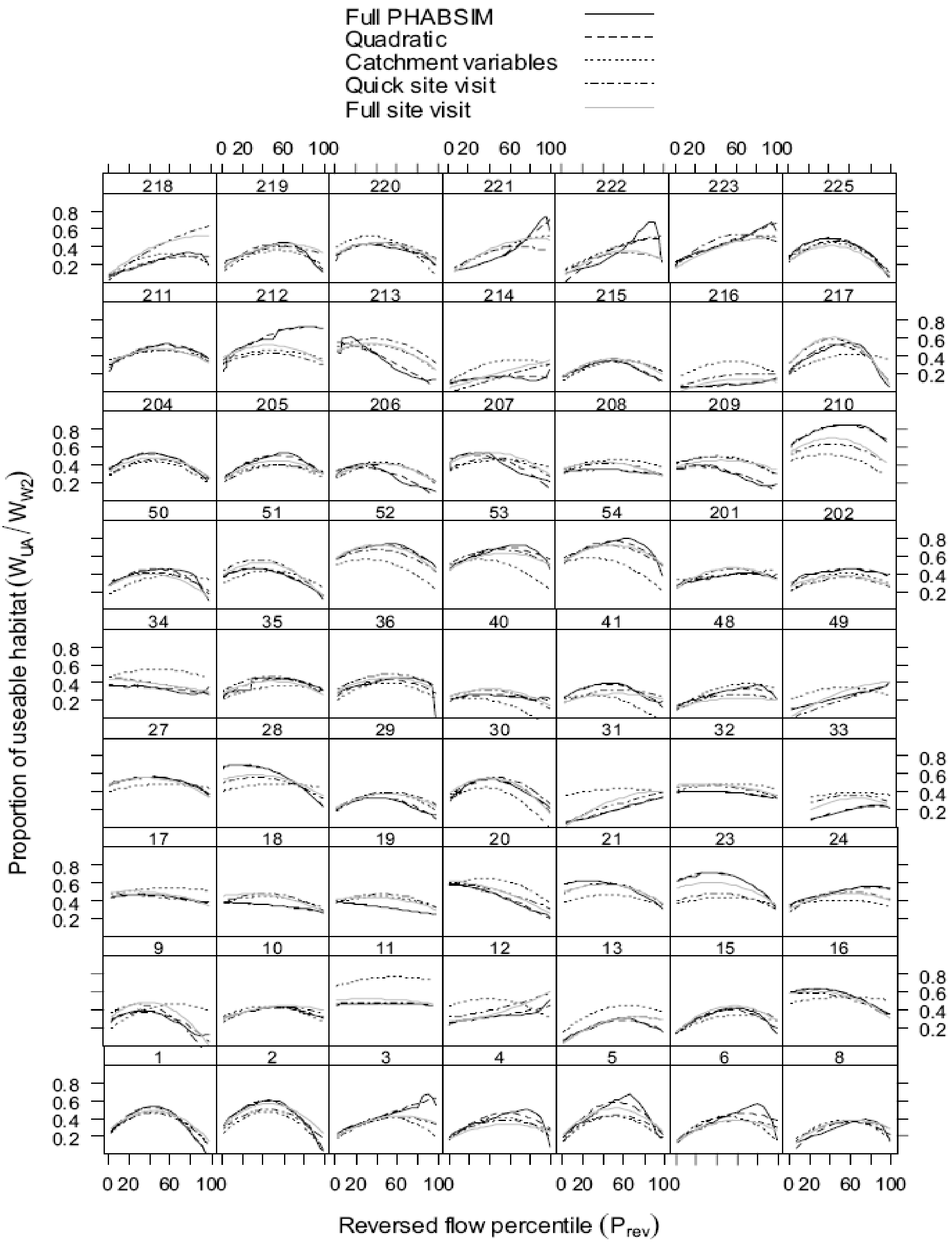
3.8 Modelling of adult salmonid returns to rivers can generate useful quantitative data on flow effects, not only in relation to migratory flows but also flows for supporting fry and parr in juvenile development habitat within the catchment. Solomon and Lightfoot (In Draft) have developed a multiple regression model for adult salmon returns on the Hampshire Avon, using a series of flow and temperature statistics and data on at-sea survival. Preliminary analysis has identified a strong relationship between the size of a returning adult cohort and the flow regime (august monthly flow) during the juvenile development of that cohort. Preliminary estimates suggest that a drop in august monthly flow during the juvenile development phase of the order of 10% is associated with a drop of a similar percentage in the numbers of individuals in the resulting adult cohort returning to the river. A similar association was identified for increases in august flows. This study argues strongly for the need to anchor flow targets to synoptic naturalised flows rather than simply seeking to protect a static flow condition. The suggested mechanism of impact is reduced juvenile habitat availability leading to reduced survival and adult recruitment rates. The consistency of this relationship across other chalk rivers and other river types is unclear but could easily be investigated with the comprehensive historical records of adult salmon runs available around the country.

Flow-habitat relationships

3.9 As discussed in Section 2, the PHABSIM model has been used at a number of sites in the UK, particularly on chalk streams and for salmonids, in a range of local investigations. It should be stressed that these studies only provide information on individual species, and typically in the UK only two species are considered (brown trout and Atlantic salmon) – the implications of flow modifications on the rest of the biological community of the river channel and margins remains unclear. The relationships generated by these studies have been collated into a multiple regression model (RAPHSA, Rapid Assessment of Physical Habitat Sensitivity to Abstraction, Booker and Acreman 2007) that can be used to estimate the relationship for unmodelled sites given key catchment/site variables (Figure 13).

3.10 In relation to defining generic flow targets, the consistency of these PHABSIM flow-habitat relationships has been looked at within river types, particularly for chalk rivers where the method has been most used (Acreman and Dunbar In Draft). Considerable variation in relationships has been found between sites in the same river type, depending on the site-specific nature of the physical habitat present. Whilst some of this variation is due to physical habitat modifications, much is due to natural variation in habitat conditions between sites, as was found in the LIFE-based analyses of Dunbar and Clarke (2005). Attempts have been made to eliminate the effect of physical habitat modification from the RAPHSA model in order to focus on the effect of flow on habitat in semi-natural conditions but, as with the work of Dunbar and Clarke, high levels of residual variation remain.

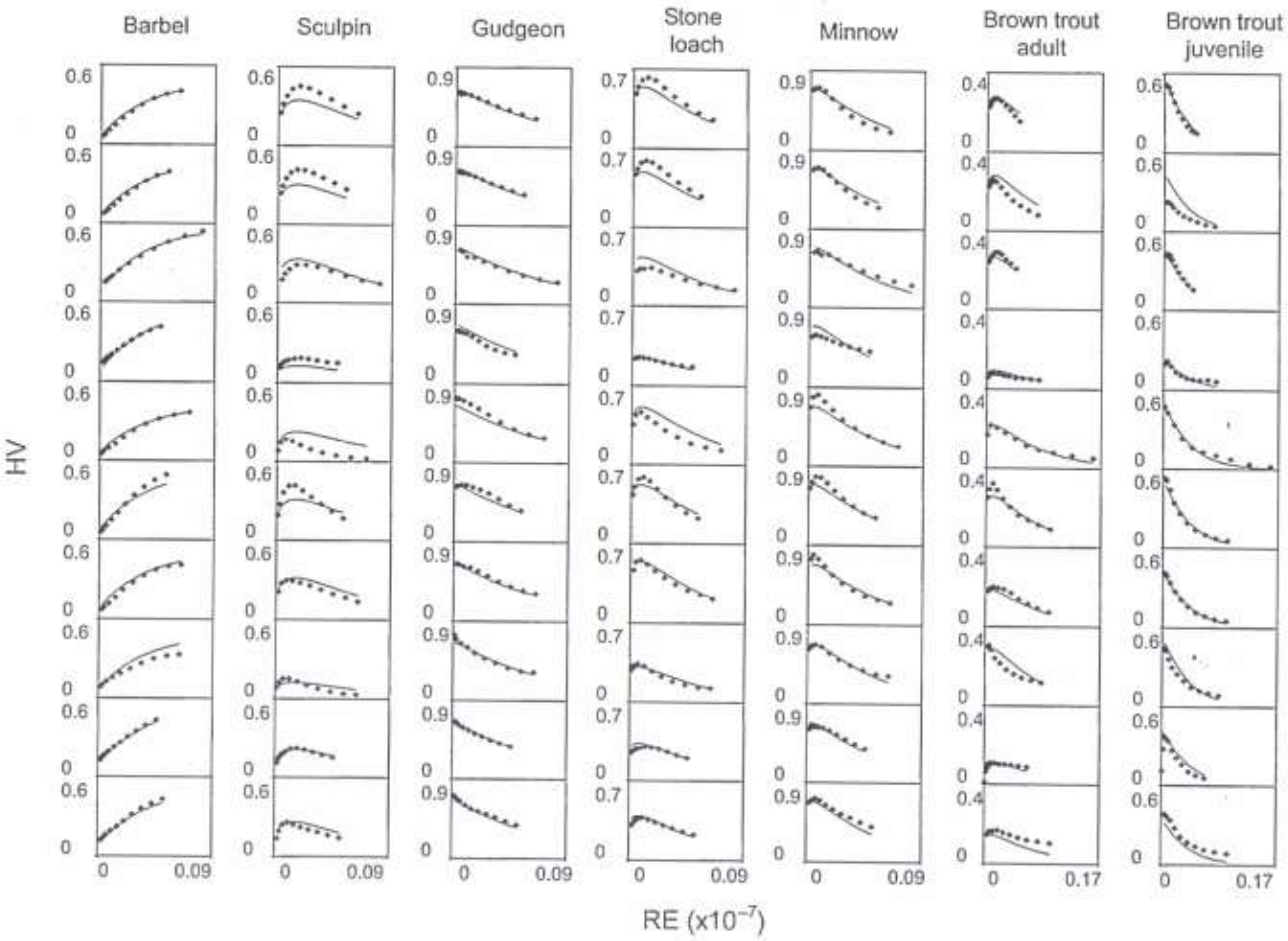
3.11 High intersite variability in flow-habitat relationships for individual species, or life stages of species, caused by natural variation in habitat should not really been seen as surprising, since the natural suitability of individual sites on a river for an individual species is known to vary widely. For instance, the suitability of glide habitat for juvenile trout is not great due to high water depth, and might not be expected to change much as a result of changes in flow. Indeed, large reductions in flow that greatly reduce water depth are likely to make such habitat more suitable for juvenile trout, but at the same time less suitable for adult trout. This highlights problems with an approach to hydroecological analysis based on individual species, rather than problems with the concept of generic relationships between flow and habitat or flow and biological assemblages. In order to interpret such species-based information in a useable way, it would be necessary to determine sites with optimal habitat of critical importance to the species (and life stage), and focus hydroecological analysis on them. A clearer pattern is likely to emerge, although any such evaluation still need to be grounded in the natural character of the river in order to avoid 'habitat gardening' for individual species.



From Booker and Acreman 2007

Figure 13 Habitat-discharge relationships for juvenile Atlantic salmon in a range of UK sites, using different levels of catchment and site information

3.12 Lamouroux and Capra (2002) demonstrated the consistency of flow-habitat relationships that can be gained by aggregating habitat characterisation to the reach-scale. Figure 14 shows the relationships between Habitat Value (a measure of habitat suitability) and Reynolds Number (a measure of flow turbulence with strong relationships to flow/discharge) for different fish species at randomly selected reaches within a defined river type characterised by trout dominance. Very consistent relationships are evident for each species, which can be related to flow variation through the strong relationships between Reynolds number and flow. This work, and that of Parasiewicz (2001, 2007) on MesoHabsim, illustrates the benefits of building in reach-level consideration of habitat characteristics in order to help define generically applicable flow targets.



From Lamouroux and Capra, 2002

Figure 14 Relationships between modelled Habitat Value and Reynolds Number using models based on reach characteristics for 10 ‘trout’ reaches in French streams

3.13 Recent attempts have been made by Booker and Dunbar (2008) to generate simple predictions of relationships between river flow and river width, depth and current velocity in UK rivers using catchment variables, in order to provide easily accessible information on the effect of flow on habitat dimensions. This work builds on the RAPHSA project and can potentially use a much wider range of sites for model development than the model based on PHABSIM outputs, due to the lower data requirements. The noise in these relationships is related to variations in at-site habitat conditions, which may be natural or anthropogenic. Restricting the dataset on which the models are based to sites in semi-natural condition would both reduce noise and provide outputs that quantify flow impacts under reference-type conditions. There are dangers, however, in this level of generality in reach-scale evaluation, associated with loss of information on sensitive habitats. Evaluations based on reach-scale habitat inventory may offer a better solution.

General comments on operational hydroecological studies

3.14 Various local hydroecological studies have been undertaken on different UK rivers to inform the definition of flow targets. However, there is no minimum specification for such investigations and they vary considerably in the extent to which they address different mechanisms of flow modification impact, different components of the biota, different components of the river habitat, and confounding anthropogenic stresses (such as physical modifications to the river channel). Investigations often involve complex analyses, or relatively simple evaluation methods that are based on pre-determined generic hydroecological relationships and/or assumptions that are not overtly characterised and/or justified. Internationally, it has been estimated that some 200 different generic methods have been developed to derive ‘environmental flows’ (Arthington *et al.* 2006), although some of these are based on common ‘parent’ methodologies.

3.15 Outputs are typically not framed in terms of the impacts of deviations from the natural/naturalised flow regime, and are typically focused on the impact of absolute values of flow volume at the low-flow end of the flow regime, leading to definition of local flow targets based on protecting low flows from dropping below a specified numerical level. The types of output from these studies are therefore often difficult to interpret in terms of the ecological impacts of anthropogenic deviations from the natural flow regime.

3.16 A collation of the results of these investigations has not been possible for this evidence paper, although an attempt has recently been made for chalk rivers (Acreman and Dunbar In Draft) that highlights the difficulties in coherent collation of quantitative outputs from local studies. The RAPHSA project (Booker and Acreman 2007), which exploited standardised outputs from a standard hydroecological technique (PHABSIM) across different local studies, is the best example of data collation and meta-analysis from the many independent hydroecological investigations that have been conducted in the UK.

4 Other relevant information

4.1 Although not primary evidence, expert judgement has been used to suggest limits on deviations from naturalised flow conditions that might be considered ecologically acceptable. A project undertaken for the UK's implementation of the Water Framework Directive assembled a panel of ecologists to try and agree acceptable limits across the range of UK rivers and for key components of the biota (Acreman *et al.* 2008). The results are presented in Table 5. The expert panel stressed the degree to which they felt their knowledge was being stretched in generating numbers of this kind. Key features of the recommendations are:

- suggested limits vary across different river types, with higher gradient rivers tending to have a higher proportion of their naturalised flow protected;
- suggested limits vary across biological components;
- seasonally varying limits for macrophytes and fish;
- the majority of the recommendations lie in the region of 10-20% of flow across seasons and flow conditions; and
- hands-off flow (HOF) conditions (ie cessation of abstraction) at low-flows are recommended for fish communities in most river types, with more protective HOFs for salmonid-dominated communities.

4.2 The river typology used, and therefore the family of targets defined, does not provide any explicit differentiation in respect of river size, which the evidence base suggests is an important factor in flow sensitivity of riverine habitats. Table 6 shows the range of river sizes found across the major river types A to D in the typology, showing a wide spread of sizes across each type. The sub-categories (A1, A2 etc), which are largely based on stream gradient, will have some level of relationship to river size but this is not possible to characterise. It is clear from the type descriptions in Table 5 that within-type variation in physical habitat conditions is also considerable. The meso-scale habitats that might be seen as more vulnerable (riffle habitat and shallow banks/margins) can be expected to occur across all river types (or at least would occur in the absence of physical habitat modifications), as can the habitats that might be seen as the least-sensitive (pool habitat and steep banks/margins). Flow sensitivity can therefore be expected to vary substantially within these types at sub-reach scale, apparent from Table 7 for the major river types A to D. The relative proportion of putatively more flow-sensitive and putatively less flow sensitive habitat does vary between types – for instance, the relative proportion (by area) of the fastest-flowing meso-habitats (rapids and riffles) declines in the order Type D>C>B>A (Table 7). This is of limited help, however, when seeking to define flow targets to protect all mesohabitats within whole reaches from reach-scale flow modifications. It is unclear whether the flow targets as defined are attempting to protect the most sensitive components of the habitat and biota in each river type, or something else.

Table 5a Summary of thresholds for supporting GES tentatively suggested by river scientists for UK river types

	Macrophytes		**Macro-invertebrates**		**Fish**	
	% flow	**Period**	**% flow**	**Period**	**% (flow – Q_{95})**	**Period**
A1	10	Mar – May	30	All year	50	Jul – Apr HOF Q98
	20	Jun – Feb			20	May – Jun HOF Q98
A2	10	Mar – May	10	All year	20	All year 10% flow < Q95 5% flow < Q99
	20	Jun – Feb				
B1	10	Mar – May	10	All year	50	Rheophilic cyprinids Jul – Jan 25% flow < Q90 20% flow < Q99 HOF Q99 Feb – Jun HOF Q90 Adult salmonids All year HOF Q95 Salmonid spawning and nursery May – Sep HOF Q95 Oct – Apr HOF Q80
	20	Jun – Feb				
B2	20	All year	20	All year	50	
C1	20	All year	20	All year	50	
C2	10	Mar – May	10	All year	50	
	20	Jun – Feb				
D1	10	Mar – May	20	All year	20	
	20	Jun – Feb				
D2	10	Mar – May	10	All year	20	
	20	Jun – Feb				
All	HOF Q97 Mar – May			HOF Q97 All year		

HOF = Hands-off Flow, ie flow under which abstraction should cease.

Table 5b Key to river types. **From Acreman et al. 2008**

Type A (A1 to A4) Alluvium/clay and/or Chalk; low altitude; low slope; eutrophic; silt/clay-gravel bed; smooth flow; predominantly C and SE England		**Type B (B1 and B2)** Hard limestone and sandstone low-medium altitude; low-medium slope; mesotrophic?; gravel-boulder (predominantly pebble-cobble), mostly smooth flow, small turbulent areas SW, NW, NE England, E Scotland, C and S Wales		**Type C (C1 and C2)** Non-calcareous shales, hard limestone and sandstone; medium altitude; medium slope; oligo-meso-trophic; pebble, cobble, boulder bed, smooth flow with abundant riffles and rapids; SW, NE England, Lake District, W Wales, Southern Uplands, Grampians		**Type D (D1 and D2)** Granites and other hard rocks; low and high altitudes; gentle and steep slopes; ultraoligo – oligotrophic; cobble, boulder, bedrock, pebble; smooth with turbulent areas – torrential; C N and W Scotland, scattered in W Wales, SW, NW and S England	
Type A1 Lowest gradients (0.8 ± 0.4 m/km) and altitudes (36 ± 25 m); predominantly clay; SE England and East Anglia & Cheshire plain	**Type A2 (hw and ds)** Slightly steeper (1.7 ± 0.8 m/km); low altitude (55 ± 38 m); Chalk catchments; predominantly gravel beds base-rich	**Type B1** Gradient: 4.1 ± 9.9 m/km; altitude: 93 ± 69 m; hard sandstone, calcareous shales; predominantly S. & SW England and SW Wales	**Type B2** Shallower than B1 (2.7 ± 10.7 m/km); altitude: 71 ± 58 m; predominantly NW England, E Scotland	**Type C1** Gradient: 5.4 ± 6.5 m/km; altitude: 101 ± 84 m; hard limestone; more silt and sand than C2; mesotrophic	**Type C2** Steeper than C1 (7.3 ± 10.8 m/km); altitude: 130 ± 90 m; non-calcareous shales; pebble-bedrock; oligo-mesotrophic	**Type D1** Medium gradient (11.3 ± 15.6 m/km); low altitude (93 ± 92 m), oligotrophic, substrate finer than D2 (incl silt & sand); more slow flow areas than D2	**Type D2** High gradient (25.5 ± 33 m/km); high altitude (178 ± 131 m); stream order 1 & 2 bed rock and boulder; ultra-oligo trophic torrential

Table 6 Percentage occurrence of different channel widths at survey sites in major river groups A – D. **From Holmes et al. 1999**

Width (m)	A	B	C	D
<5	33	24	28	50
5-10	38	30	42	41
10-20	36	38	37	29
>20	15	32	24	17

Table 7 Percentage occurrence of riffles and rapids at survey sites in major river groups A – D. **From Holmes et al. 1999**

Meso-habitat	A	B	C	D
Pools	5	9	5	13
Slacks	89	84	67	46
Runs	40	68	71	49
Riffles	5	10	14	42
Rapids	0.8	8	35	49

5 Key messages

Characterising ecological impacts

1) The published literature demonstrates the critical importance of the natural flow regime in supporting characteristic biological communities of the river channel, its riparian areas, and the associated floodplain. However, care is needed in the framing of flow targets based on the natural flow regime in a changing climate.
2) The ecological importance of the natural flow regime is strongly related to natural river morphology. Physical modifications to the river channel disrupt this relationship and need to be accounted for in, and addressed alongside, the management of the flow regime.
3) The literature provides an indication of the ecological importance of different parts of the flow regime to different components of the biota. All aspects of the flow regime seem to play an important role, including summer and winter baseflows and the magnitude and frequency of higher flows. This might be expected from the tendency of natural biological communities to maximise the use of all available habitat resource and to be shaped by resistance and resilience to the most extreme environmental conditions encountered.
4) Reduced river flows and flow variability typically shift the composition of the in-channel biota (plants, invertebrates and fish) to a more lentic character, with a loss of organisms adapted to higher current velocities.
5) Reduced flows also generate loss of in-channel and marginal habitat, resulting in increased competition and predation in remaining habitat and a consequent likelihood of loss of overall population/community abundance.
6) Artificially increased flows and water levels (which often result from impoundment that may or may not be associated with abstraction) also have ecological impacts, such as the loss of fauna associated with exposed riverine sediments and flora and fauna associated with ephemeral streams (such as winterbournes) and seasonally inundated margins.
7) The response of individual species to flow change varies widely, with some benefiting and some being disadvantaged by different changes. A community-based approach is required to evaluating flow-related impacts, rooted in the characteristic flora and fauna of the river under unimpacted conditions across the habitats that the river characteristically provides.
8) The fauna and flora of rivers with different flow regimes are adapted to those flow regimes and can be expected to respond to artificial flow modifications in different ways, necessitating consideration of river characteristics in the evaluation of effects and definition of flow targets.
9) The importance of protecting natural year-to-year variability in flow regimes has been demonstrated by some studies, allowing strong year-classes of species with different flow requirements in a way that broadens the river's characteristic suitability for biological communities.
10) The relative flow sensitivities of rivers with different environmental characteristics, and of the different mesohabitats within each river, are difficult to characterise due to the numerous mechanisms of flow-related impact (involving different parts of the flow regime) and components of the biota and habitat that are affected. Attempts to generate river typologies based on flow sensitivity to date are not demonstrably based on all key mechanisms of sensitivity or protecting the most flow-sensitive mesohabitats and biota occurring in each river type.
11) There is a strong case for considering smaller streams to be more flow sensitive than larger rivers on the basis of the scale of impact on habitat extent for a given level of flow reduction.
12) Looking across impacts on meso-scale habitats in terms of habitat character and extent and a range of biological components, higher flow sensitivities might be expected in fast-flowing, riffle-type habitat and shallow margins/banks, and lower flow sensitivities in slow-flowing, pool-type habitat, and steeper margins/banks. The picture is, however, far from clear-cut and depends on the nature of impacts considered.
13) The duration and magnitude of biological effects depends on the duration and magnitude of flow modifications and the component of the biological community considered. High

magnitude, infrequent, short duration events can have major short-term consequences but may result in little long-term damage, whilst lower magnitude, long duration modifications can lead to the biological community spending a considerable part of each year in an impacted state.

14) Modified flow regimes that result in only small deviations from the natural flow regime (ie the flow regime that would occur in the absence of abstractions and discharges) will have least impact on characteristic biological communities.
15) Natural channel morphology and high levels of biological connectivity maximise the resilience of the river ecosystem to flow-related impacts, particularly in a changing climate. Resilience is also improved by an unimpacted sediment delivery regime and unimpaired water quality. Anthropogenic impacts on these system attributes need to be controlled to realise the full benefits of a natural flow regime.

Quantifying relationships to underpin generic flow targets

1) Impacts of observed flow changes on selected components of biota and habitats have been quantified using regression models of observed flows and ecological response across a wide range of circumstances, enabling simulations of artificial flow reductions. Impacts have been related to flow reductions down to around 10% of naturalised flow statistics, including high and low flow statistics.
2) Generic quantitative characterisation of relationships between modifications to the natural flow regime and habitat/biological impact remains difficult, due to a combination of factors described in Section 6.
3) Flow modification effects on river habitat or biota do not generally occur as step changes along the flow pressure gradient – smooth relationships are more typical and judgements of acceptable levels of change have to be based on levels of deviation from a reference (unimpacted) state.
4) The consensus of a UK expert panel considering flow protection in support of Good Ecological Status was that levels of deviation of between 10 and 20 percent from naturalised flows across the flow regime might be considered adequate to protect the in-channel biological components covered by the normative definitions of the Water Framework Directive. Note these definitions do not include marginal/riparian habitats.

6 Comments on the state of the evidence base

6.1 Overall, the generic evidence to support the ecological need to protect the whole of the natural flow regime is strong, but there remains uncertainty about where to position numerical limits to define acceptable levels of flow modification from the natural regime under different circumstances. This argues strongly for a framework for target-setting that adopts an appropriate approach to uncertainty in the light of the level of environmental precaution required under different policy drivers, including the protection of SACs, SSSIs and High and Good Ecological Status under the Water Framework Directive.

6.2 The availability of adequate time series of biological data with which to match daily flow records is a serious limitation to quantitative analysis of flow/biota relationships. The most amenable data relate to the benthic macroinvertebrate community. Even here, the influence of confounding factors (such as physical habitat modification and water quality) needs careful consideration.

6.3 The published literature as briefly reviewed appears patchy in its coverage of impacts on different components of the biota and in different river types, or at least difficult to assemble in a consistent way. Hydroecological studies are generally skewed towards in-channel biota at the expense of marginal/ephemeral flora and fauna. Greater attention needs to be given to evaluating the impact of flow modifications on river habitats relying on seasonal inundation, including marginal/riparian habitats, ephemeral streams and exposed riverine sediments. Models of riparian inundation/vegetation are relatively simple to construct and can work off generalised flow/channel geometry relationships.

6.4 Most of the published literature relates to variations in observed flows at a site or range of sites. The impact of flow modifications has to be inferred from superimposing either actual or scenario flow modifications (abstractions or augmentations) on complex relationships between the observed flow regime and the habitat and/or biological response.

6.5 The many local hydroecological investigations that have taken place in the UK are highly customised and partial in their coverage of mechanisms of impact and biological end-points, generally do not explicitly handle the issue of physical modification as a confounding factor, and are largely site-based as opposed to reach-based with all of the attendant sources of variability that brings. Because of this and despite various attempts, data from the many local hydroecological investigations around the UK have yet to be collated in a coherent way that can inform the definition of generic flow targets. A decision needs to be made on whether this is really feasible or whether a new start needs to be made with new guidelines and standards for local hydroecological investigations that are geared towards meta-analysis and the derivation of generically applicable targets.

6.6 Operational monitoring in the UK, and therefore analyses based on that monitoring, is not geared to the characterisation of the impacts of modifying flows regimes on habitat space, or changes in population/community abundance caused by it. It is also not geared to the characterisation of impacts on riparian and marginal habitats and communities compared to those on in-channel components of habitat and biota.

6.7 The ability of data analyses and tools to detect flow-related impacts is dictated by the spatial, temporal and taxonomic resolution, and taxonomic coverage, of the underlying datasets. Analyses using tools such as LIFE and Dried Up generally rely on routine operational biological monitoring, which is not capable of detecting many of the impacts caused by flow modifications and water resource management more generally (including the impact of impounding structures and the impacts on ephemeral habitats and communities).

6.8 To make the most out of existing data and tools in use and under development in the UK (for example, LIFE/Dried Up and PHABSIM/RAPHSA), the problems with using site-level (as opposed to reach-level) data and focusing on selected species (and life stage) for setting flow targets at reach-scale need to be addressed from an ecological perspective.

6.9 Approaches based on reach-scale habitat characterisation, and characterisation of habitat for the whole biological community, offer greater scope for underpinning generic flow targets and need to be pursued, either through strategic R&D on representative rivers and reaches, changes to routine operational survey and analytical practices, or both.

6.10 Quantitative analyses that bring together elements of impacts on both habitat/biological character and habitat space/biological abundance are necessary to provide any meaningful evaluation of the overall effects of flow modification. These need to consider the effects on river habitat as a whole, including in-channel and marginal meso-scale habitats which between them support the entire characteristic biological community.

6.11 Analyses are needed that allow evaluation *throughout the flow regime* of the magnitude of effects arising from flow modifications that may be acceptable from an ecological and biodiversity perspective. Some analyses (flow/habitat relationships) currently handle this requirement better than others (flow/biota relationships).

6.12 There is an urgent need to further develop a suite of key tools that would allow quantitative judgements of ecologically acceptable deviations from naturalised flows in different river/reach types, addressing both changes in biological character and habitat space/volume and accounting for natural site-scale variation in response. **The most important tool required is for flow/habitat evaluation based on generalised meso-scale habitats of relevance to the entire biological community of the river corridor.** Refined Dried Up models, and perhaps (where relevant) adult salmon return models can provide valuable additional insights as long as their limitations are understood.

6.13 For the longer-term, a major programme of strategic R&D is the most certain way of generating a coherent generic evidence base of quantitative ecological responses to changes in all major components of the flow regime in a range of representative rivers/reaches with near-natural geomorphology. This work should include a standardised suite of survey and analytical methods and experimental manipulation, evaluating the full range of mechanisms of impact (including impacts on habitat character and habitat space), the full range of in-channel and marginal mesohabitats, a wide range of biological components , and addressing the issue of nested spatial scales of habitat variability. The need for such work has been stressed for many years (Armitage and Cannan 1998) but is beyond the scope of individual funding organisations. Collaborative funding across Government, the research councils and industry seems the only viable solution, and the concept of a UK Cooperative Research Partnership (URL: **www.fba.org.uk/index/CRP.html**) is the mechanism most likely to bring this about (Battarbee *et al*. 2006, Freshwater LCN 2009).

7 References

ACREMAN, M.C. and DUNBAR, M. (In Draft). Ecologically acceptable flows in chalk rivers. Report to the Chalk Rivers HAP Steering Group. CEH, Wallingford.

ACREMAN, M., DUNBAR, M.,HANNAFORD, M., MOUNTFORD, O., WOOD, P., HOLMES, N., COWX, I., NOBLE, R., EXTENCE, C., ALDRICK, J., KING, J., BLACK, A. and CROOKALL, D. 2008. Developing environmental standards for abstractions from UK rivers to implement the EU Water Framework Directive. *Hydrological Sciences Journal*, 53(6) 1105-1120.

ARMITAGE, P.D. 2006. Instream and bankside habitat in rivers. In: ZIGLIO, G., SILIGARDI, M. and FLAIM, G. (Eds.) *Biological monitoring of rivers.* John Wiley and Sons. 17-31.

ARMITAGE, P.D. and CANNAN, C.E. 1998. Nested multi-scale surveys in lotic systems – tools for management. In: BRETSCHKO, G. and HELESIC, J. (Eds). *Advances in River Bottom Ecology*. 293-314.

ARMITAGE, P.D. and PARDO, I. 1995. Impact assessment of regulation at the reach level using macroinvertebrate information from mesohabitats. *Regulated Rivers: Research and Management*, 10, 147-158.

ARMITAGE, P.D., LATTMANN, K., KNEEBONE, N. and HARRIS, I. 2001. Bank profile and structure as determinants of macroinvertebrate assemblages – seasonal changes and management. *Regulated Rivers: Research and Management*, 17, 543-556.

ARMITAGE, P.D., PARDO, I. and BROWN, A. 1995. Temporal constancy of faunal assemblages in mesohabitats: applications to management. *Archiv fur Hydrobiology*, 133, 367-387.

ARTHINGTON, A.H., BUNN, S.E., POFF, N.L., NAIMAN, R.J. 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, 16, 1311-1318.

AUBLE, G.T., FRIEDMAN, J.M. and SCOTT, M.L. 1994. Relating riparian vegetation to present and future streamflows. *Ecological Applications*, 4, 3, 544-554.

BATTARBEE, R., HILDREW, A., JENKINS, A., JONES, J.I., MABERLY, S., ORMEROD, S., RAVEN, P. and WILLBY, N. 2006. A Review of Freshwater Ecology in the UK. Report coordinated by the FBA and CEH. FBA, Windermere. URL: **http://www.fba.org.uk/docroot/samples/docs/Battarbee2005.pdf** [Accessed December 2010].

BEECHER H.A. 1990. Standards for Instream Flows. *Rivers* 1, 2, 97-109.

BICKERTON, M.A. 1995. Long-term changes of macroinvertebrate communities in relation to flow variations: The river Glen, Lincolnshire, England. *Regulated Rivers: Research & Management*, 10, 2-4, 81-92.

BIGGS B.J.F. 1996. Hydraulic habitat of plants in streams. *Regulated Rivers: Research and Management*, 12, 131-141.

BIGGS, B.J.F. 2000. Eutrophication of streams and rivers: dissolved nutrient –chlorophyll relationships for benthic algae. *Journal of the North American Benthological Society*, 19, 17-31.

BOOKER, D.J. and ACREMAN, M.C. 2007. Generalisation of physical habitat-discharge relationships. *Hydrology and Earth System Sciences*, 11, 141-157.

BOOKER, D.J. and DUNBAR, M.J. 2008. Predicting river width, depth and velocity at ungauged sites in England and Wales using multilevel models. *Hydrological Processes*, 22, 4049-4057.

BOULTON, A.J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology*, 48, 7, 1173-1185.

BOULTON, A.J. and LAKE, P.S. 1992. Benthic organic matter and detritivorous macroinvertebrates in 2 intermittent streams in south-eastern Australia. *Hydrobiologia*, 241, 2, 107-118.

CLARKE, R.T., ARMITAGE, P.D., HORNBY, D., SCARLETT, P. and DAVY-BOWKER, J. 2003. Investigation of the relationship between the LIFE index and RIVPACS: putting LIFE into RIVPACS. R&D Technical Report W6-044/TR1. Environment Agency, Bristol.

DEWSON, Z.S., JAMES, A.B.W. and DEATH, R.G. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, 26, 3, 401-415.

DUNBAR, M. and CLARKE, R.T. 2005. Producing generalised LIFE response curves. CEH Report to the Environment Agency. Environment Agency, Bristol.

DUNBAR, M.J. and MOULD, D.J. 2008. Distinguishing the Relative Importance of Environmental Data Underpinning flow Pressure assessment – Stage 2 (Dried Up 2). CEH report to the Environment Agency.

DUNBAR, M.J., LAUGE PEDERSEN, M., CADMAN, D., EXTENCE, C., WADDINGHAM, J, CHADD, R. and LARSEN, S.E. 2010a. River discharge and local scale physical habitat influence macroinvertebrate LIFE scores. *Freshwater Biology* 55, 226–242. doi:10.1111/j.1365-2427.2009.02306.x.

DUNBAR, M.J., SCARLETT, P.D., CADMAN, D., MOULD, D.J. and LAIZE, C. 2010b. Distinguishing the Relative Importance of Environmental Data Underpinning flow Pressure assessment 3 (DRIED-UP 3). CEH Report to the Environment Agency.

DUNBAR, M.J., WARREN, M. EXTENCE, C., BAKER, L. CADMAN, D., MOULD, D.J., HALL, J., CHADD, R. 2010c. Interaction between macroinvertebrates, discharge and physical habitat in upland rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems, DOI*: 10.1002/aqc.1089.

DUNBAR, M.J., YOUNG, A.R. and KELLER, V. 2006. Distinguishing the Relative Importance of Environmental Data Underpinning flow Pressure assessment (Dried Up). CEH report to the Environment Agency EMCAR Programme.

EXTENCE, C.A., BALBI, D.M. and CHADD, R.P. 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. *Regulated Rivers Research and Management*, 15, 6, 543.

FISHER, S.G. and LAVOY, A. 1972. Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam. *Journal of the Fisheries Research Board of Canada*, 29, 1472-1476.

FRESHWATER LCN. 2009. Establishing a UK Research Framework for Freshwater Conservation. Freshwater Lead Coordination Network. Available at: URL: **www.jncc.gov.uk** [Accessed December 2010].

GORE, J.A. 1977. Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia*, 55, 113-123.

GURNELL, A., THOMPSON, K., GOODSON, J. and MOGGRIDGE, H. 2008. Propagule deposition along river margins: linking hydrology and ecology. *Journal of Ecology*, 96, 553-565.

HARPER, D. M, SMITH, C., BARHAM, P., and HOWELL, R. 1995. The ecological basis for the management of the natural river environment. In: HARPER, D.M. and FERGUSON, A.J.D. (Eds). *The ecological basis for river management*. John Wiley, Chichester. 311-319.

HOLMES, N.T.E. 1996. A classification of winterbournes. A report to the Environment Agency and other research sponsors. Warboys, Cambridgeshire.

HOLMES, N., BOON, P. and ROWELL, T. 1999. Vegetation communities of British rivers: a revised classification. JNCC, Peterborough.

HULME M., JENKINS G.J., LU X., TURNPENNY J.R., MITCHELL T.D., JONES R.G., LOWE J., MURPHY J.M., HASSELL D., BOORMAN P., MCDONALD R. & HILL S. 2002. *Climate Change Scenarios for the United Kingdom*: The UKCIP02 Scientific Report, Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, UK. 120pp.

HYNES, H.B. 1961. The invertebrate fauna of a Welsh mountain stream. *Archiv fur Hydrobiologie*, 57, 344-388.

JACKSON, H.M., GIBBINS, C.N. and SOULSBY, C. 2007. Role of discharge and temperature variation in determining invertebrate community structure in a regulated river. *River Research and Applications*, 23, 6, 651-669.

JANSSEN, R., NILSSEN, C., DYNESIUS, M. and ANDERSSON, E. 2000. Effects of river regulation on river-margin vegetation: a comparison of eight boreal rivers. *Ecological Applications*, 10, 203-224.

JOHNSON A.C., ACREMAN M.C., DUNBAR M.J., FEIST S.W., GIACOMELLO A.M., GOZLAN R.E., HINSLEY S.A., IBBOTSON A.T., JARVIE H.P. and JONES J.I., LONGSHAW M., MABERLY S.C., MARSH T.J., NEAL C., NEWMAN J.R., NUNN M.A., PICKUP R.W., REYNARD,N.S., SULLIVAN C.A., SUMPTER J.P. & WILLIAMS R.J. 2009. The British river of the future: How climate change and human activity might affect two contrasting river ecosystems in England. *Science of the Total Environm*ent, 407, 4787-4798.

JOWETT, I. 1997. Instream flow methods: a comparison of approaches. Regulated Rivers: *Research & Management* 13:115-127

LADLE, M. and BASS, J.A.B. 1981. The ecology of a small chalkstream and its responses to drying during drought conditions. *Archiv fur Hydrobiologie*, 90, 448-466.

LAKE, P.S. 2000. Disturbance, patchiness and diversity in streams. *Journal of the North American Benthological Society*, 19, 4, 573-592.

LAMOUROUX, N. and CAPRA, H. 2002. Simple predictions of instream habitat model outputs for target fish populations. *Freshwater Biology*, 47, 1543- 1556.

LAMOUROUX, N., and SOUCHON, Y. 2002. Simple predictions of instream habitat model outputs for fish habitat guilds in large streams. *Freshwater Biology* 47, 8, 1531-1542.

LAMOUROUX N, CAPRA H and POUILLY M. 1998. Predicting habitat suitability for lotic fish: linking statistical hydraulic models with multivariate habitat use models. *Regulated Rivers*, 14, 1-11.

LEONARD, P.M. and ORTH, D.J. 1988. Use of habitat guilds of fishes to determine instream flow requirements. *North American Journal of Fisheries Management*, 8, 399-409.

LOHMAN, K, JONES, J R and PERKINS B D. 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. *Canadian Journal of Fisheries and Aquatic Science*, 49, 1198-205.

MAINSTONE, C.P. and CLARKE, S.J. 2008. Managing multiple stressors on sites with special protection for freshwater wildlife – the concept of Limits of Liability. *Freshwater Reviews*, 1, 175-187.

MAITLAND, P.S. 1964. Quantitative studies on the invertebrate fauna of sandy and stony substrates in the River Endrick, Scotland. *Proceedings of the Royal Society of Edinburgh*, 68, 277-301.

MCINTOSH, M.D., BENBOW, M.E. and BURKY, A.J. 2002. Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications*, 18, 569-581.

MERIGOUX, S., LAMOUROUX, N., OLIVIER, J-M. and DOLEDEC, S. 2009. Invertebrate hydraulic preferences and predicted impacts of changes in discharge in a large river. *Freshwater Biology*, 54, 1343-1356.

MONK, W.A., WOOD, P.J. and HANNAH, D.M. 2007. Examining the influence of flow regime variability on instream ecology. In: *Hydroecology and ecohydrology: past, present and future*. Eds WOOD, PJ, HANNAH, DM, SADLER, JP. John Wiley and Sons, Chichester. 165-184.

MONK, W.A., WOOD, P.J., HANNAH, D.M., WILSON, D.A., EXTENCE, C.A. and CHADD, R.P. 2006. Flow variability and macroinvertebrate community response within riverine systems. *River Research and Applications*, 22, 5, 595-615.

MOYLE, P.B. and LIGHT, T. 1996. Fish invasions in California: do abiotic factors determine success? *Ecology*, 77, 1666-1669.

NEGISHI J.N., INOUE M. & NUNOKAWA M. 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. *Freshwater Biology*, 47, 1515–1529.

NILSSEN, C., GARDFJELL, M. and GRELSSON, G. 1991. Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany*, 69, 2631-2633.

ORMEROD, S.J., WADE, K.R. and GEE, A.S. 1997. Macro-floral assemblages in upland Welsh streams in relation to acidity and their importance to invertebrates. *Freshwater Biology*, 18, 545-557.

PADMORE, C.L. 1998. The role of physical biotopes in determining the conservation status and flow requirements of British rivers. *Aquatic Ecosystem Health and Management*, 1, 25-35.

PARASIEWICZ, P. 2001. Mesohabsim: a concept for application of instream flow models in river restoration planning. *Fisheries*, 26, 6-13.

PARASIEWICZ, P. 2007. The MesoHABSIM model revisited. *River Research and Applications*, 23, 8, 893 – 903. Received: 4 June 2007; Accepted: 15 June 2007. DOI 10.1002/rra.1045.

PARASIEWICZ, P. and DUNBAR, M.J. 2001. Physical Habitat Modelling for Fish: A developing approach. Large Rivers 12 2-4, Arch. *Hydrobiol*. Suppl. 135/2-4. 239-268.

PARDO, I. and ARMITAGE, P.D. 1997. Species assemblages as descriptors of mesohabitats. *Hydrobiologia*, 344, 111-128.

PECKARSKY, B.L., HORN, S.C. and STATZNER, B. 1990. Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. *Freshwater Biology*, 24, 181-191.

PEDERSON, T.C.M., BAATTRUP-PEDERSON, A. and MADSEN, T.V. 2006. Effects of stream restoration and management on plant communities in lowland streams. *Freshwater Biology*, 51, 161-179.

PETTS, G.E. and BICKERTON, M.A. 1994. Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology*, 32, 375-386.

PETTS, G.E. and GURNELL, A.M. 2005. Dams and geomorphology: research progress and future directions. *Geomorphology*, 71, 27-47.

POFF, N.L. and ALLAN, J.D. 1995. Functional organisation of stream fish assemblages in relation to hydrological variability. *Ecology*, 76, 2, 606-627.

POFF, N.L., ALLAN, J.D., BAIN, M.B., KARR, J.R., PRESTEGAARD, K.L., RICHTER, B.D., SPARKS, R.E. and STROMBERG, J.C. 1997. The natural flow regime: a paradigm for river conservation and restoration. *Bioscience*, 47, 769-784.

RICHTER, B.D., BAUMGARTNER, J.V., POWELL, J. and BRAIN, D.P. 1996. A method for assessing hydrological alteration within ecosystems. *Conservation Biology*, 10, 1163-1174.

RIJS, T. and BIGGS, B.J.F. 2001. Distribution of macrophytes in New Zealand streams and lakes in relation to disturbance frequency and resource supply – a synthesis and conceptual model. *New Zealand Journal of Marine and Freshwater Research*, 35, 255-267.

ROSE, P., METZELING, L. and CATZIKIRIS, S. 2008. Can macroinvertebrate rapid bioassessment methods be used to assess river health during drought in south eastern Australian streams? *Freshwater Biology*, 53, 2626-2638.

ROSENFELD, J.S., POST, J., ROBINS, G. and HAFIELD, T. 2007. Hydraulic geometry as a physical template for the river continuum: application to optimal flows and longitudinal trends in salmonid habitat. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 755-767.

SADLER, J.P. and BATES, A.J. 2007. The ecohydrology of invertebrates associated with exposed riverine sediments. In: *Hydroecology and ecohydrology: past, present and future*. Eds. WOOD, P.J., HANNAH, D.M., SADLER, J.P. John Wiley and Sons, Chichester. 37-52.

SMITH, H., WOOD, P.J. and GUNN, J. 2003. The influence of habitat structure and flow permanence on invertebrate communities in karst spring systems. *Hydrobiologia*, 510, 53-66.

SOLOMON, D.J. 2005. Anthropogenic influences on the temperature regime in a chalk river. Report commissioned by the Environment Agency and Natural England. EA Science Report SC040025/SR.

SOLOMON, D.J. and LIGHTFOOT, G.W. (In Draft). Variation in salmon abundance on the Hampshire Avon – influences of climate throughout the life cycle. Report to the Environment Agency South West Region.

SUREN, A.M. and JOWETT, I.G. 2006. Effects of floods versus low flows on invertebrates in a New Zealand gravel-bed river. *Freshwater Biology*, 51, 2207-2227.

TONER, M. and KEDDY, P.A. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications*, 7, 236-246.

VALENTIN, S., WASSON, J.G. and PHILIPPE, M. 1995. Effects of hydropower peaking om epilithon and invertebrate community trophic structure. *Regulated Rivers: Research and Management*, 10, 105-119.

WAGNER, R. and SCHMIDT H-H. 2004. Year discharge patterns determine species abundance and community diversity: analysis of a 25–year record from the Breitenbach. *Archiv fur Hydrobiologie*, 161, 511-540.

WALSH C.L. & KILSBY C.G. 2007. Implications of climate change on flow regime affecting Atlantic Salmon. *Hydrology and Earth System Sciences* 11, 3, 1127-1143.

WOOD, P.J. and ARMITAGE, P.D. 2004. The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. *Archiv Fur Hydrobiologie*, 161, 1, 1-20.

WOOD, P.J. and PETTS, G.E. 1999. The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes*, 13, 3, 387-399.

WOOD, P.J., HANNAH, D.M., AGNEW, M.D. and PETTS, G.E. 2001. Scales of hydroecological variability within a groundwater-dominated stream. *Regulated Rivers: Research and Management*, 17, 347-367.

WOOD, P.J., AGNEW, M.D. and PETTS, G.E. 2000. Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes*, 14, 16-17, 3133-3147.

WRIGHT, J.F. 1992. Spatial and Temporal Occurrence of Invertebrates in a Chalk Stream, Berkshire, England. *Hydrobiologia*, 248, 1, 11-30.

WRIGHT, J.F. and BERRIE, A.D. 1987. Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management*, 1, 145-160.

WRIGHT, J.F., GUNN, R.J.M., WINDER, J.M., WIGGERS, R., VOWLES, K., CLARKE, R.T. and HARRIS, I. 2002. A comparison of the macrophyte cover and macroinvertebrate fauna at three sites on the River Kennet in the mid 1970s and late 1990s. *Science of the Total Environment*, 282-283, 1-3, 121-142.