



**Geomorphological Discontinuities and
Ecological Organisation:
A Case Study of the River Drôme**

By
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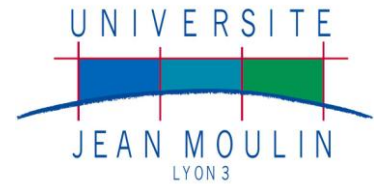
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**Discontinuités géomorphologiques
et organisation des communautés benthiques
sur le continuum fluvial de la rivière Drôme.**

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ABSTRACT

River channel changes, and patterns of in-stream macroinvertebrate community organisation, are both well explored in alluvial channels. Less is known about the behaviour of mixed bedrock-alluvial rivers, and their patterns of macroinvertebrate community structure. In response to relatively recent, widespread acknowledgment that sustainable and holistic river channel management is best achieved by a strategy that accounts for large-scale controls on long-term channel behaviour, there is a clear need to identify how spatial and temporal variation in rates and patterns of channel adjustment constrain the long-term evolution of mixed bedrock-alluvial channels, and their in-stream macroinvertebrate ecology.

The River Drôme in south-eastern France is a fascinating example of river channel change in response to a complex history of natural and anthropogenic disturbances. Previous work has documented a long-term trajectory of channel degradation, but a reach linking the upper and lower sections of the river has not been explored and is of particular interest because of its striking mixed bedrock-alluvial morphology. Over five kilometres the channel is characterised by abrupt changes in style and substrate that naturally divide the reach into six geomorphic zones. These indicate that long-term degradation is not a simple, linear evolution but a complex non-linear process. The distinct pattern of geomorphological zonation along this reach forms the central focus of this thesis, specifically in terms of its historical development, present-day macroinvertebrate community structure, and future evolution.

The first part of this thesis documents decadal changes in channel morphology between 1948 and 2006 by using GIS to analyse eight series of high-altitude aerial photography. Field work in 2005 and 2006 was used to ground truth observations. Changes in longitudinal channel profile are derived from topographic surveys from 1928, 2003 and 2005. There have been modest overall amounts of channel constriction, narrowing and incision, but there is substantial spatial and temporal variability in these trends. The present-day configuration of wide, alluvial, and narrow, bedrock zones has developed in response to a particular sequence of natural and anthropogenic events, emphasising the importance of contingency and channel sensitivity to disturbance. The reach is located 200 m downstream from le Béoux, a tributary to the Drôme, and historical changes in this sub-catchment have been manifest in the long-term behaviour of the reach. A significant flood in 1978 is the likely catalyst of present-day zonation, which locked the reach into a geometry that has constrained subsequent channel adjustments. While zonation remained distinct as recently as 2006, there is evidence that the channel is now operating under different boundary conditions to those that produced and maintained zonation before 2001. It is clear that predictions of future changes in channel morphology require a long-term perspective of channel behaviour, patterns and connectivities through time.

The second part of this thesis characterises the present-day macroinvertebrate community of the study reach. Previous work in alluvial channels has considered how

discontinuity in channel morphology influences spatial variation in patterns of macroinvertebrate organisation, but this has not been extended to mixed bedrock-alluvial channels. Relatively few studies have considered how spatial differences in channel behaviour (rather than simply channel character) may drive macroinvertebrate community organisation. Associations between channel morphology and macroinvertebrate community structure were tested by fieldwork carried out under low-flow conditions in 2006. Fifteen quantitative surber samples were collected at each of 10 sites along the reach. Local habitat characteristics, including particulate organic matter, bed sediment grain size (surface and subsurface), water quality (conductivity, temperature, pH) and flow velocity (benthic and mean) were also measured. Results indicate that the mass of particulate organic matter and the diversity of both surface and sub-surface grain size influence patterns of macroinvertebrate community structure along the reach. It is also apparent that zone-scale differences in flow and sediment regime, and differences in lateral and vertical channel dynamics are important. Variation in the frequency and intensity of bedload dispersal, which is a result of zone-scale variation in channel bed structure, is a dominant control on spatial patterns of macroinvertebrate community structure. These dynamics are the product of, and maintained by, the particular geography and history of the study reach, emphasising the 'primacy of place' and the importance of understanding how larger-scale morphological processes constrain smaller-scale patterns of macroinvertebrate biodiversity.

At present, there are plans to manage channel degradation, along the study reach and in downstream parts of the river Drôme, by restoring sediment supply to the channel. This will be achieved by the remobilisation of bedload in the Béoix sub-catchment and so it is likely that there will be future changes to the present-day morphology and macroinvertebrate community organisation in the study reach. Combining the findings of parts one and two, the third part of this thesis evaluates the likely impacts of this management strategy. It is suggested that if the channel is connected to its active floodplain, and receives a sufficient external supply of bedload, then the reach-scale dynamic of zonation is self-regulating. Successful management intervention relies upon an understanding of this behaviour. Compared to predominantly bedrock and predominantly alluvial sections of the reach, the mixed bedrock-alluvial mid-reach supports significantly more diverse macroinvertebrate communities and higher proportions of EPT taxa. These characteristics are a function of the morphological diversity of the mid-reach, which results from the particular configuration and the connectivity of the present-day zones. It is considered that if future bedload supply to the channel is not deficient or excessive to present-day flow and sediment regimes, then the present-day morphological diversity of the reach could be maintained. This would also maintain present-day patterns of macroinvertebrate community structure. It is, therefore, hypothesised that if the reintroduction of bedload from the Béoix secures the reach with a moderate volume and frequent supply of sediment, then this 'drip feed' would be a desirable management strategy.

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Discontinuités géomorphologiques et organisation des communautés benthiques sur le continuum fluvial de la rivière Drôme

Introduction

D'après Graf (1988) « l'analyse des changements fluviaux est la contribution la plus importante de la géomorphologie. On peut imaginer que nous nous situons dans une « anthropocène » où la plupart des chenaux fluviaux à l'échelle mondiale est perturbée par l'intervention anthropique. Compte tenu des changements climatiques, ces perturbations naturelles et anthropiques ont entraîné la dégradation des chenaux fluviaux, dont les conséquences morphologiques, écologiques et socio-économiques rendent les études sur la dynamique des chenaux fluviaux, leur propension actuelle au changement, et leurs ajustements éventuels à venir, une priorité scientifique.

Les changements morphologiques, et l'organisation des macro-invertébrés (le benthos) sont bien étudiés dans les chenaux alluviaux mais peu abordés dans les chenaux dessinés dans du substrat rocheux et alluvial. Suite à l'idée relativement récente, que la gestion durable et holistique des chenaux fluviaux doit être mieux développée en s'appuyant sur une stratégie en intégrant les contrôles sur l'évolution du chenal à l'échelle du bassin versant, et les dynamiques du chenal sur le long terme (ex : Brierley *et al.* 2008, Gregory et Downs 2008), l'identification des contrôles sur l'évolution des chenaux du substrat rocheux et alluviaux devient ainsi un enjeu de connaissance; comment une telle variabilité de morphologie contrôle les dynamiques temporelles et spatiales et l'organisation du benthos dans ces chenaux.

La rivière Drôme est un exemple fascinant des changements morphologiques en réponse aux perturbations naturels et anthropiques. Plusieurs études ont démontré une trajectoire de dégradation sur la Drôme aval (Landon and Piégay 1994, Landon 1999, Kondolf *et al.* 2002, Liébault 2003) (section 2.2.1), et des changements morphologiques particulièrement contrastés sont observés sur la Drôme amont (Landon et Piégay 1999, Piégay *et al.* 2004) (section 2.2.2). Un tronçon liant les secteurs amont et aval de la rivière n'est cependant pas connu. Entre Luc-en-Diois et Recoubeau-Jansac, le chenal alterne entre des segments larges et alluviaux, et étroits et rocheux, séparés par des changements morphologiques brusques. Ces discontinuités divisent le chenal naturellement en six zones morphologiques (section 2.6.1) et indiquent que l'incision n'est pas une trajectoire simple d'évolution mais un processus complexe et non linéaire. La première partie de thèse (chapitre 3) aborde cette hypothèse et examine le développement de la zonation morphologique du tronçon.

Une analyse préliminaire de la géomorphologie et de l'organisation des macro-invertébrés le long du tronçon Luc-Recoubeau, a révélé une grande variabilité spatiale (section 2.6.2, figure 2.12). Ces résultats ont servi de base pour la formulation de l'hypothèse selon

laquelle les différences de géomorphologie contrôlent l'organisation du benthos, dans et entre des zones morphologiques qui se succèdent longitudinalement. Malgré tout ces résultats n'ont pas été suffisants pour valider l'hypothèse. L'organisation du benthos dans et entre les zones morphologiques, présenté dans la deuxième partie de thèse (chapitre 4), a été examinée en s'appuyant sur des données plus détaillées et recueillies plus tard pendant la thèse.

Le tronçon de la Drôme entre Luc et Recoubeau est d'un intérêt particulier, parce qu'il se trouve 200 m en aval du Béoux. Ce sous-bassin a été choisi comme site expérimental de la recharge sédimentaire, afin de restaurer le profil en long incisé du tronçon et de secteurs encore plus incisés plus à l'aval (Liébault *et al.* 2008). Cette intervention suscite des questions fondamentales relatives à ses conséquences morphologiques et écologiques. A partir des connaissances de l'évolution historique du chenal (chapitre 3), et de la caractérisation de l'organisation actuelle des communautés de macro-invertébrés (chapitre 4), la troisième partie de thèse évalue ainsi les impacts probables de la remobilisation de sédiments dans le sous bassin amont de la Béoux (chapitre 5).

L'évolution morphologique du tronçon, 1948–2006

L'évolution morphologique du tronçon, et le développement de la zonation longitudinale actuelle, a été abordée en utilisant plusieurs séries de photographies aériennes couvrant une période de 58 ans (huit dates de 1948, 1956, 1971, 1980, 1991, 1996, 2001 et 2006) (section 3.3). Le tracé des chenaux a été dessiné en utilisant ArcGIS. Trois définitions ont été retenues (figure 3.1) et des indices de superficie et largeur ont été calculés à l'aide des scripts implémentés dans le logiciel.

- *La bande active maximale* : les îles boisées correspondant à l'emprise des chenaux en eau, des bancs de galets et de la végétation riveraine.
- *La bande active* : correspondant à l'emprise des chenaux en eau et des bancs de galets (végétation riveraine et îles boisées exclues).
- *La végétation riveraine* : la végétation sur les bancs de galets des chenaux en eau.

Les indices de sinuosité ont été calculés comme le rapport entre la longueur de la ligne centrale du chenal et la longueur de l'axe de la vallée. L'évolution du profil en long a été étudiée à partir de trois levés topographiques, fait en 1928, 2003 et 2005. Les indices de superficie, largeur et altitude ont été mesurés tous les 50 m, perpendiculairement à l'axe d'écoulement.

Entre 1948 et 2006, le tronçon a subi une incision modeste, mais les tendances globales démontrent une grande variabilité dans le temps et dans l'espace. Durant cette période, la bande active maximale s'est rétractée de 14 %, soit une superficie de 39,173 m² (\pm 894 m²) (figure 3.4 et table 3.3A). La largeur active du chenal s'est rétractée de 5 m (\pm 1 m) mais le tronçon alterne entre des secteurs qui sont larges, et des secteurs qui sont étroits

(figure 3.6). La tendance à l'incision n'est interrompue que par deux brèves phases d'expansion, en 1956 et 1996, suite aux deux grandes crues (dont le débit était deux fois supérieur au débit maximal annuel moyen) de 1951 et 1994. Entre 1928 et 2003 l'enfoncement du lit atteint une moyenne 0,8 m, mais plus que 25 % du linéaire du chenal s'est enfoncé de plus de 1 m, avec un maximum de 2,1 m au milieu du chenal.

Les différents tracés de la bande active montrent que celle-ci a diminué entre 1948 et 2006 (figure 4.13), et ce dans le cadre d'un couloir relativement stable. Le chenal de 1948 montre une grande variabilité de largeur tout au long de son tracé, et les changements sont plutôt progressifs entre les secteurs plus larges et plus étroits. En 1980, le lit s'apparente à un 'couloir' étroit et homogène dans la partie médiane du tronçon, entre les km 1.0 et 3.0 environ, et les limites de transition séparant les secteurs plus larges et plus étroits sont devenues plus courtes. Entre 1980 et 2006, la variabilité de la largeur se réduit fortement dans le tronçon d'étude. Entre 1980 et 2006, les limites entre les secteurs les plus larges et les plus étroits sont malgré tout restées les mêmes ce qui suggère que les bornes physiques actuelles ont été héritées du tracé de 1980 et qu'elles ont contrôlé l'évolution subséquente de la zonation actuelle.

Les changements actuelles de morphologie séparant les zones larges et alluviales des zones étroites et rocheuses correspondent à des ruptures statistiques (test de Pettit, $\alpha = 0,05$) dans la séquence longitudinale de largeur active du chenal de 2006 (figure 3.15). Suite à cette validation, les ruptures que l'on observe quelle que soit la date d'observation ont été considérées comme des limites de zones morphologiques. Ces ruptures confirment la stabilité des limites entre les secteurs plus larges et plus étroits durant la période 1948-2006, avec peu de variation (figure 3.16). Le développement de la zonation actuelle est décrit à partir des ruptures statistiques dans les séquences longitudinales de largeur active de tous les chenaux (section 3.4.2.3, figure 3.17). Entre 1948 et 2006 les limites des zones en aval sont plus stables que les limites des zones de l'amont, où le déplacement des limites divise le tronçon entre 1 et 3 zones. La variabilité relative de la zonation à l'amont du tronçon est considérée comme résultant de l'expansion de la végétation, et une diminution de la sinuosité.

Les changements successifs de largeur active, au cours des périodes d'observation, soulignent clairement la capacité d'ajustement du tronçon (section 3.4.2.4, figure 3.18). Depuis 1948, les zones de 2006 ont subi différents changements de largeur, mais les intensités et les directions de ces changements sont consistantes dans chaque zone au cours de chaque période. En réponse aux crues de forte intensité, les zones de l'amont (2) et de l'aval (4 et 5) se sont élargies, mais se sont rétrécies durant les périodes présentant des crues de moindre intensité. Indifférentes à l'occurrence ou l'absence d'une crue, les zones 1, 3 et 5 ne montrent aucun changement de largeur active. A présent, le milieu du tronçon est confiné dans un couloir étroit et stabilisé par des affleurements rocheux sur le fond et les berges. Compte tenu de la stabilité de largeur de la zone 3 entre 1980 et 2006, il est probable que la présence de ce couloir ait été attestée dès 1980. On peut également noter que les

changements de la zone 2 sont les plus variables comparativement à ceux de la zone 4 (figure 4.18). La différence de changement entre ces deux zones (élargissements maximaux de +459 m et +827 m, et rétrécissements maximaux de -604 m et -368 m, respectivement) pourrait indiquer une différence importante entre ces deux larges zones alluviales quant aux apports de sédiment.

Les changements cumulés de largeur active démontrent également que l'intensité de changement a diminué en moyenne durant la période 1948–2006. Les premières périodes ont subi les plus grands changements, suggérant une transformation récente de la dynamique du tronçon, et éventuellement en conséquence une diminution temporelle de l'apport de charge de fond et de la fréquence des crues.

La discussion (section 3.5) souligne l'importance des grandes crues pour les ajustements morphologiques, tant à l'échelle du tronçon qu'à l'échelle des zones. Les changements imposés par les crues n'ont pas été cependant toujours du même ordre durant la période 1948–2006, et depuis 1980 on peut ainsi constater une transformation de la manière dont le tronçon dissipe son énergie. Entre 1948 et 1956 l'élargissement de la bande active peut être expliqué par l'expansion des limites du chenal, parce que la bande active maximale et la superficie de végétation du chenal se sont élargies parallèlement. Par contre, les élargissements de la bande active de 1980, 1996 et 2006 sont accompagnés par des retractions de la largeur occupée par la végétation riveraine (de -7 %, -42 % et -58 % respectivement), sans changement de la superficie de la bande active. Ces observations mettent en lumière un changement temporel de la réponse du tronçon suite aux grandes crues, ce qui souligne la sensibilité du tronçon à ces événements. La capacité et la propension du tronçon à s'ajuster semblent également liées à une modification des apports de charge de fond et du régime hydraulique, suite aux actions anthropiques affectant le sous-bassin du Béoix.

La crue morphogène de 1978 est intervenue à un moment où le tronçon était particulièrement sensible. En 1980 un nouveau chenal étroit et droit a ainsi été créé dans le secteur médian du tronçon, parallèle à celui de 1971, en rive droite du tronçon (figure 3.19). A partir de 1886, l'installation des petits barrages, et le reboisement du bassin du Béoix (section 2.3) a provoqué une diminution progressive des apports sédimentaires au tronçon aval. Avant la crue de 1978 le déficit de la charge de fond a été soudainement exacerbé par la construction du grand barrage de Treschèrenes en 1965. Depuis 1907, les chroniques hydrologiques démontrent ainsi une réduction de la fréquence des crues (section 2.5) et la diminution temporelle de la fréquence des flux liquides et des volumes sédimentaires associés pourraient expliquer que le tronçon ait enregistré une métamorphose. Il est possible que la crue de 1978 ait dessiné un nouveau tracé suite à un phénomène de recouplement observé ailleurs et décrit comme un « floodplain stripping » (ex : Nanson 1986, Bourke 1994, Warner 1997, Largo et al. 2006). L'extraction non autorisée des graviers pourrait avoir contribué à la cause et l'effet de cette érosion, en augmentant le déficit de charge de fond ; et

la construction éventuelle de levées en rive gauche du chenal, pour empêcher l'inondation des sites d'extraction ; pourrait également avoir guidé le chenal en eau en rive droite (section 3.5.1.1).

Un deuxième impact important de la crue de 1978 était la canalisation naturelle du chenal en rive droite. Cette fixation d'un cours incisé et plus droit, surtout au milieu du tronçon, a entraîné une déconnexion du chenal en eau et de ses bancs, particulièrement en rive gauche. La végétation s'installant sur les surfaces actives de la rive gauche n'aurait donc pas été décapée par la crue. La forte rétraction de la bande active entre 1980 et 1991 s'explique alors par la longue période de développement de la végétation sur les marges actives, développement qui n'a pas été perturbé depuis au moins 1971. La végétation a également augmenté la résistance des formes fluviales à l'érosion, et a contribué à la canalisation naturelle du tronçon dans un chenal plus incisé et plus droit. L'augmentation subséquente de la puissance hydraulique a transformé la manière dont le tronçon dissipe son énergie. Après avoir atteint une extension maximale, entre 1980 et 1991, la proportion de végétation dans le chenal diminue substantiellement et rapidement entre 1991 et 2006 (figure 3.22), reflétant l'érosion de végétation et l'élargissement de la bande active. Entre 1996 et 2001, la petite et brève augmentation de la surface occupée par la végétation en l'absence d'une crue de forte intensité (figure 3.22) confirme bien que l'occurrence des crues contrôle l'extension ou au contraire la rétraction de la couverture végétale dans le tronçon.

Alors que la crue de 1994 était la plus importante de la période 1948–2006, elle n'a provoqué que des changements modestes en comparaison de ceux produits par la crue de 1978. La faiblesse relative de l'élargissement du chenal à la suite de l'événement de 1994 met en lumière l'importance de contraintes latérales au sein du tronçon, celles-là même qui sont apparues durant la crue de 1978. Peu avant 1991, la construction d'un petit seuil à l'amont du tronçon a exacerbé le déficit sédimentaire du tronçon, le déconnectant de son bassin amont. Après la crue de 1994, la bande active maximale des zones 2 et 4 s'est élargie de 10 % et 73 %, respectivement, suggérant un approvisionnement et une fourniture locale de sédiment. Il est ainsi possible que la crue de 1994 ait provoqué un fort creusement du lit, particulièrement dans les zones 1 et 3 où la roche sous-jacente est profonde relativement à la couverture alluviale (section 3.4.1.3). La capacité du tronçon à stocker et à transférer la charge de fond étant variable spatialement, cela a vraisemblablement exacerbé une redistribution discontinue des sédiments disponibles, dans et entre les zones.

En réponse à la dernière grande crue de la période 1948–2006, celle de 2003, le chenal ne s'est pas élargi. Par contre, la bande active s'est elle rétractée et la crue a provoqué une nouvelle réduction de sa sinuosité. L'incision s'est amplifiée et la déconnexion des bancs et du chenal, tout au long du tracé, est soulignée par les changements contradictoires que l'on observe suite aux crues de 1994 et 2003 : Les zones 2 et 4 ont été élargies en réponse à la crue de 1994, mais se sont rétractées après la crue de 2003 (figure 3.24).

On peut voir qu'en fixant le cours du chenal, et particulièrement le couloir étroit et droit de la section médiane, la crue de 1978 a exhumé des contrôles lithologiques latéraux et verticaux sur le tronçon, qui ont réduit sa capacité à s'ajuster. Entre 1980 et 2001, les zones alluviales 2 et 4 enregistrent des changements similaires en termes d'élargissements et de rétractions qui sont cohérents avec les hypothèses hydrologiques formulées. Au contraire, la largeur de certaines zones, particulièrement celle de la zone 3, est restée stable tout au long de la période. Par contre, il semble que cette zone 3 ait enregistré des ajustements altimétriques plus contrastés, que ceux observés sur les zones immédiatement à l'amont et à l'aval.

Il apparaît que le transport de la charge de fond des zones 1 et 2 vers les zones 4 et 5, a été facilité par le tracé simplifié de la zone 3. Une connectivité sédimentaire accrue mais complexe serait ainsi observée entre les zones 1-5. La zone 1 a servi de tapis roulant ; la zone 2 a fonctionné comme une source de sédiment ; le couloir de la zone 3 a servi de tapis roulant également, et les zones 4 et 5 ont servi de zones d'accumulation (figure 3.25). Entre 1948 et 2001, l'élargissement de la bande active et l'augmentation de la sinuosité en zone 4 peuvent rendre compte d'une accumulation de sédiment. Durant la même période, les réductions de largeur et de sinuosité et la plus forte incision en zone 2 suggèrent que ce secteur du tronçon aurait fourni du sédiment pour une redistribution à l'aval. A l'amont de la zone 2, le substrat plat et rocheux de la zone 1 n'a pas une capacité de stockage et il est probable que suite à la perte de sa couverture alluviale, ce 'tapis roulant' ait efficacement transféré la charge de fond livrée au tronçon vers le 'réservoir' de la zone 2.

La configuration du chenal, et la connectivité qui existe entre les zones, permettent de bien comprendre que les zones 2 et 4 sont « bien couplées » (Harvey 2002, Hooke 2003) et que les changements morphologiques résultant de la modification des apports sédimentaires puissent se propager tout au long du tronçon.

Entre 2001 et 2006, le rétrécissement des zones 2 et 4 et l'expansion de la zone 5 suggèrent que la zone 4 a approvisionné le chenal en charge de fond pour la redistribuer à l'aval, puisque l'apport du réservoir de la zone 2 ne suffisait pas. En 2006 c'était évident, d'après les photographies anciennes ainsi que les observations de terrain, que le chenal de la zone 2 était bien incisé au-dessous de ses bancs alluviaux. Sur le long terme, le transport de sédiment est contrôlé par la disponibilité des sédiments stockés dans la plaine alluviale (ex : Ham et Church 2002, Madej *et al.* 2009) et la déconnexion entre le chenal et sa plaine dans la zone 2 a rendu les sédiments inaccessibles pour une redistribution à l'aval. Le niveau d'enfoncement du lit ne permet plus le fonctionnement de la zone 2 comme réservoir. La déconnexion avait démarré lors de la crue de 1978 et l'incision subséquente du chenal avait provoqué une chute naturelle tout au long de la rive droite de ce secteur. Entre 2001 et 2006 une petite « avulsion », probablement pendant la crue de 2003 (figure 3.26) démontre l'augmentation de la puissance hydraulique de cette section. Il semble que l'accroissement de la végétation sur les bancs de la rive gauche ait fortement contribué à la rétraction du chenal,

renforcé la résistance des surfaces contre l'érosion et contribué à la canalisation et l'enfoncement du chenal dans la zone de recoupement.

Entre 2001 et 2006 les tendances en termes de rétraction, d'incision et de réduction de sinuosité à l'échelle du tronçon ont réduit les différences morphologiques existant entre les zones de 2001. Même si les limites des zones sont toujours discernables, il apparaît que la dynamique de zonation a changé, de telle sorte que le transport et le stockage de sédiment ne fonctionnent plus à l'échelle des zones, mais entre les trois secteurs du tronçon (figure 3.28).

Ces deux structures spatiales longitudinales ont été retenues dans l'étude de l'organisation du benthos. Dans le cadre de la restauration de la charge de fond, la zonation est tout à fait intéressante si les zones possèdent un caractère benthique distinct. Il est ainsi important de savoir quelles conséquences auront les changements de morphologie sur les communautés de macro-invertébrés, parce que l'organisation spatiale du benthos n'est pas très bien connue. L'organisation du tronçon en trois secteurs distincts pourrait indiquer que le chenal est déjà en phase de transition, ce qui renforce l'intérêt de bien comprendre l'organisation du benthos.

L'organisation actuelle des macro-invertébrés du tronçon

L'organisation des macro-invertébrés est bien connue dans les chenaux alluviaux, alors que celles existant dans les chenaux où alternent substrats rocheux et alluviaux mérite encore une analyse détaillée. De plus, la variation de l'organisation du benthos a rarement été mise en rapport avec les processus fluviaux. A plusieurs échelles d'observation, de nombreux travaux ont montré que la variation de la structure des communautés de macro-invertébrés reflète des différences dans les conditions physiques d'habitat. Cela concerne principalement la vitesse du courant et la nature du substrat (ex : Statzner et Higler 1986, Brown et Brussock 1991, Grubaugh *et al.* 1996). De telles considérations soulignent que l'habitat n'est pas une forme statique mais bien dynamique, sous le contrôle des processus géomorphologiques aux échelles plus petites.

Un seul type d'habitat a été échantillonné dans le tronçon afin que la variabilité morphologique locale ne soit pas un facteur confondant susceptible de bruite l'étude de la variation longitudinale de l'organisation des macro-invertébrés. Plusieurs auteurs ont constaté que les seuils sont les habitats les plus divers et les plus abondants (ex : Brown et Brussock 1991, Parsons et Norris 1996, Principe 2008) et bien représentatifs du peuplement des macro-invertébrés au sein d'un chenal donné (Blocksom *et al.* 2008). Suite à ces observations, les seuils ont été retenus pour étudier l'organisation des macro-invertébrés dans cette étude. Le cortège benthique (représenté par quinze échantillons de macro-invertébrés) ainsi que 18 variables physiques (dont quinze réplicats) et ont été échantillonnés sur 10 sites distribués longitudinalement sur le tronçon (figure 4.1).

Même si le but final est de caractériser l'organisation spatiale du benthos, les conditions physiques du tronçon sont d'abord étudiées (section 4.4.1), afin de disposer d'un

contexte physique robuste, bien compris pour l'interprétation de l'organisation des macro-invertébrés (section 4.4.2). Les relations entre la morphologie et les indices biologiques sont ensuite étudiées (section 4.4.3).

Pour analyser la structure spatiale des conditions physiques du tronçon, 12 variables ont été retenues (table 4.2). La structure de zonation identifiée précédemment n'est finalement ni validée par les données univariées, ni par les analyses multivariées. En fait, les données univariées révèlent l'existence d'une structure faite de trois secteurs successifs au sein du tronçon. Cette configuration repose sur des indices de granulométrie et de tri, la vitesse du courant benthique, et l'abondance de la matière organique. Elle comporte ainsi un secteur en amont (sites 1-3), un secteur médian (sites 4-7) et un secteur aval (sites 8-10) (section 4.4.1.1, figures 4.6-4.8). Les analyses en composantes principales (ACP) indiquent qu'il n'y a pas de grande variabilité spatiale des variables physiques (sections 4.4.1.2 et 4.4.1.3, figures 4.9 et 4.10), exception faite de l'abondance de la matière organique et de la vitesse du courant benthique des sites 1, 2 et 3. Ces deux variables sont statistiquement plus structurantes et sont plus élevées, dans le secteur amont comparativement aux secteurs médian et aval (section 4.4.1.1, tables 4.3 et 4.4).

Pour étudier l'organisation du benthos, 5 indices biologiques (abondance, richesse, diversité, dominance, et égalité) ont été calculés. Une moyenne de 15 valeurs a été prise pour représenter chacun des indices sur chacun des sites.

La zonation n'est pas évidente dans les données univariées mais trois secteurs peuvent malgré tout être observés (figure 4.13).

Les comptes d'abondance des 150 échantillons de macro-invertébrés ont été analysés avec une ACD (une analyse détendancée des correspondances) (section 4.4.2.2). La zonation peut être étudiée grâce aux projections factorielles de l'ACD, même si les groupements d'échantillons ne correspondent pas exactement aux zones morphologiques (figure 4.15). La structure de trois secteurs est également apparente dans la restitution graphique de l'ACD. Il y a une bonne discrimination entre les échantillons des sites 1, 2 et 3 et ceux des sites 4-10. Les échantillons des secteurs médians (sites 4-7) et aval (sites 8-10) peuvent être différenciés mais se recouvrent partiellement (figure 4.16). Les sites à l'amont du tronçon (1, 2 et 3) sont par contre significativement différents des sites 4-10. La particularité de ce secteur amont se caractérise par un écart d'abondance des macro-invertébrés: 73 % de tous les taxa sont plus abondantes sur les sites 1, 2 et 3.

Quant aux tests post-hoc, ils indiquent que les différences concernant la diversité, la dominance et l'égalité des communautés de macro-invertébrés sont statistiquement plus significatives entre les trois secteurs qu'entre les zones. Par contre, les différences en matière d'abondance sont plus significatives entre les zones qu'entre les trois secteurs (section 4.4.2.2, tables 4.8-4.11). On peut donc voir qu'il y a des différences spatiales concernant la structure des communautés de macro-invertébrés. Les deux structures spatiales que nous

avons identifiées auparavant, la zonation et les trois secteurs, sont toutes les deux importantes pour l'interprétation de l'organisation des macro-invertébrés du tronçon.

Même si les variables physiques et les indices biologiques de diversité, dominance et égalité, ne sont pas structurés selon les trois secteurs du tronçon, il n'y a des corrélations entre celles-ci (section 4.4.3). Une relation statistique positive est observée entre l'abondance d'un échantillon en macro-invertébrés et sa masse de matière organique. A l'échelle des dix sites, la diversité moyenne du benthos est liée à la diversité de la granulométrie des sédiments de surface, et démontre de plus une relation statistique négative avec la diversité de la granulométrie des sédiments de subsurface.

Les analyses multivariées ACC (analyses des correspondances canoniques) confirment qu'il n'y a pas de corrélation forte entre les variables physiques et les comptes d'abondance des macro-invertébrés. En cohérence avec les résultats de la précédente ACP, les échantillons pris dans les sites en amont (1, 2 et 3) sont différenciés des autres échantillons aval avec des quantités de matière organique et une vitesse de courant benthique plus élevées (figure 4.17).

La structure en trois secteurs qui est exprimée par les indices de granulométrie (figures 4.7 et 4.8), peut indiquer que les dynamiques de stockage et de transport de la charge de fond opèrent à l'échelle des secteurs (section 3.5.2.3, figure 3.25). On peut voir que la zonation représente un patron de perturbation *historique*, et que les trois secteurs indiquent un patron *actuel* des dynamiques morphologiques. Il est ainsi possible que la structure des trois secteurs représente la forme *future* du tronçon.

La particularité des sites 1, 2 et 3 qui enregistrent une vitesse du courant benthique et des quantités de matière organique plus élevées, peut être expliquée par un substrat particulier de la zone 1 et l'apport, le transport et le stockage de matière organique qui se manifestent entre les trois sites amont (section 4.5.1). Le substrat de la zone 1 est plat et rocheux, avec des nappes de gravier présentes dans les petites dépressions rocheuses du fond du lit. La juxtaposition des différents substrats crée des patrons hydrauliques plus divers que celui des sites entièrement alluviaux ; cette diversité physique est en effet accrue compte tenu de courants benthiques plus rapides et d'une plus forte variation du courant dans les sites 1 et 2. Les sites 1 et 2 retiennent également une masse de matière organique plus abondante que la moyenne de l'ensemble des dix sites, une masse presque deux fois plus importante que celle qui a été relevée dans le site 3. L'hypothèse de connectivité sédimentaire du tronçon (figure 3.25) émise précédemment permet d'interpréter la zone 1 comme un tapis roulant, fournissant efficacement la charge de fond à la zone 2. Il est probable que la masse de matière organique dans le site 3 s'explique par le même processus. Dans les sites 1 et 2, la capacité de stockage en sédiment ou en matière organique ne peut pas se faire sur le long terme, et il est possible que l'abondante masse de matière organique du site 3 reflète un processus de stockage de toute la matière organique fournie au tronçon (figure 4.20).

Les échantillons des sites 1, 2 et 3 se différencient par le courant benthique et les masses de matière organique, mais il est probable que la matière organique joue un rôle plus important que le courant pour expliquer la différence relative à l'abondance des macro-invertébrés du tronçon. Près de la moitié (42 %) des macro-invertébrés ont été collectés sur les sites 1, 2 et 3. L'abondance benthique d'un échantillon ne montre aucun lien statistique avec le courant benthique ($r = 0.18$) mais il y a par contre une relation statistique positive entre l'abondance et la masse de matière organique d'un échantillon ($r = 0.70$, $\alpha 0.05$). La majorité de tous les taxons est la plus abondante dans le site 3 ce qui par ailleurs (figure 4.21) démontre l'importance relative de la matière organique.

En plus des plus grandes abondances observées sur les sites 1, 2 et 3, la restitution graphique de l'ACD souligne bien que l'abondance benthique est également structurée entre les zones (figure 4.15). La zonation n'est pas retranscrite dans les distributions des taxons (figure 4.21) mais peut être interprétée à partir de la proportion des Ephéméroptères, Plécoptères et Trichoptères (EPT) dans un site (figure 4.22). A l'exception des sites de la zone 4, il est évident que la proportion des EPT varie peu entre les deux sites d'une zone alors que la différence de la proportion des EPT entre les zones est significative. Sullivan *et al.* (2004) ont reconnu par ailleurs une différence significative de la proportion des EPT entre les secteurs fluviaux stables et ceux plus instables du fait d'ajustements latéraux et verticaux. La différence concernant la proportion des EPT entre les sites de la zone 4 est donc importante tout comme l'égalité relative des sites 5, 6 et 7 et leur différenciation des sites 8, 9 et 10. Cela nous amène à réfléchir sur les effets résultant de changements morphologiques plus récents (2001-2006, section 3.5.2.2) : l'incision à l'amont de la zone 4 et l'accumulation de la charge de fond à l'aval de la zone 4 et dans la zone 5.

L'abondance est un indicateur du nombre absolu d'individus, mais n'exprime pas l'abondance relative des différents taxons. Les indices de diversité, dominance et égalité reflètent les différences d'abondance relative des différents taxons et donc les processus de compétition et d'exclusion, par exemple. Les résultats montrent que les indices d'abondance et les indices de diversité, dominance et égalité ne sont pas structurés dans la même façon. Tandis que l'abondance et la proportion des EPT reflètent les zones, les indices de diversité, dominance et égalité mettent en lumière une structure longitudinale en trois secteurs. Les différences concernant le style fluvial, la géométrie et la morphologie du lit dans et entre toutes les zones contrôlent le transport et le stockage de sédiment dans le tronçon. Les ajustements morphologiques plus récents (2001-2006) indiquent que cette dynamique a changé, de telle sorte que la redistribution de la charge de fond opère entre trois secteurs, plutôt qu'entre les limites des zones plus discernables. La correspondance entre la dynamique du tronçon et la structure des indices biologiques a mené à l'hypothèse que les différences de perturbation, associées aux différents régimes sédimentaires et hydrauliques des zones, ont une influence prédominante sur l'organisation du benthos (section 4.5.3). Les différences du style fluvial, de la géométrie et de la morphologie des zones entraînent davantage de

variations en matière d'ajustement transversal et vertical. Les zones larges et alluviales (2, 4 et 5) ne sont pas latéralement contraintes et leurs échanges avec la plaine alluviale peuvent alimenter le benthos avec une matière organique plus riche que celle des zones 1, 3 et 6. Il est ainsi probable que la contrainte verticale, exercée par le substrat rocheux, entraîne les différences en matière d'échange entre le substrat hyporhéique et le substrat de surface. Dans les chenaux alluviaux les échanges transversaux et verticaux exercent une influence d'égale importance sur l'organisation du benthos (ex : Junk *et al.* 1989, Stanford et Ward 1993), mais il est admis qu'il y a une plus grande variation des taux de stockage et de transport de la charge de fond et que la redistribution de la charge de fond a une influence plus forte. La résistance variable du lit des chenaux du substrat rocheux et alluvial entraîne une discontinuité substantielle des processus de transport de la charge de fond. La signification d'une telle variabilité est connue depuis peu dans le cadre d'ajustements fluviaux sur le long terme (Stark *et al.* 2009) mais a surtout une influence fondamentale sur l'organisation du benthos.

Le secteur à l'amont du tronçon abrite un benthos statistiquement moins divers et plus dominé que le benthos du tronçon médian. La charge de fond n'est pas souvent délivrée au tronçon, et quand elle arrive, les sédiments sont efficacement transférés en masse sur la zone 2 aval. Il est possible qu'un tel régime sédimentaire crée des perturbations du lit peu fréquentes mais intenses.

Le benthos de l'aval du tronçon est aussi statistiquement moins divers et davantage dominé que le benthos du tronçon médian. L'accumulation de sédiment à l'aval de la zone 4 et dans la zone 5 est susceptible d'exercer des perturbations du lit qui sont plus fréquentes mais moins intenses que celles du secteur en amont.

Le benthos du tronçon médian est statistiquement plus divers, plus équilibré, et composé d'une proportion d'EPT plus grande que celui des secteurs de l'amont et de l'aval. La zone 3 se caractérise par une morphologie du lit particulière, ce qui entraîne une forte différence en termes de transport et de stockage de la charge de fond en comparaison avec les processus régissant les autres zones. Les affleurements rocheux sont discontinus spatialement entre les nappes alluviales ; la sélection granulométrique ainsi que la réduction de la taille des sédiments de surface dans le tronçon médian (section 3.4.1.3, figure 4.13) peut suggérer que les affleurements rocheux interrompent le transport de sédiment, agissant comme des « barrières topographiques ». Les changements relativement dynamiques du profil topographique suggèrent davantage que les processus de transport et de stockage dans le tronçon médian sont relativement fréquents. Il semble ainsi que la morphologie particulière de la zone 3 crée des perturbations du lit plus fréquentes et modérées en comparaison avec celles des secteurs à l'amont et à l'aval du tronçon.

Il est bien établi que les variations de l'intensité et de la fréquence de perturbation contrôlent la distribution de macro-invertébrés (ex : Poff et Allan 1995, Death et Winterbourn 1995), entre les nappes qui subissent l'érosion, l'accumulation ou restent stables (Matthaei et

al. 1999, Effenberger *et al.* 2006, Olsen *et al.* 2007). Il est ainsi clair que le benthos est plus diversifié et équilibré dans les nappes qui subissent une érosion fréquente (Miyake *et al.* 2005, Effenburger *et al.* 2008) mais d'une intensité modérée (Miyake and Nakano 2002). Une telle perturbation engendre un effet sur le long terme (Matthaei et Townsend 2000) ainsi que sur le court terme (Mochizuki *et al.* 2008) et donc l'organisation actuelle du benthos peut résulter des régimes de perturbation régis par la géométrie et la morphologie des zones. Brown (2003, 2007) a montré que les perturbations sont amorties par l'hétérogénéité morphologique et un tel mécanisme est ainsi probablement plus efficace dans le chenal médian suite à la complexité des éléments structuraux, qui apportent une diversité de refuge pour la colonisation des macro-invertébrés. Cette hypothèse est renforcée par le fait que la diversité du benthos dépend d'un habitat lui-même contrasté et dynamique (Wilson 1994) afin que l'exclusion compétitive puisse se manifester dans les conditions de perturbation intermédiaire (Connell 1978, Ward et Stanford 1983, Townsend *et al.* 1997).

Le déplacement des individus est régi par la résistance et la résilience des taxa aux perturbations (ex : Poff et Ward 1990, Resh *et al.* 1994, Death et Winterbourn 1995), ce qui contrôle leur capacité à obtenir de la nourriture et un refuge. Le mécanisme d'exclusion compétitive exige un « effet sélectif » quant aux traits physiologiques, telles que la taille, la flexibilité et la forme des corps des taxons.

La relation statistique observée entre la diversité de la granulométrie et la diversité du substrat dans le tronçon reflète le mécanisme d'exclusion compétitive. Les sédiments de surface plus triés (la granulométrie étant alors moins contrastée) abritent un benthos relativement diversifié (figure 4.19), indiquant qu'un processus d'érosion a exclu les taxons qui n'ont pas pu résister au déplacement. De la même manière, la relation inverse observée entre la diversité de la granulométrie des sédiments de subsurface, et la diversité du benthos, met en lumière une capacité variable des individus à se réfugier dans le substrat de subsurface. Une granulométrie de subsurface plus diverse explique l'existence d'espaces interstitielles plus divers et donc susceptibles d'abriter une plus grande diversité de traits physiologiques.

L'idée qu'un effet sélectif puisse expliquer les différences des indices biologiques entre les zones, en fonction des différents régimes sédimentaires et hydrauliques, et des perturbations associées, souligne que la distribution des macro-invertébrés reflète l'adaptation des individus à l'hétérogénéité spatiale et temporelle de leur habitat. Dans ce cas, l'« habitat » semble opérer à l'échelle des zones qui contrôlent la variation des processus d'ajustement morphologique.

Strayer *et al.* (2006) suggèrent qu'il est plus efficace de décrire les distributions biologiques à l'échelle des processus de contrôle dominants, parce qu'ils indiqueront le cadre dans lequel les processus aux échelles plus grandes opèrent pour régir l'organisation du benthos. Entre Luc-en-Diois et Recoubeau-Jansac, la redistribution de la charge de fond est considérée comme le contrôle dominant de l'organisation des macro-invertébrés. Le transport

et le stockage de sédiment sont contrôlés par les différences de géométrie et de morphologie entre les zones. A leur tour, la géométrie et la morphologie discontinues du tronçon ont été créées et maintenues par l'apport de la charge de fond au tronçon et l'activité hydraulique, qui sont eux-mêmes contrôlés par la dynamique de la couverture végétale du bassin de la Béoux, qui est finalement elle-même un contrôle s'exprimant à long terme et à une échelle spatiale plus petite. L'organisation du benthos est alors contrôlée par une hiérarchie des processus, soulignant l'élément clé de la « Hierarchical Patch Dynamics Theory » (Lu et Woucks 1995, Poole 2002). Un changement de la couverture végétale dans le sous-bassin du Béoux entraîne un changement de l'apport de la charge de fond et de l'activité hydraulique du tronçon. A leur tour, les modifications du régime sédimentaire et hydraulique entraînent un changement dans la dynamique de transfert et de stockage des sédiments dans le tronçon, ce qui a in fine des implications pour la zonation du tronçon. Un changement de zonation crée un changement du régime de perturbation. Ultérieurement, les différents régimes de perturbation modifient à leur tour l'organisation des macro-invertébrés. Les analyses de l'évolution morphologique du tronçon, apporte une meilleure compréhension des conditions actuelles du tronçon, et de l'organisation du benthos. Tous ces éléments sont ainsi utiles dans le cadre de la restauration de la charge de fond au tronçon.

Les évolutions morphologiques futures, et les réponses du benthos

Même si en 2006 des tendances à la rétraction et à l'incision caractérisent le chenal à l'échelle du tronçon, et que la distinction des zones tend ainsi à se réduire, il est peu probable que de tels changements conduisent à la suite d'une succession d'étapes vers une trajectoire de dégradation qui soit inexorable. Compte tenu de la variabilité permanente de la capacité et de la propension du tronçon à s'ajuster, il est peu probable que celui-ci développe une morphologie homogène tout au long de son tracé. A présent la géométrie du tronçon est fixe, surtout dans les zones 1, 3 et 6. La discontinuité des contrôles latéraux ne permettra pas l'élargissement ou la rétraction du chenal à l'échelle du tronçon et maintiendra une morphologie discontinue. Il apparaît que la topographie du substrat rocheux sous la couverture alluviale n'est pas homogène, et il est donc peu probable que le chenal s'incise uniformément jusqu'à atteindre ce substrat tout au long de son tracé. Il y a des affleurements du substrat rocheux dans les secteurs où le lit est incisé d'environ 1.0 m, mais ces expositions rocheuses ne sont pas toujours observables dans les secteurs du tronçon qui ont subi un même niveau d'incision. L'exposition discontinue du substrat rocheux est un point important, parce qu'elle affecte variablement les processus de transport et stockage de sédiment, tout au long du tronçon.

En 2006 le chenal s'était incisé dans sa plaine alluviale, tout au long du tronçon, et il semble que dans l'avenir la déconnexion entre le chenal et ses marges les plus actives devrait favoriser plus d'incision et une diminution de la sinuosité. La fréquence des crues et les apports sédimentaires sont en train de se réduire et la réactivation moins fréquente des bancs

de galets permet ainsi l'expansion de la végétation. La végétation augmentant la résistance des bancs à l'érosion, elle provoque une concentration de l'eau dans un chenal plus étroit et contribue à l'enfoncement du lit. Un enfoncement plus marqué augmentera la déconnexion entre le chenal et ses marges alluviales, le phénomène s'auto-alimente et s'inscrit ainsi dans une boucle de rétro-réaction.

En 2005 les gestionnaires locaux ont cependant réaligné le tronçon dans la zone 2, et il est possible que l'intervention ait pu perturber ce cycle de dégradation. Le réalignement a dévié le cours du chenal de la rive droite vers la rive gauche, recoupant le tracé naturel. Le chenal a été réaligné dans une tranchée étroite et droite dans la partie amont de la zone 2, et a reconnecté le chenal à sa plaine alluviale expliquant l'arrivée de sédiments dans la partie aval de la zone 2 (figure 5.2). Il est ainsi possible que cette reconnexion réactive le fonctionnement de la zone 2 en mettant à sa disposition une source de sédiment à redistribuer à l'aval du tronçon.

Dans un scénario de laisser-faire, il est possible que sur le court terme la réactivation de ce réservoir puisse réactiver la connectivité sédimentaire qui régit la dynamique de zonation. Dans le cadre actuel d'une réduction généralisée des apports sédimentaires au tronçon, il est malgré tout probable que sur le long terme les tendances à la rétraction et à l'incision se maintiennent à l'échelle du tronçon et que l'incision et la déconnexion entre le chenal et les sources de sédiment soient rapidement observées dans la zone 2 et se propagent par la suite dans les zones aval.

Il est ainsi probable que sur le long terme, l'incision dans la partie amont de la zone 2 accélère le transfert de charge de fond à la transition entre la zone 2 et la zone 3, où le chenal se rétrécit, formant un goulet. De ce fait, on peut voir que la tranchée a servi à déplacer le chenal de la rive droite vers la rive gauche. Pendant la période d'analyse il apparaît que le goulet a réduit l'entrée de la charge de fond dans le couloir de la zone 3, où la géométrie du lit contrôle le transfert vers la zone 4. Il est fort probable que l'accumulation de sédiment au niveau de ce goulet ait produit le changement de tracé en rive droite du chenal lors de la crue de 1978 (figure 3.19), et une forte accumulation de sédiment au niveau de cette barrière peut éventuellement entraîner un nouveau changement de cours en rive gauche. Adjacent au goulet, la rive gauche du chenal était antérieurement une partie de la bande active (figure 5.3) et si un recoupement se manifeste il est possible que le chenal réoccupe un chenal ancien de cette zone. Si le chenal recoupe le goulet en rive gauche, et rejoint le chenal dans la zone 3, une augmentation de l'apport de sédiment vers l'aval est fort probable. L'exhaussement du lit, associé avec une augmentation de l'apport sédimentaire, nuirait la diversité structurale de zone 3 et ralentirait le transfert de sédiment à la zone 4. Il est possible qu'un tel changement entraînerait l'apport local de sédiment et l'incision dans la zone 4, et des dépôts aval dans les zones 5 et 6, parce que l'apport de charge de fond des zones 2 et 3 ne serait plus suffisant. Compte tenu de l'existence d'un seuil à la limite aval du tronçon, l'exhaussement de cet

secteur aval pouvait provoquer des crues susceptible de déborder dans la plaine agricole adjacente.

Si le réalignement du chenal permet de reconstituer une zonation sur le court terme, il est probable néanmoins que l'organisation actuelle du benthos ne changera pas, parce que les transferts longitudinaux (le transfert de sédiment), transversaux (les échanges avec la plaine alluviale) et verticaux (les échanges avec la subsurface) continuent à contrôler l'organisation du benthos de la même manière que dans le cas de la situation présente.

Sur le long terme, un processus de recoupement changerait les attributs benthiques du tronçon. A présent, la diversité morphologique du secteur médian est à l'origine de perturbations du lit qui sont modérées mais fréquentes, et qui expliquent l'existence d'un benthos plus diversifié et d'une proportion des EPT plus grande que ceux des secteurs de l'amont et de l'aval. Suite au recoupement, un exhaussement du lit sera à prévoir et celui-ci réduira la diversité morphologique, la variabilité hydraulique, et simultanément les processus de transfert et stockage de la charge de fond. Ces changements réduiront ensuite la diversité du benthos, et la proportion des EPT du chenal dans le secteur médian. A présent, l'incision et l'exhaussement des zones 4 et 5, respectivement, provoquent des perturbations du lit moins intenses et plus fréquentes que celles observées dans les secteurs amont et médian. Le benthos associé à de telles perturbations est moins diversifié et plus dominé que celui des secteurs amont et médian et donc un recoupement pourrait également réduire la diversité et augmenter la dominance du benthos dans le secteur aval. Du fait de la raréfaction des apports de charge de fond, le lit du secteur amont subit des perturbations plus intenses mais aussi plus rares. Compte tenu de la réduction des apports sédimentaires au tronçon, il est probable que sur le long terme, un tel régime ne changera pas, et que cela n'aura par conséquence pas d'effet sur le benthos.

Si la restauration de la charge de fond alimente le tronçon par des apports réguliers, ni trop fréquents ni trop conséquents en volume, il est possible que la zone 2 puisse fonctionner comme un réservoir et préserver la dynamique de zonation. Les transferts longitudinaux (le transfert de sédiment), transversaux (les échanges avec la plaine alluviale) et verticaux (les échanges avec la subsurface) pourraient alors maintenir la dynamique de zonation, celle-ci continuant à agir sur l'organisation du benthos dans les mêmes conditions qui prévalent actuellement préservant ainsi l'organisation actuelle du benthos.

La restauration de la charge de fond a pour but de limiter l'incision du tronçon proprement dit mais aussi des tronçons de la Drôme plus à l'aval. Il est probable que cette intervention atténuera bien l'incision du tronçon, mais elle n'aura malgré tout pas un effet homogène. Les processus de connectivité du tronçon devraient ralentir la recharge en sédiment à l'aval du tronçon. Le transfert de sédiment est une dynamique qui n'est ni linéaire ni simple. Un exhaussement du lit du tronçon ne serait donc pas une bonne mesure de restauration (Madej et Ozaki 1996). En revanche, la conservation d'une zonation morphologique suggère que le tronçon ait une dynamique autorégulatrice. Le rétablissement

de cet équilibre, avec un chenal mieux connecté à ses marges, constituerait un bon indice de succès (Beechie *et al.* 2008, Madej *et al.* 2009).

Afin de conserver la zonation actuelle du tronçon, et prévenir une métamorphose de la morphologie et une détérioration du caractère benthique du tronçon, la restauration de la charge de fond apparaît comme une stratégie de gestion désirable. Pourquoi faut-il conserver la zonation actuelle du tronçon ? Elle n'est qu'une configuration particulière des différents patrons que le chenal a exhibé pendant la période considérée dans les analyses. Depuis 1948 le chenal montre un agencement variable de zones morphologiques tant en nombre qu'en longueur (section 3.4.2.3, figure 3.17). On peut voir que si le chenal est connecté à ses bancs, notamment dans la zone 2, et si l'apport de charge du fond au tronçon suffit à tenir le fonctionnement de cette zone comme réservoir sédimentaire, la dynamique de zonation peut alors s'autoréguler. Il est important de comprendre la dynamique du tronçon, quelle que soit la stratégie de gestion. Tenir compte en effet du comportement du tronçon, devrait augmenter les chances de succès des politiques mises en oeuvre (Brierley et Fryirs 2009).

Comparé au substrat principalement rocheux du secteur amont, et au substrat alluvial du secteur aval, le substrat du secteur médian est hétérogène et abrite un benthos plus diversifié, moins dominé et une plus grande proportion d'EPT. De ce fait, il est possible que la diversité de la morphologie rocheuse et alluviale du tronçon actuel accueille un benthos plus diversifié et moins dominé, et une plus grande proportion d'EPT que les chenaux observés au cours des années précédentes, en particulier ceux de 1948, 1956 et 1971, qui sont tous alluviaux. On peut ainsi considérer que le tronçon actuel est sans doute écologiquement plus intéressant que les différents états antérieurs. Cette observation suscite des questions quant aux « conditions de référence » qu'il convient de définir (un état de la morphologie et des conditions écologiques existant avant une perturbation anthropique) et à l'idée souvent admise que les environnements fluviaux contemporains sont plus dégradés aujourd'hui qu'ils ne l'étaient il y a plusieurs décennies. La diversité écologique associée à la morphologie rocheuse et alluviale qui est mise en lumière ici comparativement à celle des sections en tresses renouvelle ainsi les résultats de précédents travaux (ex : Rempel *et al.* 2000, Robinson *et al.* 2002, Tockner *et al.* 2006, Gray et Harding 2009) et la considération des sections en tresses comme « îlots d'habitat préférentiel » (Jähnig *et al.* 2009). Si la biodiversité d'un chenal principalement alluvial n'est pas plus désirable que celle d'un chenal rocheux, il est possible que la restauration des chenaux multiples n'augmentera pas la diversité d'habitat et le benthos qui y est associé.

On en conclut alors que la conservation de la zonation du tronçon est écologiquement importante. La préservation des processus contrôlant la diversité morphologique maintiendrait en effet la diversité benthique. Les attributs morphologiques et écologiques du secteur médian dépendent bien sur de l'hétérogénéité du substrat dans ce tronçon, mais également de la configuration et des connexions existant dans et entre les zones 1 et 2. De même, les caractéristiques morphologiques et écologiques des zones 4 et 5 dépendent du

fonctionnement des zones 1, 2 et 3. Les processus des zones 1, 2, 3, 4 et 5 contrôlent le stockage de sédiment dans la zone 6. Dès lors, la dynamique de zonation fonctionne comme la somme de ses composantes et en conséquence les caractéristiques morphologiques et écologiques du secteur médian ne peuvent être reproduites sans un agencement particulier de la géométrie et de la morphologie du chenal, et des processus et connexions qui sont à l'origine de cette configuration particulière. La géométrie et la morphologie du chenal sont contraintes par les contrôles lithologiques latéraux et verticaux au sein du chenal. Autrement dit, la zonation et l'organisation du benthos dans le tronçon sont le résultat de la géographie et de l'histoire du tronçon.

Si l'apport de charge de fond n'est pas excédentaire ou inférieure à la capacité de transport actuelle, la diversité de la morphologie sera maintenue. On peut ainsi voir que si la restauration de la charge de fond assure des apports modérés et fréquents, une telle action serait une stratégie morphologiquement bénéfique pour le maintien de la diversité benthique.

1. Introduction

1.1. Thesis Definition

The first part of this thesis investigates the evolution of the present-day morphology along a five kilometre reach of the Drôme River, France. Between Luc-en-Diois and Recoubeau-Jansac, the channel is characterised by a striking, discontinuous pattern of bedrock, alluvial and mixed bedrock-alluvial sub-reaches, suggesting that complex temporal and spatial dynamics underlie what at first appears to be a linear trajectory of reach-scale degradation. To evaluate this hypothesis, decadal changes in channel planform are examined over a 58 year period, between 1948 and 2006, by using eight series of high-altitude aerial photography. Changes in longitudinal channel profile are observed using topographic surveys from 1928, 2003 and 2005.

In the second part of this thesis, the organisation of in-stream macroinvertebrate fauna is examined along the same reach. Particular attention is given to whether differences in channel behaviour and not just channel morphology influence spatial patterns of macroinvertebrate organisation between the bedrock, alluvial and mixed bedrock-alluvial sub-reaches. This hypothesis was developed following initial observations of in-stream channel features and channel behaviour, and patterns of macroinvertebrate community structure which emerged from data collected during this early fieldwork campaign. Associations between channel morphology and macroinvertebrate community structure were fully tested by subsequent fieldwork.

In an applied context, the reach of the Drôme River that forms the central focus of this thesis is of particular interest, because it is located 200 m downstream from the Béoux sub-catchment, a site chosen for the experimental remobilisation of sediment to rehabilitate channel degradation both along the five kilometre study reach and in downstream parts of the Drôme (Liébault *et al.* 2008). The third part of this thesis evaluates the likely impact of this management intervention on both channel morphology and the present-day organisation of in-stream macroinvertebrate communities. These predictions are based on an understanding of long-term channel behaviour, inherent variation in the capacity and the propensity of the channel to adjust, and an understanding of influences on the in-stream organisation of macroinvertebrate taxa gained in parts one and two.

Thus, this study provides historical, present-day and future perspectives of river channel form, dynamics, and associated patterns of in-stream macroinvertebrate organisation. The key themes explored in this thesis and introduced in the following review are river channel evolution, historical contingency, channel sensitivity, scale, patterns of in-stream macroinvertebrate organisation, and long-term, catchment-scale perspectives of river channel management.

1.2. Context

1.2.1. River Channel Evolution

River channels adjust continuously through time, in response to changes in their controlling conditions. A conventional view of this process is that, in the short term, channels adjust to changes in flow and sediment load (Schumm and Licity 1965), to achieve an equilibrium state of grade (Gilbert 1917, Mackin 1948), whereby the channel does not tend towards an *overall* state of aggradation or degradation (Leopold and Bull 1979). An excess input of sediment relative to flow energy can instigate aggradation and channel widening, while excess amounts of flow energy relative to sediment load can result in channel incision.

More recent concepts of complexity and non-linearity contest the concept of an equilibrium state (e.g. Phillips 1992), not least because the view of a graded channel is dependent upon the spatial and temporal scales of observation (e.g. Turner *et al.* 2003). Nonetheless equilibrium remains an important concept that is very useful in developing an understanding of river channel dynamics. On any given timescale, it is clear that a channel exhibits a natural range of variability around its mean form or long-term trajectory of evolution. As a river channel evolves it thus exhibits non-linear behaviour (e.g. Werner 1999, Phillips 1992). For example, Zanoni *et al.* (2008) observed that between 1803 and 2005 the general overall narrowing of a 16 km reach of the Tagliamento River was characterised by highly dynamic and cyclic behaviour. Phases of narrowing were followed by phases of widening, as a result of temporal changes in sediment supply and transport, which were associated with flood activity and within-channel vegetation. Brewer and Lewin (1998) also observed planform cyclicity along a reach of the river Severn, at Llandinam in mid Wales. Over a 150 year period increases in flood activity and magnitude triggered the development of a braided channel, while periods of reduced flood activity caused the channel to adjust from a braided to a single thread, low sinuosity channel.

In the long term, climate and geology are dominant controls on flow and sediment yield (Schumm and Licity 1965). Different climates control different intensities and frequencies of flood activity, and different bedrock lithologies undergo different rates of weathering and thus volumes of sediment production. Land use, and vegetation cover in particular, is an important intermediary of the two. The cohesive strength of tree and vegetation roots stabilises gullies and hillslopes, and the cover provided by the canopy buffers the weathering and transport of colluvial sediment to the channel during rainstorm events (e.g. Bravard 2002, Gomez *et al.* 2003). Thus, the large-scale deforestation of catchment vegetation can increase sediment yields, leading to channel aggradation (e.g. Madej and Ozaki 1996, Brooks and Brierley 1997), while an increase in catchment vegetation can have the opposite effect of channel degradation, by reducing sediment supply and changing flow regimes (e.g. Keestra *et al.* 2005, Boix-Fayos *et al.* 2007). The Drôme River in south-eastern France is a particularly remarkable example of how, at the catchment scale, managed afforestation and natural reforestation has

contributed to a large sediment deficit and considerable channel degradation. Between 1928 and 1996, the lower 70 km of the channel incised by an average of 2.9 m, and as much as 5 m in places. Between 1948 and 1991 a 42 % reduction in the active width of the channel was also recorded (Landon 1996).

Changes in flow and sediment yield can also cause channel metamorphosis, in the sense that sudden changes in channel form may occur when critical threshold limits are exceeded (Schumm 1973), either as an immediate, or lagged response. By interrupting gradual, long-term adjustments floods can act as external 'triggers' of channel metamorphosis causing changes in channel form. Brewer and Lewin (1998) observed that large floods triggered switches in channel planform from meandering to braiding, while periods of reduced activity were coincident with the metamorphosis of a braided to single-thread and less sinuous channel.

Irrespective of magnitude, however, the morphological effects of a flood event are contingent upon the condition of the channel at the time of impact. The propensity of a channel to change, and the capacity for a channel to adjust, are variable in both time and space, and so a given flood event may instigate a different response at a different point in time. For example, Warburton *et al.* (2002) observed that between 1815 and 1993 a 1.4 km reach of Swinhope Burn, in northeast England, retained a stable meandering pattern, but in response to four major floods, this was interrupted by an abrupt and short-lived change to a straight and partly divided channel during the early part of this period. Following a change in sediment regime, major floods during the latter part of their study period caused no evidence of major morphological change. During their 150-year study period Brewer and Lewin (1998) also observed that levels of flood activity which had previously instigated the metamorphosis of a single-thread to braided channel no longer caused such a response. This change in channel behaviour along the Severn River was attributed to an increase in channel stability. Kochel (1988) also highlighted the importance of historical contingency in his example of the Pecos River, Texas. Floods with estimated return intervals of 2000 and 500-800 years, that occurred in 1954 and 1974, respectively, also caused contrasting morphological changes. The earlier flood event induced substantial erosion, and twenty years later the second event instigated minor morphological changes, because the channel was still adjusting to the previous impacts of the 1954 flood. These examples further highlight that the interpretation of channel evolution as deterministic or stochastic is controlled by the spatial and temporal scale of observation (Church 1996).

In addition to flow and sediment regimes, there is increasing recognition that within-channel and riparian vegetation is a fundamental control on channel evolution (e.g. Gurnell *et al.* 2009). The cohesive strength of roots increases the resistance of channel bars and banks to erosion (e.g. Abernethy and Rutherford 2000, Simon and Collinson 2002) and has been observed to instigate channel metamorphosis from braided to single thread planforms (Tal and Paola 2007). A riverbed is an 'arena in which vegetation attempts to establish itself, while

the river tries to scour it away' (Hicks *et al.* 2008). During periods of reduced flood activity, the encroachment of vegetation along channel margins has been observed to cause channel narrowing, with floods acting as 'vegetation resetting events' (Wallick *et al.* 2008) by causing channel expansion (e.g. Winterbottom 2000, Tiegs and Pohl 2005).

River channels are connected to their catchment by a network of longitudinal, lateral and vertical linkages (Bravard and Gilvear 1996) and so their flow and sediment regimes are contingent upon both the geography and history of their catchment landscape. Thus, 'every stream is likely to be individual' (Hynes 1975) and this 'primacy of place' (Phillips 2001) offers some explanation for the finding that models of channel evolution developed in one particular catchment do not adequately describe variation in channel form in another (e.g. Beechie *et al.* 2008). Ideas of contingency, threshold, sensitivity and scale are important for, and resonate with, the recognition that there is no universal template for understanding river channel adjustment (Leopold and Langbein 1963).

This is perhaps particularly true of mixed bedrock-alluvial channels. Such channels are good examples of non-linear systems with complex geographies. While alluvial channels are 'authors of their own geometries' (Leopold and Langbein 1962), in that they are generally unconstrained and able to freely adjust, once incised to bedrock, a channel is strongly constrained and able to 'chronicle its own cataclysms' (Baker and Pickup 1987). The structural resistance of bedrock can force substantial adjustments in channel form, such as the avulsion of a new channel through adjacent, less resistant alluvial floodplains by the catastrophic stripping of sediments (e.g. Warner 1997, Heritage *et al.* 1999). The intermittent bedrock and alluvial characteristics of the channel boundary creates substantial variability in resistance to erosion (Thompson and Wohl 1998), and thereby spatial and temporal variability in the propensity and the capacity of a channel reach to undergo change.

Patterns, rates and processes of adjustment in bedrock-controlled channels are receiving increasing attention, in part because it is recognised that they set the boundary conditions for subsequent, long-term channel evolution (e.g. Wobus *et al.* 2006, Attal *et al.* 2008, Stark *et al.* 2009). Sediment transport and alluvial cover play a fundamental role in bedrock channel erosion and to date, there has been particular interest in how channel alluvium moderates rates and processes of channel incision. This is a balance between a 'tools' effect, whereby bedload promotes incision of the channel bed, notably by processes of abrasion and quarrying; and a 'cover' effect, in which bedload acts as a mobile 'cover' shielding the channel bed from incision (e.g. Sklar and Dietrich 2001, Turowski *et al.* 2008). These effects are transient, and spatially variable, because of temporal and spatial fluctuations in flow regime and sediment supply (Finnegan *et al.* 2007).

However, despite this interest, and in comparison with purely alluvial rivers, relatively little is known about the behaviour and processes of adjustment in mixed bedrock-alluvial channels: 'There is little information on bed lowering rates in rock-confined channels, practically no information on recession rates of channel margins...[and] few studies have addressed *reach-scale* sediment dynamics (Carling 2006, p.2, my emphasis).

The first part of this thesis therefore aims to:

- Examine the decadal evolution of a mixed bedrock-alluvial channel reach;
- Identify spatial and temporal variability in overall trends of channel adjustment; and
- Investigate how this has been influenced by larger-scale and long-term controls on flow and sediment yield.

1.2.2. Channel Morphology and In-Stream Macroinvertebrate Community Structure

The geomorphological processes that shape the physical structure of a river channel operate over different spatial and temporal scales, which have been organised in different conceptual frameworks that share a common view: a river channel is embedded within a multi-scaled hierarchy, in which small-scale features are shaped by short-term processes, and constrained by larger scale features, which result from long-term processes (e.g. Frissell *et al.* 1986, Montgomery and Buffington 1997, Thomson *et al.* 2001). Because of the unique historical and morphological context of each catchment, hierarchical frameworks of channel structure and function that have been developed in one catchment are unlikely to apply to another (Frothingham *et al.* 2002), and especially to mixed bedrock-alluvial channels, in which spatial and temporal channel dynamics differ markedly from the predominantly alluvial settings in which hierarchical classifications of channel structure and function were developed.

The physical structure of a river channel provides a physical template for interpreting the organisation of in-stream macroinvertebrate fauna. Discrete changes in physical habitat conditions typically reflect parallel changes in the composition of a macroinvertebrate community (Southwood 1977, Townsend and Hildrew 1994), as different macroinvertebrate taxa are 'filtered' between localities by their different requirements and tolerances of temperature, light, nutrients, oxygen, flow velocity and substrate (Poff and Ward 1990, Death and Winterbourn 1995). For example, taxa found in shallower, fast-flowing environments and on coarser substrates possess holdfast structures to maintain their attachment to the substrate for feeding, while taxa found in deeper, slow-flowing environments and on finer sediments may be adapted to burrow into the substrate to avoid hydraulic stress (e.g. Wallace and Merrit 1980, Mackay 1992).

However, this 'top-down' morphological approach does not account for biotic processes and interactions, which also regulate the composition of a macroinvertebrate community. Trophic interactions can significantly influence the distribution of macroinvertebrate taxa by predation and competition (Schmera *et al.* 2007), and it has been

shown that community structure is influenced by the invasion of foreign taxa (Smiley and Dibble 2005). There is evidence that macroinvertebrate taxa respond to their 'streambed landscapes' (Palmer *et al.* 2000) in the sense that local variation in macroinvertebrate organisation (e.g. Brooks *et al.* 2005) may be explained by patterns of active pathways of macroinvertebrate dispersal across the channel bed (Rice *et al.* 2008) and within the flow (Lancaster *et al.* 2006). It has also been observed that biotic processes can regulate channel bed morphology by 'engineering' the substrate. Mayfly (Ephemeroptera) burrowing can enhance water and sediment exchange (Charbonneau and Hare 1998). Caddis fly (Trichoptera) nets can 'armour' the stream bed (Statzner *et al.* 1999) and stabilise gravel (Cardinale *et al.* 2004), significantly increasing the threshold at which gravel is entrained into the flow (Johnson *et al.* 2008). These small-scale biotic interactions contribute to patterns of macroinvertebrate organisation that are apparent at larger scales (Lamouroux *et al.* 2004) and their significance cannot be discounted. A recent review of 158 published data sets found that only 50 % of variation in macroinvertebrate community structure could be explained by environmental and spatial variables (Cottenie 2005), lending importance to the 'bottom-up' influence of biotic processes and interactions.

Notwithstanding the importance of biotic processes such as predation, competition and dispersal, it has been argued that the behavioural and morphological adaptations of different taxa develop in response to different physical habitat conditions (Leibold *et al.* 2004) such that the physical habitat template is of fundamental and undeniable importance. In addition it is generally impractical to take a bottom-up approach given the relative paucity of knowledge about the biological processes that affect biological interactions and distribution patterns at larger scales. In practice, a morphological, top-down approach has prevailed in developing our wider understanding of in-stream macroinvertebrate organisation, and so associations between channel morphology and patterns of in-stream macroinvertebrate community structure are well-established in alluvial channels.

From river source to river mouth, systematic downstream changes in macroinvertebrate community structure reflect downstream changes in temperature and productivity (Vannote *et al.* 1980). Along this continuum, broad zonation in macroinvertebrate community structure (Ilies and Botosaneanu 1963) reflects downstream zonation in organic biomass (Culp and Davies 1982) and stream hydraulics (Statzner and Higler 1986), and parallels the distinction of sediment source, transfer and deposition, between headwater, mid-order and floodplain zones (Schumm 1977). However, the perception of continuity relies upon the scale of observation (Turner *et al.* 1993, Wright and Li 2002). It is clear that at smaller scales of resolution, downstream gradients of channel morphology and in-stream macroinvertebrate ecology are non-linear. Anthropogenic and natural perturbations, such as dams (Ward and Stanford 1983) and tributaries (Bruns *et al.* 1984) interrupt linear downstream gradients to create a discontinuum (Perry and Scafeffer 1985, Poole 2002) and instigate patterns of heterogeneity.

At the catchment scale (10^4 km), the introduction of water and sediment at tributary junctions forces numerous changes in habitat composition, including punctuation of the downstream fining of river bed grain size (Rice and Church 1998). This has been shown to interrupt downstream gradients of macroinvertebrate community structure (Rice *et al.* 2001a, b; Kiffney *et al.* 2006). Within channel links, little attention has been given to macroinvertebrate community structure between channel reaches (10^1 km) that have different planforms. Some recent work has identified significant differences in macroinvertebrate community composition between reaches characterised by different channel styles and considered this variation to reflect differences in geomorphic units and channel bed composition (Chessman *et al.* 2003). Channel reaches (10^1 km) are characterised by different compositions of geomorphic units (10^{-1} km) such as riffles and pools. Considerable attention has been given to differences in macroinvertebrate community structure at this scale and it is well established that riffles are more diverse and abundant than pools, for example (e.g. Brown and Brussock 1991, Parsons and Norris 1996, Beisel *et al.* 1998). Within a riffle, at sub-metre scales (10^{-3} km), median bed particle size has been related to variation in macroinvertebrate richness and evenness (Brosse *et al.* 2003) and differences in abundance (Pedersen and Friberg 2007). The head of a riffle has been observed to support significantly higher mean macroinvertebrate abundance and richness than the downstream part of a riffle, as a function of the relatively greater amount of interstitial space (Davy-Bowker *et al.* 2006).

While it is clear that patterns of macroinvertebrate organisation are constrained by physical habitat, it is also apparent that relatively few studies have examined the underlying morphological processes responsible for creating and maintaining these corresponding patterns. The categorisation of 'habitat' as a static spatial entity neglects to consider that habitat is dynamic, in the sense that it is constructed and maintained by morphological processes, of bedload erosion and deposition, for example. This has led to relatively recent, widespread recognition that understanding the links between morphological dynamics and ecological variability should be a research priority (e.g. Clarke *et al.* 2003, Vaughan *et al.* 2009). It is also recognised that local variation is not dominated by local controls but results from processes operating and interacting between different scales (e.g. Brosse *et al.* 2003, Parsons *et al.* 2003, Galbraith *et al.* 2008) and thus an understanding of local variability requires an appreciation of larger-scale and longer-term processes constraining the organisation of macroinvertebrate taxa.

Compared to alluvial morphological units, bedrock is less well explored as an in-stream habitat for macroinvertebrate communities. A few studies have compared bedrock outcrops with alluvial depositional and cobble riffle habitats, and observed significant differences in macroinvertebrate community structure between these substrate types (Wohl *et al.* 1995, Grubaugh *et al.* 1996, Robson and Chester 1999). In instances where bedrock has been observed to support significantly higher abundance and/or diversity than channel alluvium, this has been related to the greater surface area provided by stands of *Podostemum*

ceratophyllum (hornleaf river weed) covering the bare bedrock (Grubaugh *et al.* 1996, Hutchens *et al.* 2004). Chadwick and Huryn (2007) also observed that compared to riffles and runs, bedrock was dominated by moss, but conversely supported significantly less rich macroinvertebrate communities. Other citations of macroinvertebrates and bedrock are observations that Simuliidae (black fly) is characteristic of bedrock surfaces (Boyero and Bosch 2004, Halwas and Church 2005, Principe *et al.* 2007).

There is little, if any information on how macroinvertebrates are organised in mixed bedrock-alluvial channels, between juxtaposed reaches characterised by contrasting morphologies, and flow and sediment regimes. The role of morphological processes in creating and maintaining patterns of macroinvertebrate community structure in such channels is, at present, unknown. Given their dynamic nature, mixed bedrock-alluvial channels provide a unique opportunity to explore links between processes of channel adjustment and variability in the distribution of in-stream macroinvertebrate taxa. To understand how these ecological patterns are regulated by processes of channel adjustment, it is also necessary to recognise longer-term controls on variation in flow regime and sediment supply, which operate externally to the reach, at the catchment scale.

The second part of this thesis therefore aims to:

- Characterise the organisation of in-stream macroinvertebrate taxa within a mixed bedrock-alluvial channel;
- Explore associations between spatial patterns of macroinvertebrate community structure and physical channel characteristics, and, specifically, the morphological dynamics of the channel;
- Investigate how patterns of macroinvertebrate organisation are constrained by different internal mechanisms and external controls operating at different spatial and temporal scales.

1.2.3. Future Changes in Channel Morphology and Macroinvertebrate Community Structure

For river systems that have been disturbed and disequibrated, the prediction of future changes in channel morphology is a critical part of river channel management. Under a changing climate, and following the large scale and widespread anthropogenic disturbance of fluvial landscapes, it is necessary to understand how river channels and their in-stream ecology are likely to respond to future changes in flow regime and sediment supply. The political and economic implications of river channel changes led Graf (1988) to suggest that 'the most significant social and economic contributions of the science of geomorphology lie in the analysis of change in fluvial systems'.

The majority of European rivers are now disturbed by anthropogenic intervention. Man's role in 'changing the face of the earth' (Thomas 1956), from natural to cultural

landscapes, has been shaped by a history of political and economical changes. Meybeck (2003) has gone so far as to propose that rivers are part of a contemporary 'Anthropocene' period of Earth history, during which natural processes are dominated by human actions past and present. For example, it is estimated that approximately only 10 % of rivers in the entire Alpine region are still 'pristine' or in a 'near natural' condition (Martinet and Dubost 1992, cf. Habersack and Piégay 2008). Throughout the nineteenth and twentieth centuries, in response to requirements for improved flood protection and navigation, hydropower, agricultural development and industrial expansion, the widespread regulation of flow and sediment regimes has disturbed the majority of European rivers (e.g. Petts *et al.* 1989), many of which now tend to overall degradation. Channel constriction, narrowing and incision have been observed in piedmont rivers of south-eastern France (Liébault and Piégay 2002), Italy (Surian 1999, Rinaldi 2003), and Austria (Muhar *et al.* 2000).

River channel degradation is a particular management priority because of the associated morphological, ecological, and socio-economic consequences, such as lowering of the groundwater table, the loss of in-stream habitat, and the undermining and subsequent collapse of bridges (e.g. Bravard *et al.* 1999, Kondolf *et al.* 2002). Equally, the way in which degradation is managed can have substantial morphological, ecological and socio-economic consequences. The local installation of small engineering infrastructure, such as check-dams, can alleviate channel incision in the short term, but in the long term they can have the opposite effect and increase downstream erosion (e.g. Castillo *et al.* 2007, Boix-Fayos *et al.* 2008). In 1996, in the central Pyrenees, the collapse of check-dams resulted in the death of 87 people during a rainstorm event that generated discharge levels equivalent to a one in two year flood event (White *et al.* 1997). These examples are only two of many that have led to relatively recent, widespread acceptance that historically commonplace short-term and small-scale engineering interventions target the symptoms, rather than of the cause of channel degradation (e.g. Leeks *et al.* 1988), and that sustainable and successful management is best achieved by a strategy that adopts a large-scale perspective of long-term channel behaviour (e.g. Downs and Gregory 2004, Brierley *et al.* 2008, Gregory and Downs 2008).

A key management objective for a river channel that has been disturbed and disequibrated, such that it tends towards overall degradation or aggradation, is to restore an equilibrium state. However, this often fails to recognise the non-linear behaviour of river channels. For example, the assumption that channel incision may be alleviated and reversed by the reintroduction of bedload does not account for spatial variation in channel behaviour, and the changing propensity and capacity of the channel to adjust through time. The successful restoration of channel degradation relies on an understanding of this variability and how the channel is likely to respond to future changes in flow and sediment regime. This includes a recognition of how the channel has responded to historical changes in flow and sediment regime, and controls on the routing of flow and sediment within the channel. The downstream propagation of flow and sediment can be impeded by internal or external

perturbations, in the form of barriers, buffers and/or blankets (Fryirs *et al.* 2007). In evaluating how a channel may respond to changes in flow and sediment regime, it is important to understand the dynamics and functioning of channel reaches, in terms of their sediment connectivity (Hooke 2003). Understanding spatial and temporal changes in connectivity provides a basis from which to predict likely future trajectories of change in morphology (e.g. Fryirs and Brierley 2000, Fryirs *et al.* 2007). An understanding of spatial and temporal changes in the functioning of channel reaches, in terms of their regimes of bedload supply and transfer, will also inform predictions of future changes in macroinvertebrate community structure by revealing changes in the dynamics and functioning of habitat.

The main aims of the third part of this thesis are to:

- Project future changes in channel morphology along a mixed bedrock-alluvial reach, in response to changes in flow and sediment load. This prediction will be based on the thorough understanding of long-term and large-scale controls on channel evolution gained in the first part of this thesis.
- Speculate on future changes in macroinvertebrate community organisation, based on any correspondence between patterns of channel adjustment and macroinvertebrate distribution observed within the second part of this thesis.

1.3. The Drôme River

Historical morphological changes along the Drôme River, in south-eastern France, are fascinating examples of channel change in response to management interventions. Substantial channel incision and narrowing have been documented along the lower Drôme (Landon and Piégay 1994, Landon 1999, Kondolf *et al.* 2002) and remarkably different channel changes have been assessed in the upper Drôme (Landon and Piégay 1999, Piégay *et al.* 2004). Morphological changes have also been examined in sub-basins throughout the catchment (Liébault *et al.* 1999, Liébault and Taillefumier 2000, Liébault 2003). However, there is a significant gap in this detail. A distinctive reach linking the upper and lower Drôme has not been explored, despite recognition that it is one of three sites in the Drôme basin characterised by severe degradation (Liébault *et al.* 2008).

Located in the upper part of the Drôme, a five kilometre reach between Luc-en-Diois (Luc) and Recoubeau-Jansac (Recoubeau) is characterised by abrupt changes in style and substrate between wide and alluvial, and confined, narrow and bedrock sub-reaches (hereafter referred to as zones). This morphological diversity is representative of large sections of the river Drôme as a whole, and is akin to the analogy of 'beads on a string' that has been used to describe the Italian river Tagliamento (Ward *et al.* 1999). Abrupt transitions occur between the zones and suggest that complex sub-reach dynamics underlie simplified trends of channel narrowing and incision. The historical development and the present-day dynamics of this diverse channel structure, its present-day ecological characteristics, and the likely future

evolution of the reach are not at present understood. The reach thereby provides a unique opportunity for the investigation of the main thesis aims summarised below.

In an academic sense, this information will contribute to currently limited perspectives on the evolution of mixed bedrock-alluvial channels, and how they respond to changes in flow and sediment load; and provide insights into how the structural diversity and dynamics of a mixed bedrock-alluvial channel regulate in-stream patterns of macroinvertebrate community organisation.

In an applied sense, this research may also contribute information useful for the guidance of management decisions associated with channel stability and the conservation of in-stream biodiversity. Channel changes and their ecological implications are of particular interest in the European Community at present, within the context of the European Water Framework Directive (WFD) and its recognition that the former hydromorphological and aquatic habitat diversity of most streams in Central Europe has been lost. The WFD acknowledges that understanding river channel hydromorphology is a key element in achieving 'good ecological status' by 2015 (European Commission 2000). In France, regional-scale management schemes (SDAGE) were enforced in 1992, under new water laws to manage the state and quality of fluvial environments in large watersheds, such as the Rhône. As a tributary to the Rhône, the Drôme basin is subject to local planning schemes (SAGE), under the control of under the control of local water authorities (CLE), which aim to (i) limit anthropogenic impact on bedload transport and channel geometry, (ii) encourage restoration of natural geomorphic processes and (iii) improve aquatic habitat conditions (Piégay *et al.* 2002). These objectives invoke issues of sediment transfer and connectivity along the Drôme and SAGE guidelines thus require an understanding of long-term channel behaviour at sub-reach scales.

Concerns over the implications of degradation along the Drôme have generated interest in reactivating coarse sediment supply in the upper part of the catchment, to reverse degradation and incision along downstream reaches (Liébault *et al.* 2008). Located 200 m upstream from the reach that is examined in this thesis, the Béoux sub-catchment has been chosen as a site for the long-term remobilisation of sediment. The experiment is particular significance because, in the context of the aims of the Water Framework Directive, no practical example of river basin management exists for the Alpine region (Habersack and Piégay 2008). The experiment has also created interest in restoring channel degradation by reactivating coarse sediment supply in rivers of north-eastern Italy (Surian 2009), yet the morphological and the ecological impacts of this type of intervention are not yet clear, and remain to be evaluated.

It is likely that the planned remobilisation of sediment in the Béoux will have implications for the future morphological and ecological character of the study reach, because it will involve changes in morphological dynamics and the provision and character of in-stream habitat. By confirming the present-day trajectory of morphological changes between Luc and Recoubeau, it will be possible to speculate on how the reach may respond to an altered

sediment regime, should the planned sediment remobilisation in the Béoux sub-catchment be successful. Combined with a detailed characterisation of in-stream macroinvertebrate community organisation, specifically between morphological zones, it will be possible to speculate on the possible ecological impacts of future morphological changes under these two scenarios.

1.4. Thesis Aims and Objectives

To summarise, the overall aims of this thesis are to:

- (1) understand the long-term evolution of a mixed bedrock-alluvial channel, at the reach scale;
- (2) identify spatio-temporal variability in long-term trends of channel adjustment and how this has been influenced by larger-scale controls;
- (3) characterise the present-day distribution of macroinvertebrate communities within of a mixed bedrock-alluvial channel;
- (4) explore associations between the organisation of macroinvertebrate taxa and the physical characteristics, specifically the morphological dynamics of the channel; and
- (5) speculate on possible future trajectories of change in channel morphology and macroinvertebrate community structure, given the understanding of present-day channel condition and propensity for change.

1.5. Thesis Structure

This thesis is organised into four main parts. Chapters 2, 3, and 4 contribute observation, data, theory and interpretation necessary for a synthesis of possible future changes in channel morphology and macroinvertebrate community organisation in chapter 5 (figure 1.1).

Chapter 2 introduces the river channel in which the main thesis aims and objectives will be examined, describing and illustrating present-day channel form and characteristics for reference throughout the thesis. This chapter also considers the present-day setting of the reach and historical changes within it that will likely be of importance for the interpretation of morphological changes.

Chapter 3 documents decadal changes in channel morphology between 1948 and 2006, using GIS to analyse eight series of high-altitude aerial photography. Particular consideration is given to spatio-temporal variation within overall trends and the development of present-day morphological zonation. Three longitudinal profiles, surveyed in 1928, 2003 and 2005 are used to analyse change in channel elevation.

Chapter 4 characterises the present-day organisation of macroinvertebrate taxa along the study reach, using data derived from quantitative Surber samples collected in the field under low-flow conditions in 2006. Associations between channel morphology and patterns of macroinvertebrate community structure are evaluated using local habitat characteristics that were measured simultaneously.

Chapter 5 discusses the main findings of chapter 3 and 4 to predict possible future changes in channel morphology and in-stream macroinvertebrate community organisation in light of management plans to rehabilitate channel degradation along the study reach.

Chapter 6 draws together the main thesis findings and relates them to current perspectives of river channel change and macroinvertebrate community organisation.

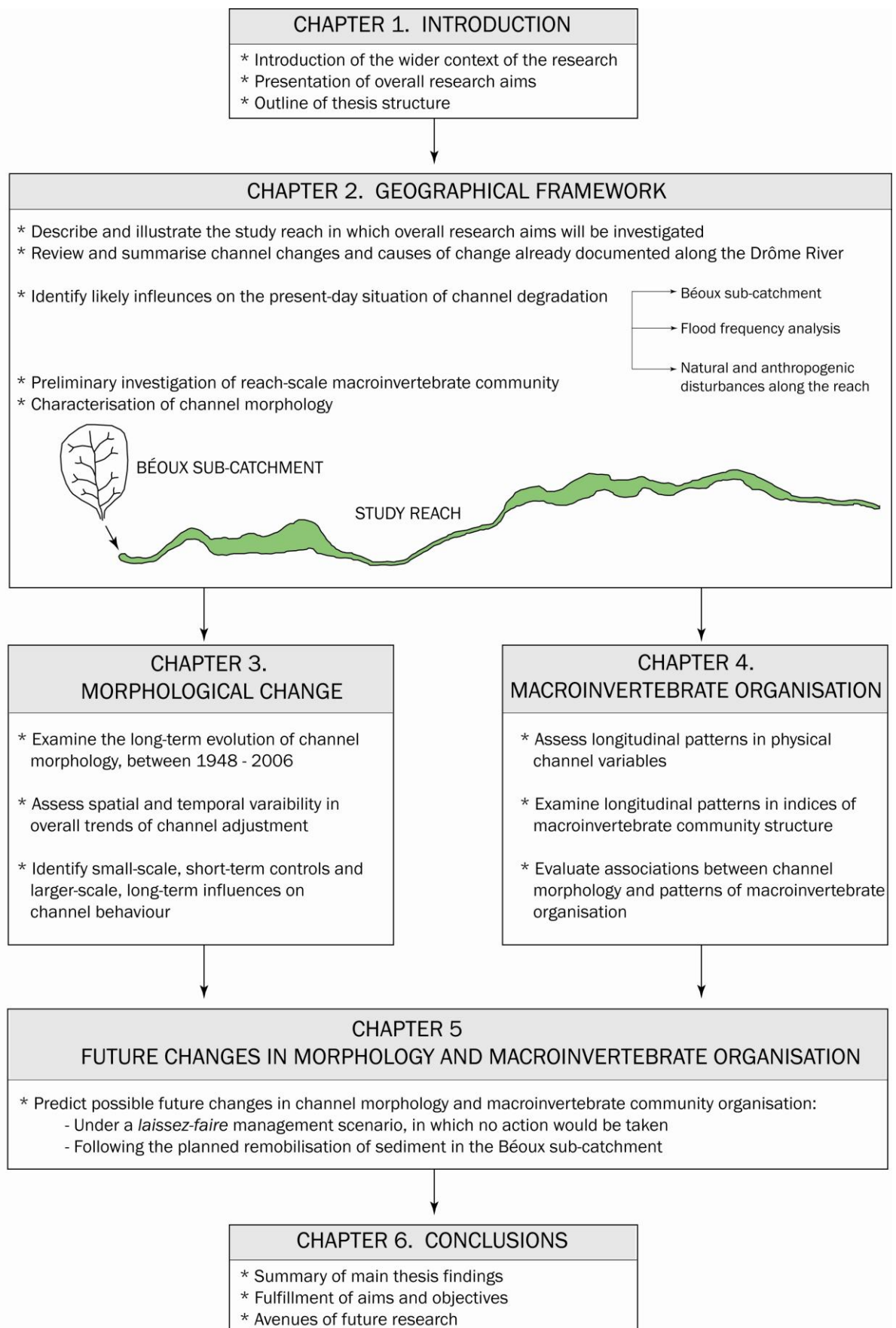


Figure 1.1. Schematic diagram of thesis structure.

2. Geographical Framework

2.1. Introduction

This chapter introduces the five-kilometre reach of the river Drôme in which the study aims and objectives will be examined. The historical morphological changes and causes of channel adjustment already established along the river Drôme, along the lower and upper reaches of the channel are first summarised (section 2.2). To provide some context for the apparent situations of channel degradation and incision, both natural and anthropogenic changes in sediment supply are then identified in the immediate geographical setting of the reach, specifically within the Béoux sub-catchment (section 2.3) and along the reach itself (section 2.4). Changes in flood frequency are also considered for the study period of interest (section 2.5). Initial assessments of the morphology and macroinvertebrate ecology of the study reach are then presented (section 2.6) and the six channel zones that characterise the study reach are described and illustrated for reference throughout the thesis.

2.2. The River Drôme

The Drôme River is 106 km long. It is a left bank tributary of the mid-Rhône River in south-eastern France (figure 2.1), underlain by Mesozoic marls and limestones and drains both the Diois and Vercors mountains, that range in elevation from 800 m – 2000 m, over a catchment area of 1642 km². The flood regime is nival, with an annual snowmelt flood that typically occurs in March. The flood regime is further influenced by a Mediterranean climate that generates large flashy floods in both spring and autumn.

Figure 2.1 (following page) *Location map of the Drôme River.*

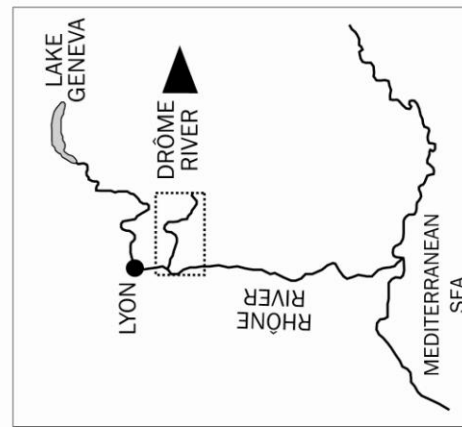
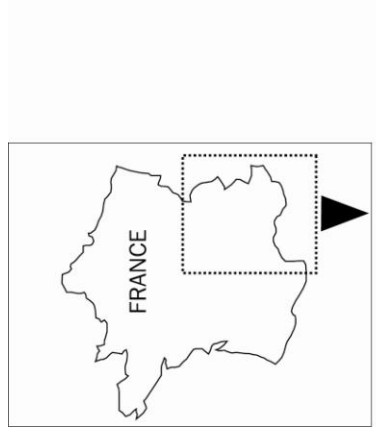
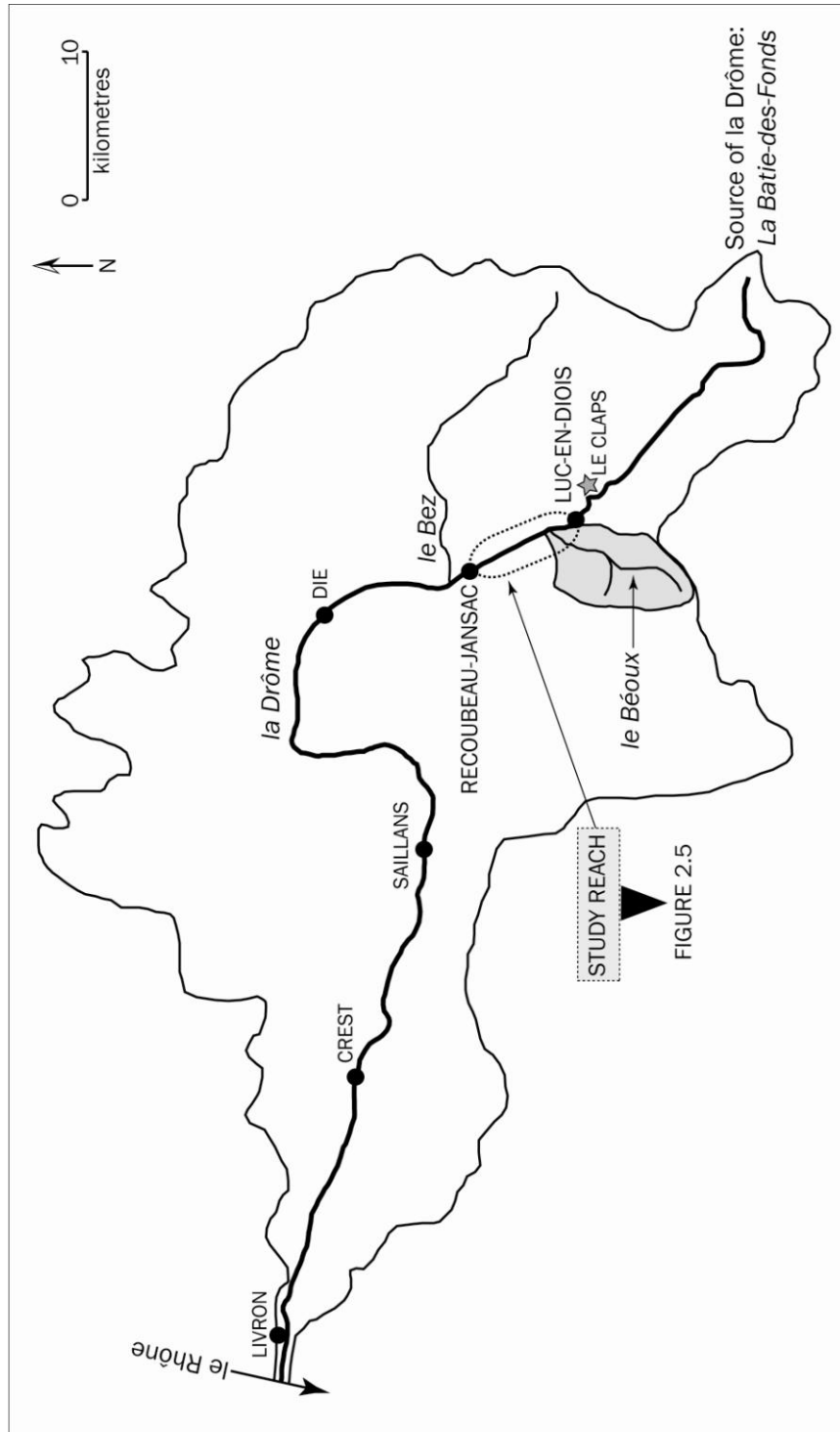


FIGURE 2.5

2.2.1. The Lower Drôme, le Bez to le Rhône

Since 1850 channel incision and narrowing have been observed in mountain streams and piedmont rivers throughout south-eastern France, including the Drôme catchment, with an abrupt increase in the rate of these changes since 1950 (Liébault and Piégay 2002). Between 1928 and 1986 the downstream 84 km of the Drôme underwent substantial incision that approached 5 m in places. Between 1948 and 1991 the width of the active channel narrowed, on average, by 42 % (Landon *et al.* 1998) with as much as 60 % narrowing observed along some reaches (Kondolf *et al.* 2002). This degradation has been related to three main causes.

First, channel incision and channel narrowing have been related to extensive afforestation throughout the catchment (Landon and Piégay 1994) that was enforced between 1887 and 1914 by RTM (Restauration des Terrains en Montagne/mountain landscape restoration) schemes (Liébault and Zahnd 2001). Prior to this period of afforestation small check-dams and other direct interventions were widely installed to stabilise hillsides and steep torrents. These collective actions were undertaken following realisation in the mid-nineteenth century that severe land degradation, associated with agricultural pressures and exacerbated by the climatic instability of the Little Ice Age, was responsible for aggradational problems within the main stem Drôme. In the early 1900s a further increase in forest cover was caused by the natural reforestation of agricultural land abandoned by widespread depopulation (Liébault 2003). The substantial increase in forest cover has reduced hillslope erosion, runoff and sediment yields, increasing the resistance of the Drôme basin to climatic events (Piégay *et al.* 1997). There has been a reduction in the magnitude of peak flows since 1925 (Landon *et al.* 1998) and a decrease in flood frequency throughout the twentieth century (Liébault 2003).

Channel degradation along the lower Drôme has also occurred in response to gravel mining. The early RTM interventions had ceased by the 1950s, when the onset of government authorised gravel extraction between 1950 and 1985 created a further bedload deficit. Channel incision and narrowing has been associated with substantial extractions along the lower Drôme and at certain tributary confluences (Landon 1999, Kondolf *et al.* 2002).

A third cause of degradation along the downstream reaches of the Drôme has been embankments, which have constrained the channel since the late eighteenth century (Gemaehling and Chabert 1962). In 1998, Landon *et al.* reported that 37 % of the lower Drôme was protected by dykes, which contributed to channel incision and narrowing by increasing unit stream power and limiting the supply of sediment by bank erosion.

2.2.2. The Upper Drôme, la-Batie-des-Fonds to le Claps

These studies of channel change have concentrated on the lower Drôme between river kilometres 36 and 106, between the Bez confluence and the Rhône confluence. The upper Drôme, from its source at La-Batie-des-Fonds to le Claps, approximately 2 km upstream of Luc-

en-Diois (figure 2.1), is characteristically different in terms of historical changes in channel morphology.

In 1442 a catastrophic landslide known as 'le Claps' occurred along the band of Tithonian limestone running north-east to south-east through the upper catchment, close to river kilometre 26 (Brocard and van der Beck 2006). By damming the river, the rockfall naturally separated the lower Drôme from the upper Drôme, and created two upstream lakes; one small (le petit lac, of approximately 60 km²), and one large (le grand lac, of approximately 3,000 km²) (Landon and Piégay 1999). There was substantial sedimentation in these lakes through time, both by natural accumulation, and by an unsuccessful attempt of Carthusian Monks to 'dry out' these upstream reservoirs (Froment 1988). Le Claps separated the upstream and downstream reaches of the Drôme until 1839, when a tunnel was constructed through the enormous rock barriers damming the flow. The lakes were naturally drained into the Drôme and gradually reconnected the upstream and downstream reaches. The contemporary upper Drôme, above le Claps, is a narrow and single thread channel flowing through a wide, flat floodplain that was previously le grand lac. Despite the history of changes in the upstream part of the Drôme, contemporary sediment yields remain high (Landon and Piégay 1999). However, the upper Drôme continues to act as a natural sediment trap that requires periodic dredging, reducing downstream bedload supply (Piégay *et al.* 2004). This suggests that the Béoux catchment has been, and continues to be, the most important source of coarse sediment to the study reach. The overall channel degradation seen between Luc and Recoubeau may, of course, be influenced by interruption of bedload supply from the upper Drôme, but the study reach is likely more sensitive to changes in the immediate supply of bedload from the Béoux sub-catchment.

2.3. The Béoux Catchment

Approximately 200 m upstream of the study reach, the Béoux tributary is the principal supply of bedload to the study reach, joining the Drôme on the left bank (figure 2.1). Since the start of the twentieth century, the Béoux sub-catchment has undergone considerable land use changes, specifically afforestation and the implementation of check dams, which have substantially reduced sediment supply to the Drôme. These practises were not limited to the Béoux catchment, but formed part of the RTM schemes that were enforced throughout the Drôme basin (section 2.2).

Between 1886 and 1914, only 12 % of the Béoux sub-catchment was afforested (Liébault 2003). Forest cover increased to approximately 78 % by 2005 (Marcaggi 2005), following the natural reforestation of abandoned agricultural land. This substantial increase in vegetation cover has caused a significant reduction in sediment supply to the Drôme. A reduction in bedload supply to the channel was also augmented by the installation of small weirs and check dams prior to and during the same period as afforestation practises, to

reduce erosion from hillsides and torrents. Sediment supply was further restricted in 1965 by the construction of a 10 m high dam across le Torrent de Trescherènes, a main tributary to le Béoux. In 1982 the dam was heightened to 15 m, and has had a substantial impact on the reduction in channel bedload, accounting for approximately 57 % of all sediment retained by flood defence structures in the sub-catchment (95,000 m³, Liébault and Beullens 1997).

Gravel mining was not authorised along the Béoux, but between 1971 and 1996 potential sites of extraction can be interpreted on aerial photography just downstream of the Béoux–Drôme confluence. It is possible that a bedload deficit created by extraction has further reduced supply to the study reach. Upstream of the Béoux confluence, there is possible evidence of gravel mining in substantial channel incision of up to 3 m that can be seen between long profiles taken in 1928 and 2003.

2.4. Anthropogenic Disturbance between Luc and Recoubeau

Between Luc-en-Diois and Recoubeau gravel mining was also unauthorised and undocumented, and cannot be verified. However, the possibility of gravel extraction cannot be discounted, and has likely further contributed to a bedload deficit along the study reach. The reach is easily accessible from the main D93 road between Luc and Recoubeau, and tracks can be seen on aerial photography that lead through the riparian canopy to farmland at close proximity. It is possible that unauthorised gravel extraction by riparian landowners was carried out to provide aggregate for the construction or maintenance of farm tracks, and to prevent inundation of farm land. Potential sites of extraction have been identified by careful observation of aerial photography (figure 2.2). Between 1971 and 1991 upstream sites can be seen in zone 2 and in 1980, downstream in zone 4. Between 1996 and 2001, gravel was potentially also extracted from the upstream part of the reach for the construction of a small water treatment reservoir that can be seen by 2001. While the volumes of gravel that may have been extracted from these sites is insufficient to account entirely for reach-scale incision, this mining activity may have contributed to bedload deficits along the reach.

In addition to the possibility of gravel extraction, change in sediment supply to the reach may have been further influenced by a change in land use along a small mid-reach section of the left bank. A small site of grazing has been interpreted on the photographs of 1956 and 1971 (B, figure 2.2). By 1980 this area appears to have been abandoned and is densely forested, although by 1991 and until 2006 it was clear of riparian cover.

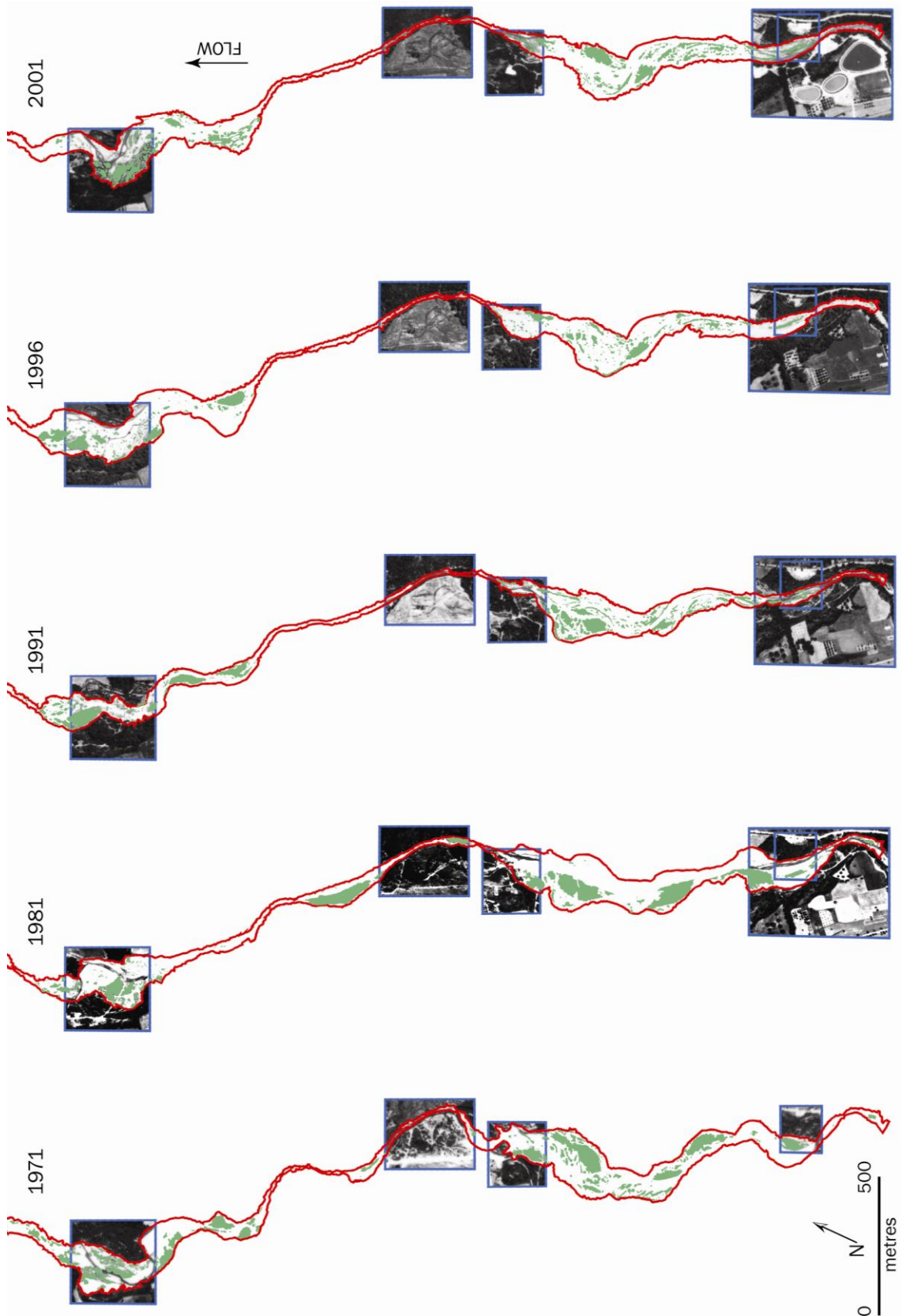


Figure 2.2 Possible historical sites of gravel mining and grazing between Luc and Recoubeau.

During the study period, the channel has been further affected by the construction of two small weirs that mark the upstream and downstream limits of the reach. The upstream weir was likely installed shortly prior to 1991, when it is first evident on photography, perhaps to prevent erosion propagating downstream from sites of unauthorised gravel extraction close to the Béoux confluence. The effectiveness of small management structures, in controlling the propagation of channel incision, is dependent on the relative timing of their installation (Simon and Darby 2002). It has also been observed that check dams can increase downstream erosion (Castillo *et al.* 2007, Boix-Fayos *et al.* 2008) and it may be possible that the relatively recent construction of the weir at the upstream end of the study reach may have served to increase downstream channel incision during the latter part of the study period.

The downstream weir crosses the channel underneath a road bridge in Recoubeau. It is not apparent on 1995 photography and there is no record of it until the early 2000s. It is unlikely therefore to have had a substantial impact on historical channel changes, but has possibly influenced more recent changes in morphology along downstream parts of the study reach. 3 km downstream of the bridge, gravel mining was authorised at the Bez confluence and it is likely that the weir was installed to stop the bridge from being undermined by regressive upstream erosion. The final 500 m of the reach has also been constrained through time by a left bank dike, and so this downstream part of the reach is most affected by anthropogenic intervention than any other. It is also easily accessible from the road and further affected during the summer months by people that come and bathe in the channel and build structures using the channel gravel.

In addition to the upstream reduction in sediment supply from the Béoux catchment, these anthropogenic interventions have modified the availability of sediment along the reach. Channel adjustments during the study period will be influenced by the redistribution of these modified bedload yields. The reworking of channel sediment is influenced by the history of flood events affecting the reach, and any changes in flood regime.

2.5. Changes in Flood Regime

Since 1907, discharge has been recorded at the Luc-en-Diois gauging station approximately 800 m upstream of the study reach. By combining these daily records with additional archived information, previous work has shown an overall decrease in the magnitude and frequency of maximum annual discharge since 1850 (Landon *et al.* 1998). Between 1907 and 2002 annual peak flows stabilised, but flood frequency (defined as days when daily average discharge exceeded $Q_{1.5}$) declined by almost 50 %, with a rapid reduction in the number of flood days per decade from approximately 1950 (Liébault 2003). These long term trends established in the historical record may be important for predictions of future changes in channel morphology and macroinvertebrate community organisation (chapter 5). The changes in flood frequency identified during the latter half of the century suggest that this

period is the most appropriate for evaluating flood events as possible explanations for the morphological changes observed in chapter 3.

The annual series of daily average discharge was therefore analysed for the study period (1948-2006). During this period, average daily discharge was $2.5 \text{ m}^3\text{s}^{-1}$, the mean annual flood (MAF) was $30.6 \text{ m}^3\text{s}^{-1}$ and the maximum flood was $108.0 \text{ m}^3\text{s}^{-1}$ in 1994 (figure 2.3). Flood return intervals were estimated from the annual maximum series using a log-Pearson type III distribution (figure 2.4, table 2.1).

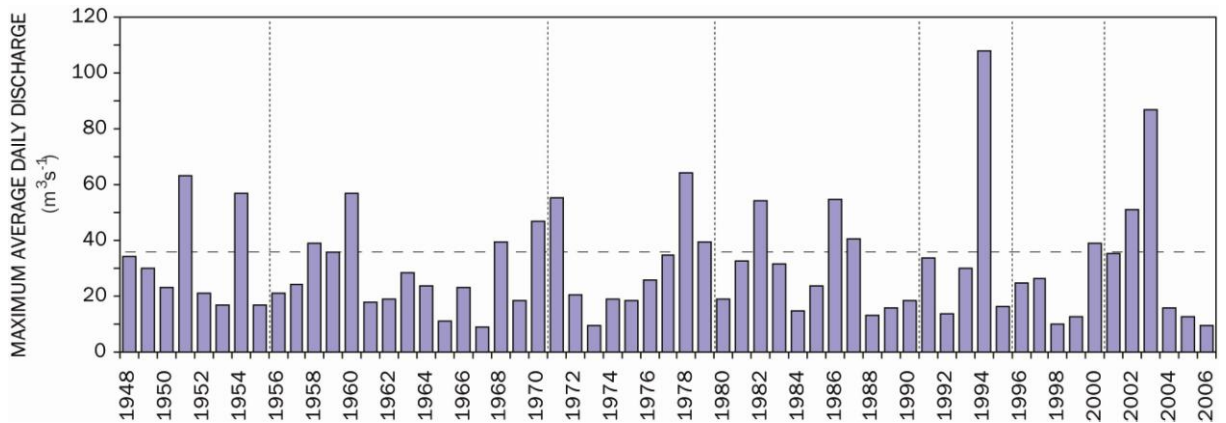


Figure 2.3. Maximum average daily discharge, 1948-2006. Dashed horizontal line indicates MAF, dashed vertical lines indicate epochs examined in chapter 3.

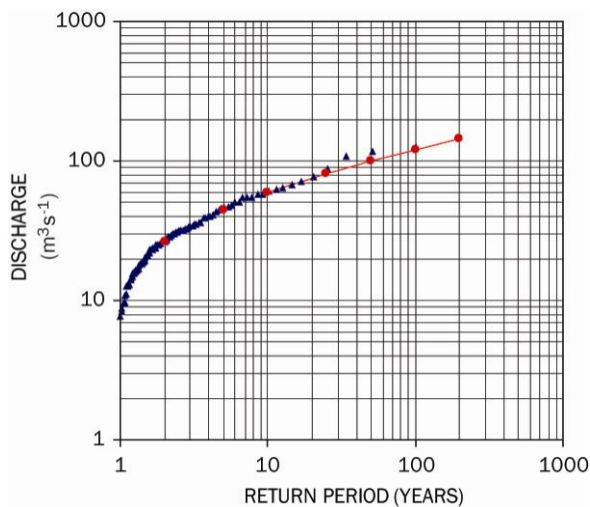


Figure 2.4. Recurrence intervals (red circles) estimated from the record of maximum average annual discharge at Luc-en-Diois between 1948 and 2006 (blue triangles), using a Pearson log III adjustment.

RECURRENCE INTERVAL (YEARS)	ESTIMATED Q (m^3s^{-1})	EXCEEDENCE PROBABILITY (%)
1.5	19.9	0.7
2	25.4	50
5	41.8	20
10	54.9	10
25	74.0	4
50	90.2	2
100	108.1	1
200	127.9	0.5

Table 2.1 Recurrence intervals and flood magnitudes estimated from the record of maximum average annual discharge at Luc-en-Diois between 1948 and 2006, using a Pearson log III adjustment.

These statistics provide the general context of flood activity during the study period, but it is also useful to derive some additional indices that provide a measure of relative changes in flood activity between the seven epochs in which morphological changes are assessed in chapter 3. Maximum daily average discharge, and the number of days on which various flood thresholds were exceeded, were determined for each epoch from the average daily discharge record (table 2.2). The number of days on which bankfull discharge (Q_b) was exceeded during each epoch was also estimated. Without direct observations of bankfull discharge at the gauging station or within the study reach, Q_b was estimated as the discharge corresponding to a return interval of $Q_{1.5} = 19.9 \text{ m}^3\text{s}^{-1}$. Previous studies have shown broad variation in the return interval of bankfull discharge (Williams 1978, Petit and Pauquet 1997), however an average return period of 1.5 to 1.6 years is widely reported (Leopold *et al.* 1964, Emmett and Wolman 2001, Lenzi *et al.* 2006) and has previously been used as a reasonable approximation of bankfull at Luc-en-Diois (Liébault 2003). In the absence of more detailed hydraulic observations or direct bedload transport measurements, the six indices presented in table 2.2 provide the best means of assessing flood activity as a possible explanation for morphological changes observed during the study period. Consistent with previous observations of long-term flood frequency (Landon *et al.* 1998, Liébault 2003), there has been a clear reduction in the number of days when different flood thresholds were exceeded, with higher frequencies in the early part of the study period, and lower frequencies toward the end of the study period.

	1948-56	1956-71	1971-80	1980-91	1991-96	1996-01	2001-06
MAXIMUM AVERAGE DAILY Q (m^3s^{-1})	63	57	64.3	54.9	108	39.2	86.8
RECURRENCE INTERVAL (YEARS)	16.4	11.7	17.4	10.0	99.8	4.5	44.8
No DAYS > MEAN ANNUAL FLOOD	10	13	6	7	4	2	6
No DAYS > Q_5	7	4	1	2	3	0	3
No DAYS > Q_{10}	5	2	1	0	1	0	2
No DAYS > $Q_{1.5}$ (Q_b)	25	37	18	18	9	9	11

Table 2.2 Indices of flood frequency for each epoch of morphological change examined in chapter 3.

2.6. Initial Field Assessments of Geomorphology and Macroinvertebrate Community Structure between Luc and Recoubeau

Preliminary reconnaissance fieldwork was conducted in 2005 to examine the geomorphology of the study reach and collect preliminary data to assess the composition of the reach-scale macroinvertebrate community. This section presents the findings of this initial work which provided important reference information for the development and future testing of the main thesis aims and objectives.

2.6.1. Zonational Channel Geomorphology between Luc and Recoubeau

Between Luc and Recoubeau the most striking geomorphological feature of the channel is its great diversity and, in particular, the presence of six distinctive geomorphological zones over its relatively short length of five kilometres. The six zones were identified in the field by contrasting channel styles and substrates separated by abrupt transitions. The six zones that are clear in the field are also evident on aerial photography in downstream changes of channel width between wider and narrower sub-reaches (figure 2.5). Former channel boundaries and floodplain terraces observed on aerial photography were validated during the initial field visit and detailed geomorphological mapping of in-stream channel features was also carried out.

Zone 1 (figure 2.6) is a relatively narrow (average total width 25 m, maximum 36 m) bedrock channel with a patchy alluvial cover (photos A and B). The maximum depth of alluvium is approximately 30 cm. The smooth, undulating bedrock is hummocky with both rounded and sharp crests. Large boulders create areas of flow separation and accumulations of relatively fine sediment (sand and gravels < 16mm) (photos C and E), and in places bedrock depressions are lined with loose, unconsolidated gravels. Flow diverges through the zone and is channelled in places by bedrock runnels (photo D). Flow is deep and slower flowing in parts where bedrock has created pool-like environments. Shallower alluvial patches of coarse gravels create riffle-like environments, but on the basis of Froude number alone. Zone 1 is the shortest sub-reach in terms of downstream distance, extending 500 m from the upstream weir. Large steps in bed elevation mark the end of this section and the transition from a confined to a wide gravel bed channel.

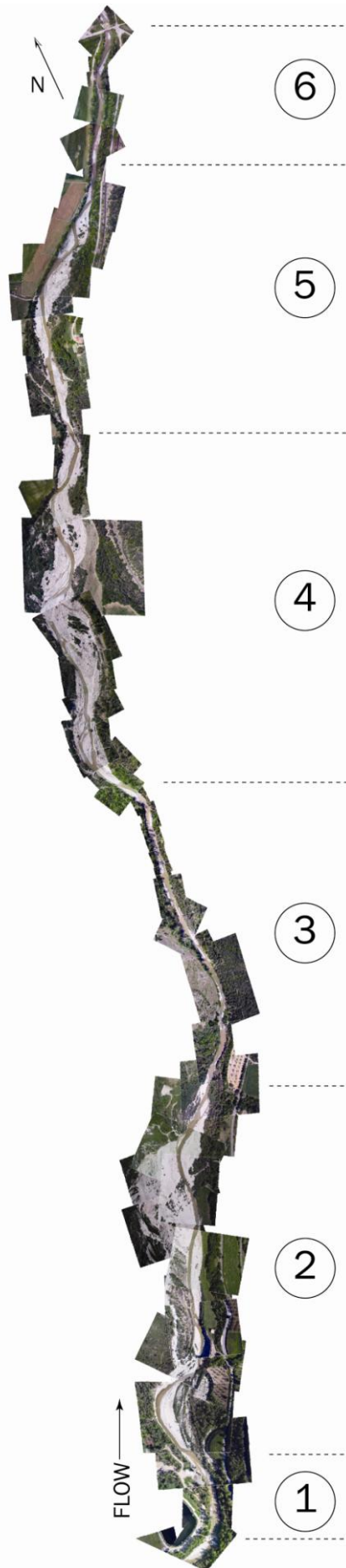


Figure 2.5. Low-altitude aerial photo stitch of the reach between Luc-en-Diois and Recoubeau-Jansac. Dashed lines indicate zone boundaries delineated in the field; numbers in circles refer to zones.

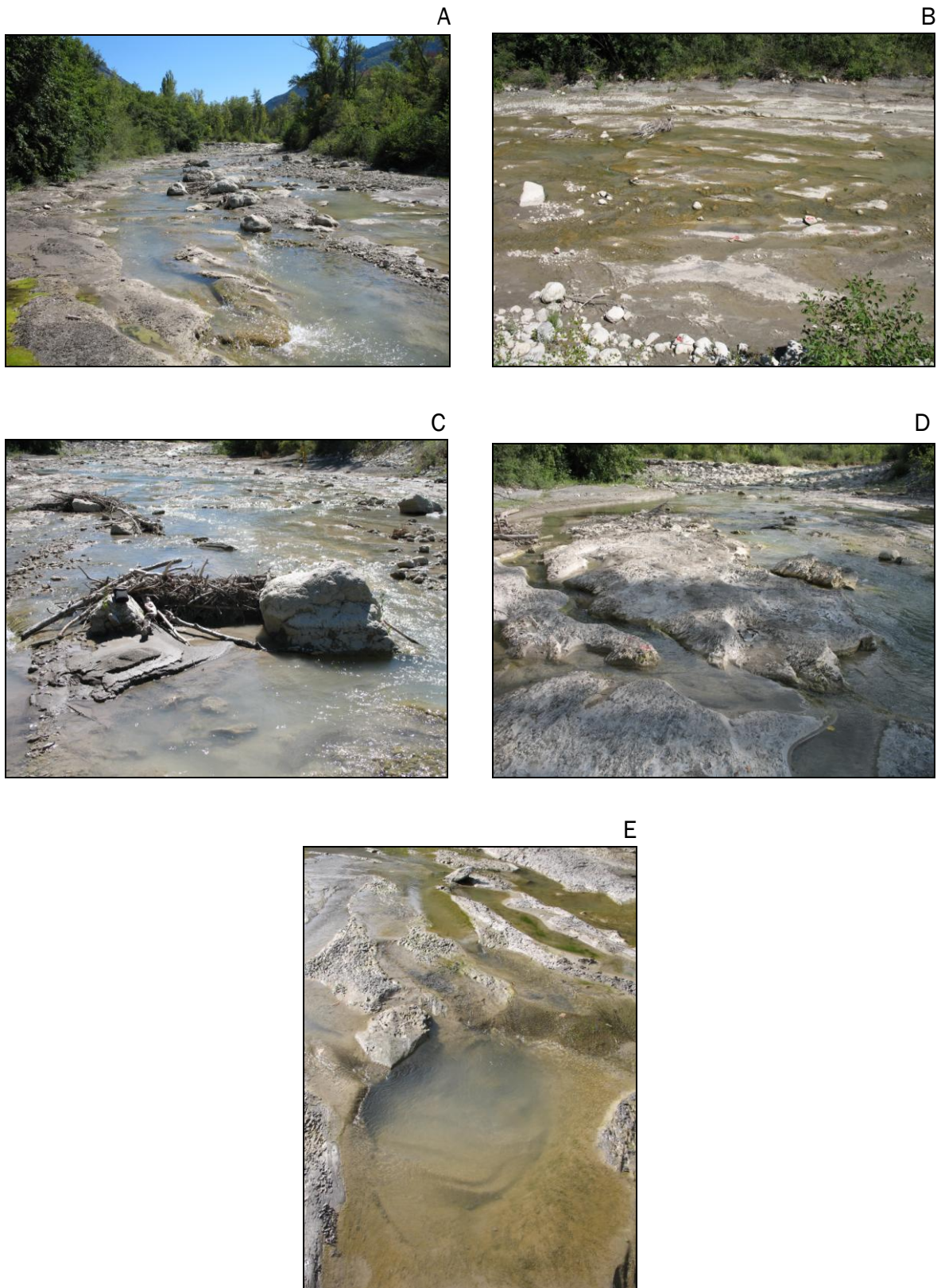


Figure 2.6. Channel features in zone 1. (A, upstream view and B, lateral view; flow from right to left) the channel is bedrock, with gravel patches and boulders; (C, upstream view) boulders and woody deposits create areas of flow separation and the accumulation of fine sediments; (D, upstream view) a runnel cuts through the bedrock on the left side of the image, channelling the flow; (E, upstream view) a bedrock pothole lined with deposits of fines.

Zone 2 (figure 2.7) is a wide alluvial zone (average total width 92 m, maximum 198 m) extending approximately 1250 m downstream. The main low-flow channel meanders away from zone 1 before it meets high, vertical channel banks on the right (photo A). Flow is funnelled downstream through an incised, straight channel along the right side of the active floodplain boundary (photo B). The channel bed is predominantly unconsolidated sands, gravels and cobbles. Bedrock is not an important element in this zone, but small amounts of bedrock are exposed at a few very deeply incised locations. The wide gravel bar on the left side of the channel is unconstrained and channel constriction is indicated by vegetation encroachment (photo C). The channel narrows from the apex of the wide left bar to a bottleneck at the transition to zone 3.

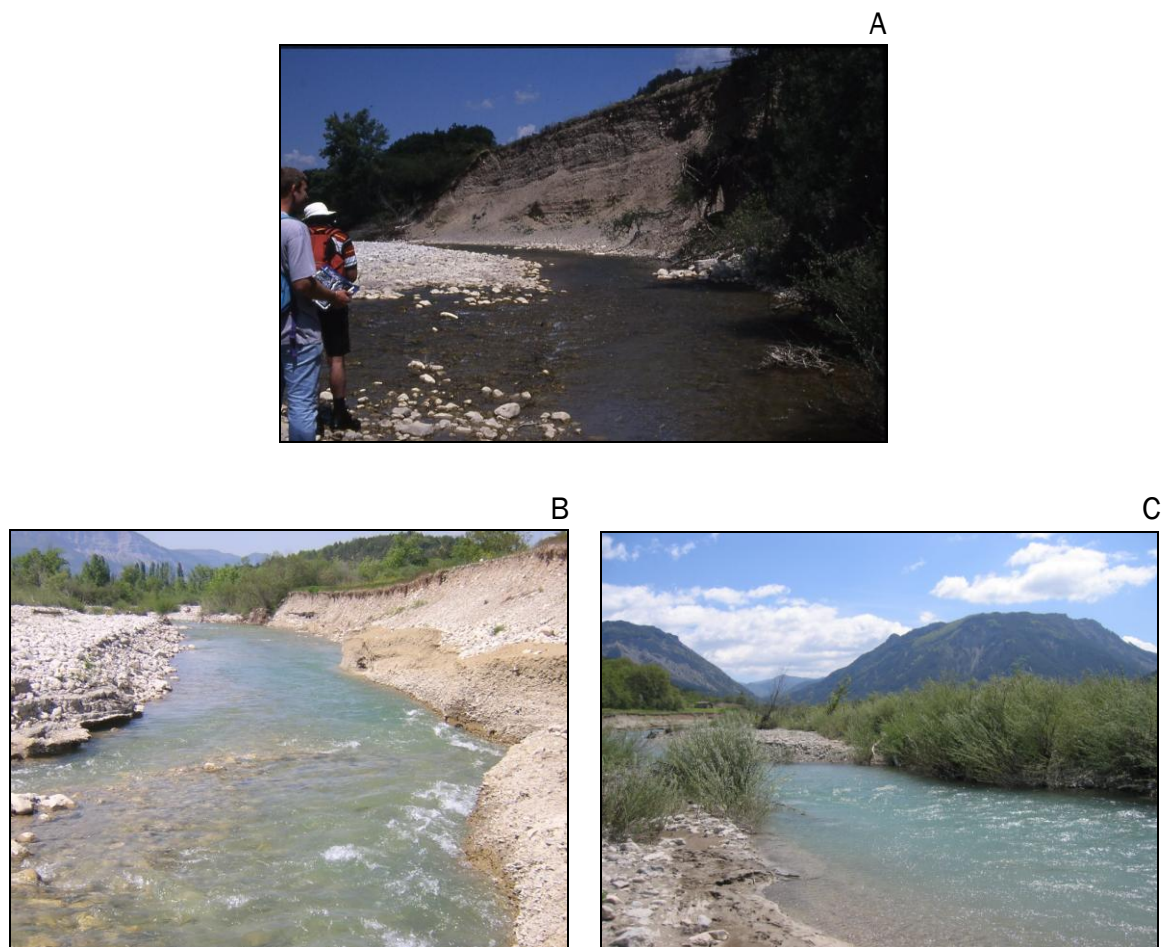


Figure 2.7. Channel features in zone 2. (A, downstream view) high and undercut right bank; (B, downstream view) flow is channelled by a straight, incising 'chute' along the right side of the floodplain; (C, upstream view) substantial vegetation encroachment of the right bank.

Zone 3 (figure 2.8) is a characteristically narrow and straight, mixed bedrock-alluvial channel (average total width 18 m), approximately 1000 m long. The channel is constrained by bedrock along the right bank and for the upper part along the left bank (photo A), entrenched into a deep, rectangular slot between upper and lower zones that are wider and unconstrained. Within this narrow 'corridor' the channel separates around gravel bars in places (photo B), but these short alluvial sections are interspersed with bedrock that forms approximately 50% of the channel substrate. There is substantial irregularity in the topography of the channel bed through this zone. At the upstream boundary there are steps in the channel bed (photo C), and chutes and runs (photo F) contrast with shallower gradients of pools and riffles that characterise alluvial zones. Outcropping bedrock structures appear to be important controls on downstream fluxes of flow and sediment as they create a complex environment of highly variable resistance, which is reduced in sections where bedrock is flat and bare (photo D). Larger bedding planes generate patches of flow separation and turbulence (photo E). The channel is constrained along the right bank until the downstream transition to zone 4, where the active floodplain expands and the channel enters a wide, alluvial zone (figure 2.9A).

Zone 4 (figure 2.9) is wide (average total width 80 m, maximum 124 m), approximately 1250 m long and the most sinuous reach. At the transition from zone 3 (photo A) the main low-flow channel bifurcates through wide gravel bars before rejoining into a single thread meandering channel. The active channel area is a complex of multiple bar surfaces at different elevations, inactive high-flow channels and unit bars that suggest that zone 4 has been formerly braided and formerly undergone aggradation (photo B). Under low-flow conditions there are shallow lentic waters in some of these disconnected channels, suggesting that they are reactivated under flood conditions. Other inactive channels are well-consolidated with sand and silt. There are dense clusters of vegetation on bar surfaces and along bar crests (photo C). In 2006 the channel appeared to be disconnected from the right bank through most of the zone (photo D) but well connected to the left bank riparian forest.



Figure 2.8. Channel features in zone 3. (A, lateral view) bedrock constraint in the left bank upstream in the zone, and a deep pool in the channel bed; (B, downstream view) the channel anabranches around gravel bars and cuts deep runs, particularly along the right side of the active channel; (C, downstream view) large steps in the channel bed and outcropping bedding planes on the right side of the image; (D, upstream view) juxtaposition of bedrock and alluvium, that is in places a shallow cover over the bedrock; (E, upstream view) outcropping bedrock creates a diverse hydraulic environment; (F, upstream view) a rapidly incising alluvial run, and bedrock constraint in the right bank.

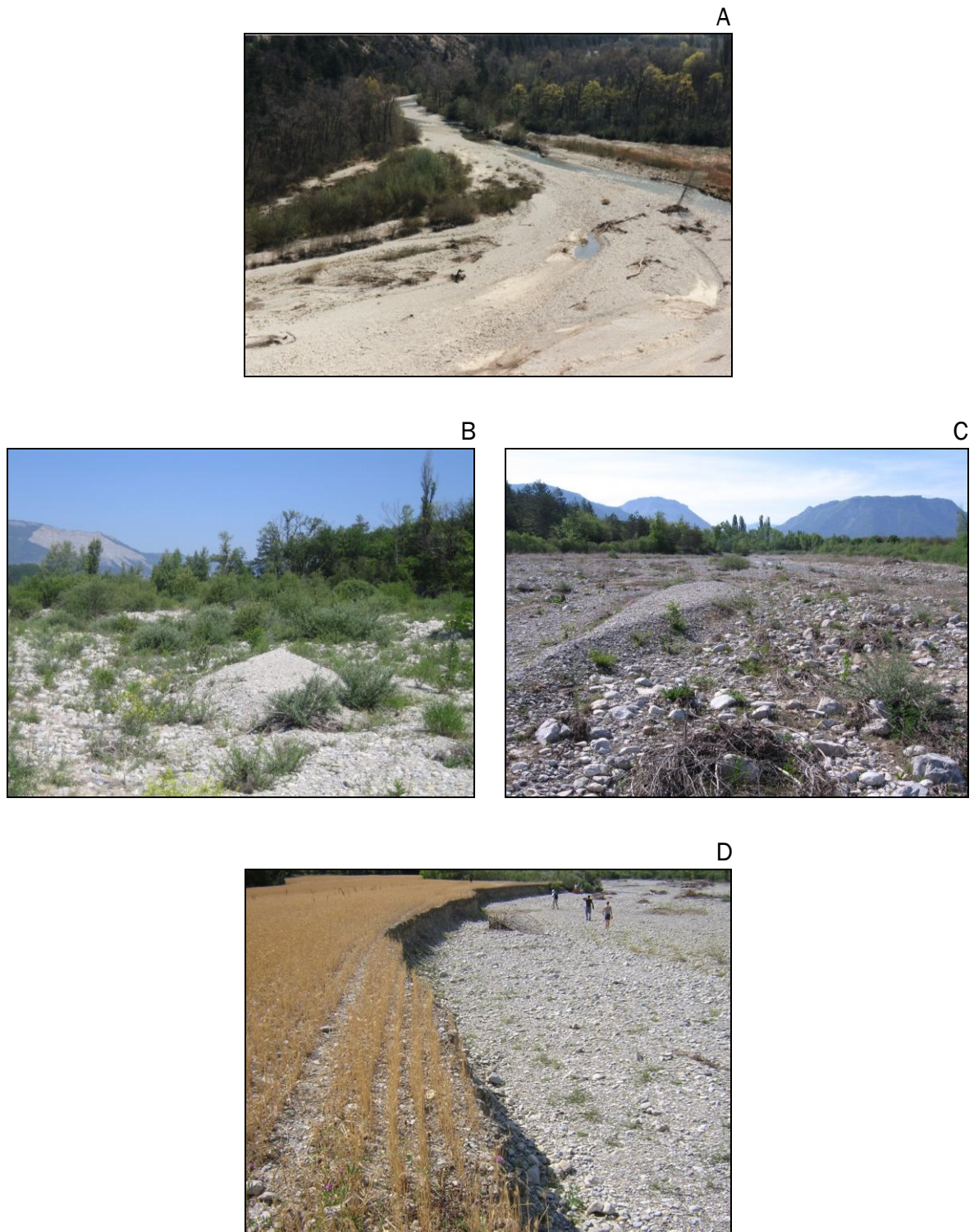


Figure 2.9. Illustrations of zone 4. (A, upstream view) the transition from zone 3 to zone 4; (B, downstream view) unit bar and dense vegetation establishments, (C, upstream view) unit bar, woody deposits and a wide range of grain sizes; (D, upstream view) the right bank terrace.

Zone 5 (figure 2.10) is alluvial, but narrower than zone 4 (average total width 46 m, maximum 68 m). The channel is single thread and meanders between gravel bars over approximately 800 m (photo A). There is one prominent site of bedrock outcropping in this zone that is coupled with a deep pool immediately downstream (photo B). These features also mark the end of zone 5 and the transition into zone 6.

Zone 6 (figure 2.11) is a narrow channel (average total width 19 m) confined by a left bank dike, and right bank bedrock. It is the final 500 m of the study reach, and meanders between small and almost overlapping lateral bars. Frequent changes in bar form on all past and present aerial photography indicate that under high flow these bars are submerged and reworked. The downstream limit of both zone 6 and the study reach is marked by a small weir underneath the road bridge at Recoubeau. The channel is accessible from the road and during summer months is often disturbed by people that bathe in it and build small dams across the channel.

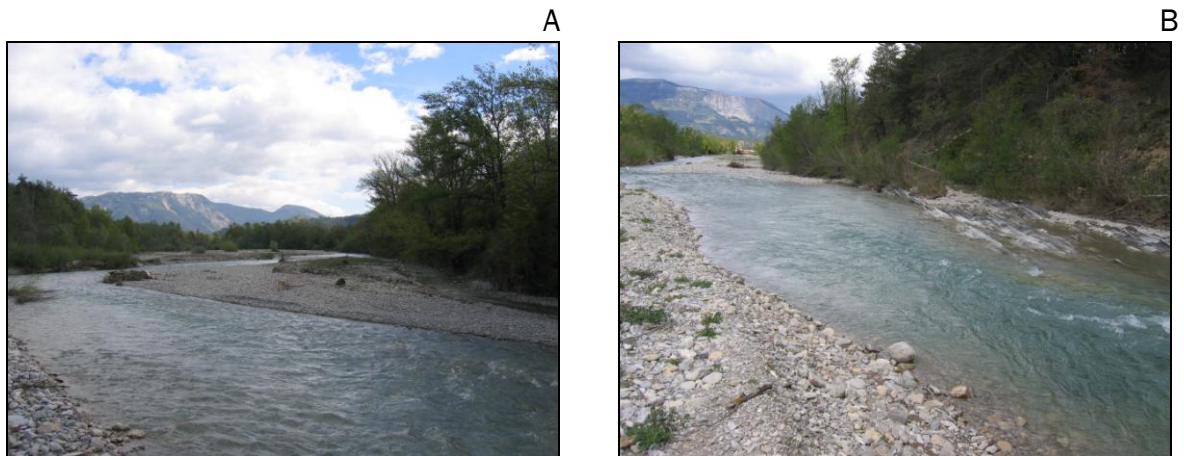


Figure 2.10. Illustrations of zone 5. (A, downstream view) The channel is single thread, meandering between shallower bars with (B, downstream view) a single site of exposed bedrock near the transition to zone 6.



Figure 2.11. Lateral overlapping bars and bedrock exposure on the right bank in zone 6 (downstream view).

2.6.2. Preliminary Survey of Macroinvertebrate Organisation

During the initial reconnaissance fieldwork of May 2005, a preliminary survey of the reach-scale macroinvertebrate community was carried out. A total of 44 quantitative Surber samples were collected in riffle or riffle-like habitats at 20 sites along the reach (figure 2.12A), to gain an initial understanding of in-stream macroinvertebrate community organisation. Samples were preserved in the field, and on return to the laboratory, macroinvertebrates were sorted and counted at family level. Distinct spatial variation was evident in longitudinal patterns of community structure (figures 2.12B–D), suggesting that the distribution of macroinvertebrate taxa may be related to differences in channel morphology between the zones. This cursory observation provided enough insight to establish this hypothesis, but the data was not adequate to further test it. The downstream organisation of the macroinvertebrate community was further examined by a second, detailed sampling program carried out during August and September 2006 (chapter 4).

2.7. Summary

Between Luc-en-Diois and Recoubeau-Jansac, the Drôme River has undergone a significant reduction in coarse sediment supply. This has been influenced by historical changes along the Upper Drôme, but is more directly caused by land use changes and dam installation in the upstream Béoux catchment since 1887. A number of anthropogenic interventions along the reach, notably the installation of a small weir at the start of the reach shortly prior to 1991, may have more recently caused a further reduction in bedload. Alongside changes in flood regime documented for the historical record since 1907, and within the context of the study period (1948–2006), these changes establish a context for the channel incision apparent along the channel at the present day. Overall changes in channel morphology and the development of the morphological zonation that characterises the present-day channel will now be examined in detail in the following chapter.

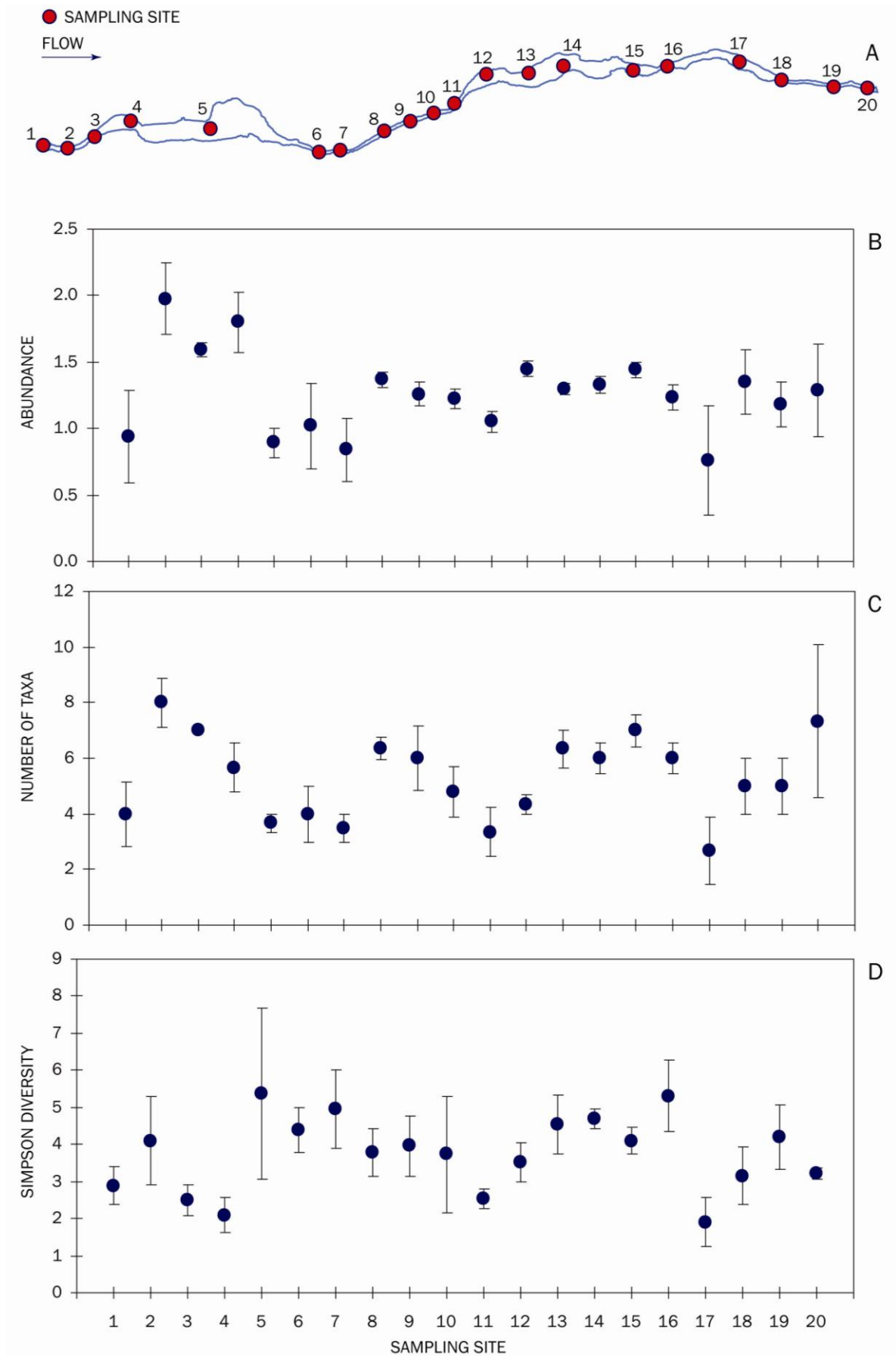


Figure 2.12 The twenty sites initially examined by reconnaissance fieldwork in May 2005 (A). Downstream changes in macroinvertebrate abundance (B), the number of macroinvertebrate taxa (C) and macroinvertebrate diversity (Simpson's index) (D).

3. Historical Changes in Channel Morphology between Luc-en-Diois and Recoubeau-Jansac, 1948 – 2006

3.1. Introduction

The overall aims of this chapter are to investigate historical changes in channel morphology along the five kilometre unstudied reach of the Drôme, between Luc-en-Diois and Recoubeau-Jansac, during a 58 year period (1948–2006); to examine the evolution of the present-day mixed bedrock-alluvial channel morphology (chapter 2), by observing the development of the present-day pattern of zonation and sub-reach changes in channel morphology within and between eight epochs of this overall timeframe; and to evaluate current trajectories of morphological change, at the zone scale and at the reach scale. The possible causes of channel adjustments are discussed, including the importance of large floods and their timing relative to external changes in sediment supply and flood activity, sub-reach sensitivity to adjustment, and sub-reach dynamics of bedload redistribution. Given recent interest in rehabilitating channel degradation in this upstream part of the Drôme, it is particularly important to understand the spatio-temporal variability of channel behaviour. Any management intervention aiming to restore channel degradation may have limited success if the marked variability in channel form and behaviour are not better understood. A historical perspective of channel evolution between Luc and Recoubeau, and an understanding of present-day dynamics responsible for present-day morphological zonation will inform predictions of future trajectories of change in channel morphology (chapter 5) and, together with an understanding of in-stream macroinvertebrate community organisation (chapter 4), and the likely impact this will have on in-stream ecology.

3.2. Aims and Objectives

This chapter aims to establish:

- Overall, reach-scale changes in channel morphology between Luc and Recoubeau, between 1948 and 2006
- Spatial and temporal patterns of sub-reach changes in channel morphology
- The evolution and likely causes of zonal channel geomorphology
- Stages and/or thresholds of change during the 58 year study period

3.3. Data Sources and Methodology

The evolution of channel planform was examined using eight sets of high-altitude aerial photography, captured over a period of 58 years (1948-2006) (table 3.1). Changes in channel elevation were examined using three longitudinal profiles surveyed in 1928, 2003 and 2005.

YEAR	SCALE	CONTRAST
1948	1:30,000	B+W
1956	1:25,000	B+W
1971	1:25,000	B+W
1980	1:25,000	B+W
1991	1:17,000	COLOUR
1996	1:25,000	B+W
2001	1:25,000	COLOUR
2006	DIGITAL	COLOUR

Table 3.1. Attributes of the eight sets of aerial photography used in this study.

3.3.1. Aerial Photography

River channel planform was mapped from aerial photography using ArcGIS software. Images were obtained georeferenced from the UMR 5600 unit in Lyon, France. Three definitions were used to consistently identify boundaries and digitise polygons of the channel and mid-channel vegetation on each of the eight sets of photography (figure 3.1).

Total Channel Area (A_T) and Width (W_T): The entire channel area and width between the maximum extent of the adjacent bank-side vegetation canopy, including any mid-channel islands or clusters of vegetation.

Active Channel Area (A_{GB}) and Width (W_{GB}): The total channel area and width excluding all mid-channel islands and clusters of vegetation (the subscript GB refers to gravel and bedrock).

Area of Vegetation (A_V): The surface area of vegetation within the total area ($A_T - A_{GB} = A_V$).

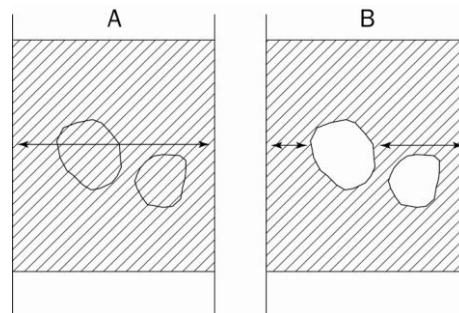


Figure 3.1 Definitions of (A) total and (B) active channel areas (diagonal lines) and widths (arrows).

The channel boundary was identified using the maximum extent of the adjacent bank-side vegetation canopy. Where the canopy extended over the channel, the boundary was extrapolated between obvious adjacent bank-side points. These criteria have been used in previous studies that have identified channel boundaries from aerial photography, and encountered the effect of canopy shadowing (e.g. Gurnell 1997, Winterbottom 2000, Tieggs and Pohl 2005). Alternative use of the bankfull channel has been shown to overestimate channel width (Gurnell 1997) and introduces error from differences in stage height between dates.

Georeferencing error cannot be reported for the images used, because they were received without their georeferencing files. Small displacement in the channel boundary between sets of images was not considered to affect the comparison of areal measurements. The main source of error introduced between the sets of images is likely to be inconsistent identification of the channel boundary, as a function of variation in image contrast and scale (table 3.1, section 3.3.3). Measurements of area and width were calculated automatically using expressions in ArcGIS before the data was exported for analysis. Two templates were created to extract consistently located measurements of area and width from each photograph, and enable measurements to be directly compared between years.

To calculate areas, each total channel boundary was intersected using a template of 100 polygon segments (appendices I and II). The template was created by digitising transects every fifty metres along and perpendicular to the channel centreline. These transects delineated the top and bottom boundary of each segment, and the total channel boundary delineated both sides of each segment for each year (figure 3.2A). Within each of the 100 polygon segments, benchmark transects were digitised every ten metres along, and perpendicular to the channel centreline. This created a template of 500 channel widths that was intersected using the total channel boundary to generate five width measurements per segment (figure 3.2B). At the reach scale, all five hundred measurements of width were averaged to generate a single value for each year. At the segment scale, the five measurements within each segment were averaged to generate a single width value per 50 m segment (appendices III and IV). Channel sinuosity was calculated as the ratio between the total channel centreline, and the straight-line distance of the reach.

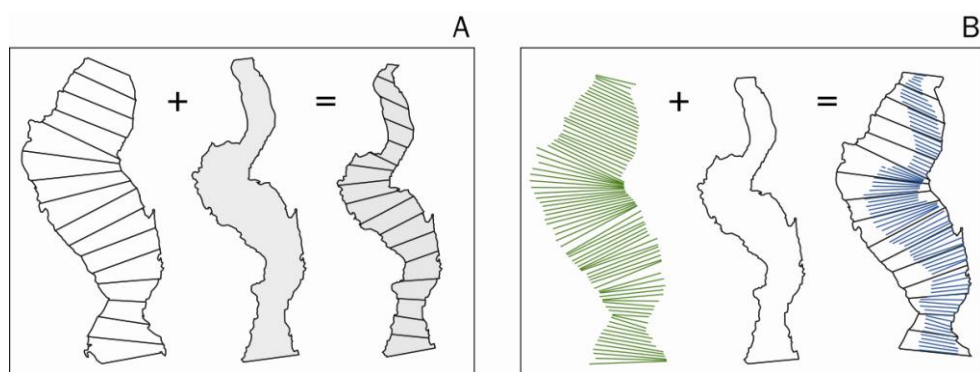


Figure 3.2. Examples of segment and width templates used to extract channel areas (A) and widths (B).

Unexpected construction of an embanked trench through zone 2 was completed in September 2005 by local river managers, under local planning guidelines to facilitate the remobilisation of sediment through the reach. The trench cuts through two meander bends, and diverts the main flow away from a very high right-bank terrace (figure 2.7A), where channel incision and bank erosion were extensive, and flow had previously been funnelled downstream along a 'chute' to zone 3 (figure 2.7B). The embankments extend downstream for approximately 400 m and have shortened the present-day wetted channel centreline through zone 2 by approximately 210 m. Despite this intervention, it is valuable to include the 2006 photography. The previous set of aerial photographs was captured in 2001 and so the inclusion of the 2006 photographs extends the time series for analysis by five years. This widens the perspective of long-term morphological adjustment, and enables the integration of concurrent research on in-stream macroinvertebrate community organisation. In order to avoid confounding the account of natural channel adjustment in zone 2, by changes effected as part of this management intervention, the channel boundary of the small entrenched section was replaced by that identified on high-resolution aerial images captured in 2005, just prior to the construction of the trench. On account of differences in image resolution, the 2005 imagery was not incorporated as a separate photo series in the analysis.

3.3.2. Longitudinal Profiles

Three longitudinal profiles were used to examine change in channel elevation. The 1928 and 2003 survey data were received from the UMR 5600 unit in Lyon, France, and the 2005 profile was surveyed in May 2005 as part of the fieldwork for this thesis. Each profile was surveyed as water surface elevation under low-flow conditions. To calculate elevation at the mid-point of each channel segment, slope was extrapolated between the segment boundaries from known surveyed points (appendix V).

3.3.3. Evaluating Methodological Accuracy

In order for estimates of channel change to be significant, they must exceed the error incorporated in extracting measurements from and between the data sources. Combining maps and aerial photography can result in the measurement of insignificant changes (Hopley *et al.* 2007) and limit confidence in final estimates of change (Zanoni *et al.* 2008). In this study, maps were not combined with aerial photography to avoid introducing additional error. The aerial photography used in this study was captured at variable scales, with differences in contrast and scale between the seven sets (table 3.1). The most direct source of error in this study is therefore the consistent identification of the channel boundary between images of variable scale and contrast. Channel and vegetation boundaries can be clearly distinguished on black and white images, but are less easily identified on the three sets of colour photos due to the relatively reduced contrast.

3.3.3.1. Mapping errors

To test the consistency of channel boundary identification between images of variable scale and contrast, and thereby quantify a threshold 'digitising error' above which changes in the channel boundary are significant, repeat digitisation of channel boundaries was carried out. This method has been used in previous studies that have mapped channel boundaries from aerial photographs, to evaluate consistency in channel boundary identification (Gurnell *et al.* 1994, Brewer and Lewin 1998, Van Steeter and Pitlick 1998). The channel boundary was digitised four times in each of five different channel sectors. Together the five sectors comprised between 21 and 30 % of the total channel area and included the range of different planforms (narrow and wide) and variable extents of overhanging vegetation. It is considered to be a reasonable assumption that, although only part of the total channel area was tested, operator error would remain consistent over the remaining channel area. Sectors were consistently located between the photo sets by digitising the same template segments (a total of 25 out of 100 segments). Five photo sets (1948, 1956, 1991, 2001, 2006) represent the combinations of scales and contrasts of all eight sets of aerial photographs and so these were used for the repeat digitisation of channel boundaries (note that the photographs of 1971, 1980 and 1996 are of the same scale and contrast to the photographs of 1956, table 3.1).

3.3.3.2. Error in channel area

Error in the measurement of channel area (SE_{total}) for each different combination of photograph scale and resolution was quantified by first calculating the standard error of the four measured areas, SE_{meas} . It was assumed that this value was representative of the entire reach, but to obtain an absolute error for the total area it was necessary to scale up this error by the ratio of the total channel area (A_{total}) to the area measured during repeat digitisation (A_{meas}), as follows:

$$SE_{total} = \sqrt{[(A_{total} / A_{meas}) \cdot SE_{meas}^2]}$$

The error term for overall change in channel area during the study period, between 1948 and 2006, was calculated as follows

$$\sqrt{[SE_{total\ 1948}^2 + SE_{total\ 2006}^2]}$$

giving a value of 894 m².

3.3.3.3. Error in channel width

To assess error in channel width, the template of width transects ($n = 500$) was intersected with each of the four total channel boundaries digitised to assess error in area. This provides repeat measurements (x 4) of 90 channel widths along the reach, each of which

yields a standard error. Error in channel width (SE_{width}) for each combination of photograph scale and resolution was then quantified by averaging the 90 standard errors. The error term for overall change in channel area during the study period, between 1948 and 2006, was calculated as follows

$$\sqrt{[SE_{width\ 1948}^2 + SE_{width\ 2006}^2]}$$

giving a value of 1.0 m².

PHOTO TESTED	1948	1956	1991	2001	2006
SCALE	1:30,000	1:25,000	1:17,000	1:25,000	DIGITAL (63 cm)
RESOLUTION	BLACK + WHITE	BLACK + WHITE	COLOUR	COLOUR	COLOUR
REPEAT DIGITISATIONS (m ²)	61474	74636	63867	70648	75720
	61086	74807	64275	71669	75503
	61035	74664	63650	71119	75516
	61579	74922	63892	70799	73710
SE_{meas}	137	66	130	226	470
A_{total}/A_{meas}	4.60	4.71	3.45	3.56	3.23
STANDARD ERROR IN AREA (m ²)	293	144	241	426	845
STANDARD ERROR IN WIDTH (m)	0.5	0.5	0.5	0.8	0.8

Table 3.2. Estimates of variation in channel area and width digitised on each different combination of photograph scale and resolution.

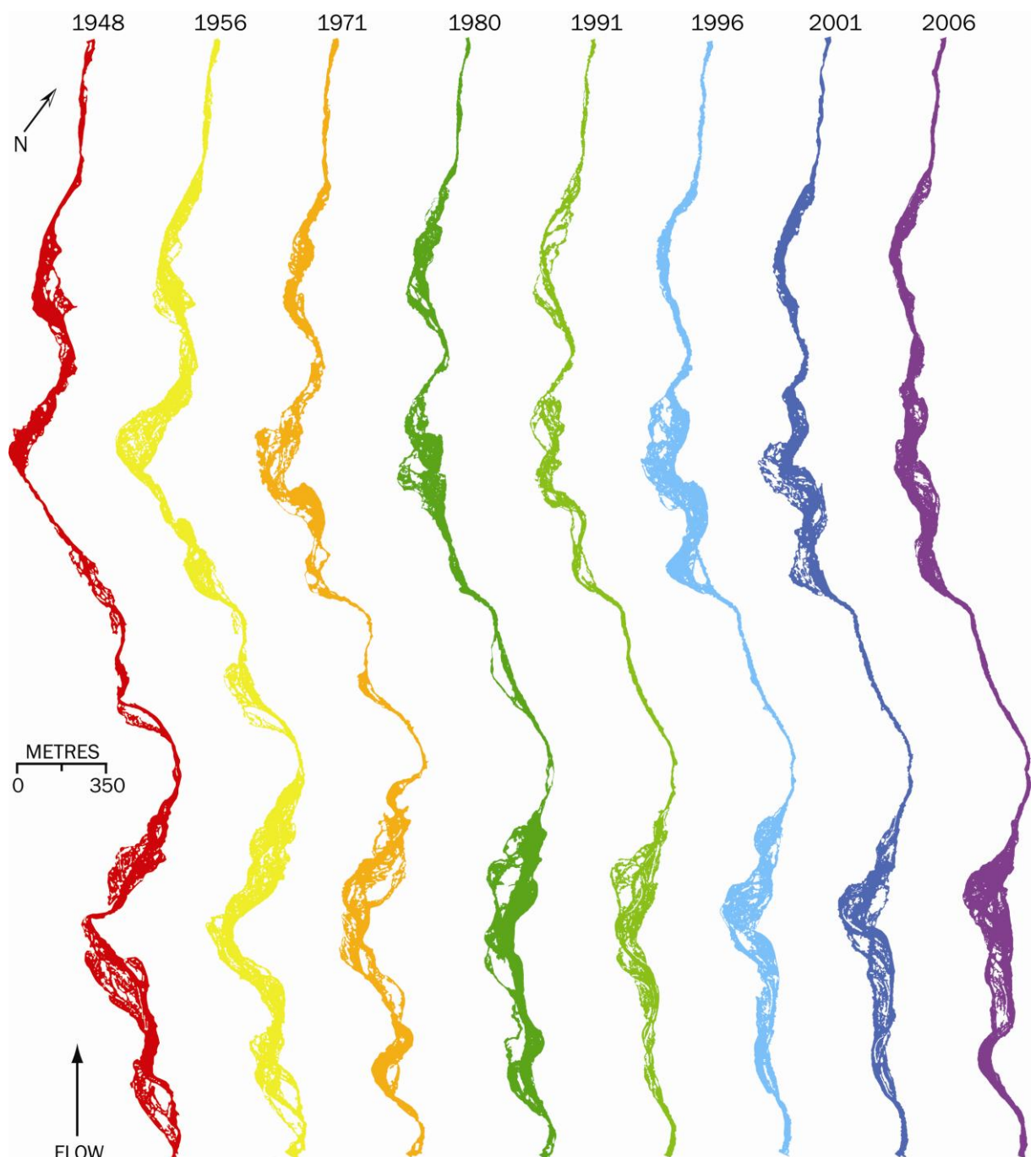
Figure 3.3 (following page) Channel planform, 1948-2006.

3.4. Results

3.4.1. Reach-Scale Changes in Channel Morphology

3.4.1.1. Channel constriction and narrowing

Between 1948 and 2006 the reach underwent overall channel constriction and the development of distinctive sub-reaches characterised by differences in width (figure 3.3). Following initial channel expansion between 1948 and 1956, the overall trajectory of channel constriction is interrupted only by a short-term increase in channel area in 1996. Total channel area (A_T) decreased overall by approximately 14 %, an absolute loss of approximately 39,173 m² \pm 894 m² (figure 3.4 and table 3.3A).



A

	CHANNEL AREAS (m ²)			PERCENTAGE OF TOTAL CHANNEL AREA (%)		ABSOLUTE AND (%) CHANGE DURING EPOCH (m ²)			RATE OF CHANGE (m ² yr ⁻¹)				
	A _T	(ERROR)	A _{GB}	A _V	A _{GB}	A _V	A _T	A _{GB}	A _V	n YRS	A _T	A _{GB}	A _V
1948	281954	(± 293)	233401	48548	83	17	69802 (+25)	67421 (+29)	2452 (+5)	8	8725	8428	306
1956	351756	(± 144)	300822	51000	86	14	-65809 (-19)	-74084 (-25)	8257 (+16)	15	-4387	-4939	550
1971	285947	(± 144)	226739	59257	79	21	-1971 (-1)	2257 (+1)	-4274 (-7)	9	-219	251	-475
1980	283977	(± 144)	228995	54983	81	19	-63760 (-22)	-64868 (-28)	1463 (+3)	11	-5796	-5897	133
1991	220217	(± 241)	164128	56446	75	26	39596 (+18)	63064 (+38)	-23818 (-42)	5	7919	12613	-4764
1996	259813	(± 144)	227191	32628	87	13	-7139 (-3)	-16332 (-7)	9218 (+28)	5	-1428	-3266	1844
2001	252674	(± 426)	210859	41846	83	17	-9893 (-4)	14517 (+7)	-24439 (-58)	5	-1979	2903	-4888
2006	242781	(± 845)	225376	17407	93	7							
OVERALL 1948-2006	-39173	(± 894)	-8025	-31141									

B

	AVERAGE CHANNEL WIDTH (m)		ABSOLUTE AND (%) CHANGE DURING EPOCH (m)	
	W _T	(ERROR)	W _T	W _{GB}
1948	59	(± 0.48)	15 (+25)	14 (+29)
1956	74	(± 0.47)	-14 (-19)	-16 (-25)
1971	60	(± 0.47)	3 (+4)	3 (+7)
1980	62	(± 0.47)	-13 (-21)	-14 (-27)
1991	49	(± 0.51)	9 (-18)	14 (+37)
1996	58	(± 0.47)	-2 (-3)	-3 (-6)
2001	56	(± 0.76)	-2 (-4)	3 (+6)
2006	54	(± 0.84)		
OVERALL 1948-2006	-5	(± 0.97)		1

Table 3.3. Channel areas (A) and channel widths (B), 1948–2006.

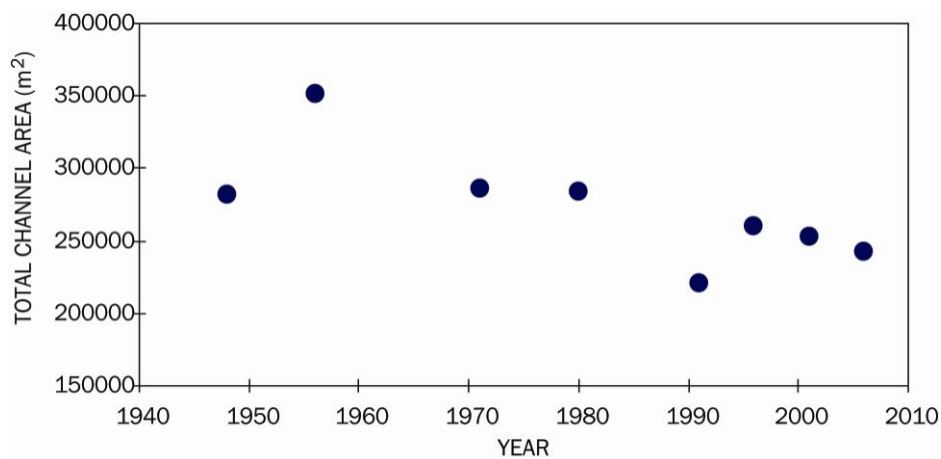


Figure 3.4. Total channel areas, 1948–2006. Error (± 1 standard error) bars have not been shown because they are smaller than the symbol size (table 3.3A).

In 1948 the channel was relatively wide and sinuous (mean total width = $59 \text{ m} \pm 1 \text{ m}$) compared to successive years. Transitions between sub-reaches of contrasting width were relatively gradual and mid-channel vegetation was established along the length of the reach. A similar planform was maintained until 1956 despite reach-scale expansion of channel area (+25 %) and an increase in sinuosity (figure 3.3). Channel constriction is first recorded by 1971, when a clear distinction between wider and narrower sub-reaches is first apparent. There was also an increase in channel sinuosity and mid-channel vegetation establishment in wider sub-reaches. Between 1971 and 1980 there was virtually no net change in total channel area, but the channel underwent substantial straightening. The most notable change occurred mid-reach with the creation of a new straight channel through the right bank floodplain. In 1980 mid-channel vegetation was mainly limited to the left side of the channel. Between 1980 and 1991 the channel narrowed, and there was an increase in sinuosity. Over the next five years (1991–1996) planform was maintained, despite total channel expansion of approximately 38 %. By 1996 there was a clear reduction in mid-channel vegetation, notably in downstream parts of the channel, where island establishments appear to have joined the riparian forest. Between 1996 and 2006 trajectories of constriction and straightening continued and abrupt changes between wider and narrower channel areas became more distinct. By 2006 the reach had developed a discontinuous channel pattern of wide and narrow sub-reaches that correspond to the six geomorphological zones identified by field observation (chapter 2).

The reduction in total channel area was matched by an overall reduction in average total channel width ($-5 \text{ m} \pm 1 \text{ m}$) (figure 3.5 and table 3.3B). The modest overall narrowing of the channel was, however, accompanied by a substantial increase in the range of channel widths (figure 3.5, error bars) as overall changes in area have been highly variable between sub-reaches that have undergone widening and narrowing (figure 3.6).

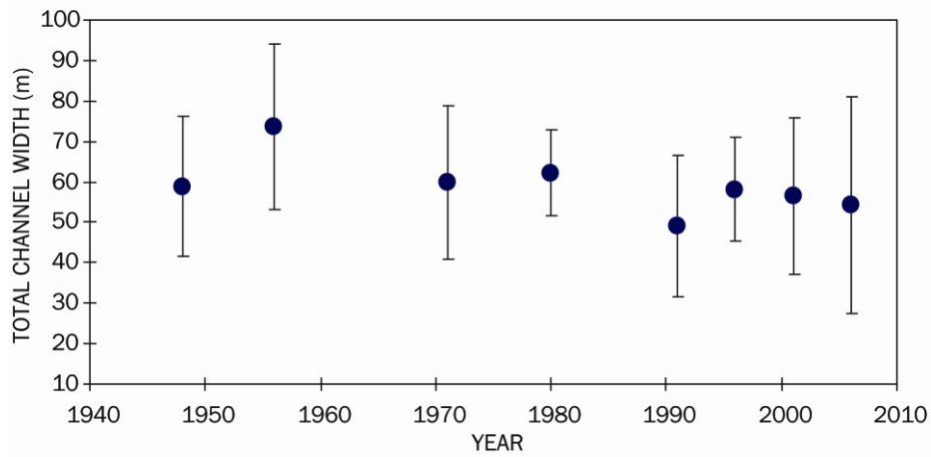


Figure 3.5. Total channel width (m), 1948–2006 (centre point = average, error bars = range of the 500 width measurements).

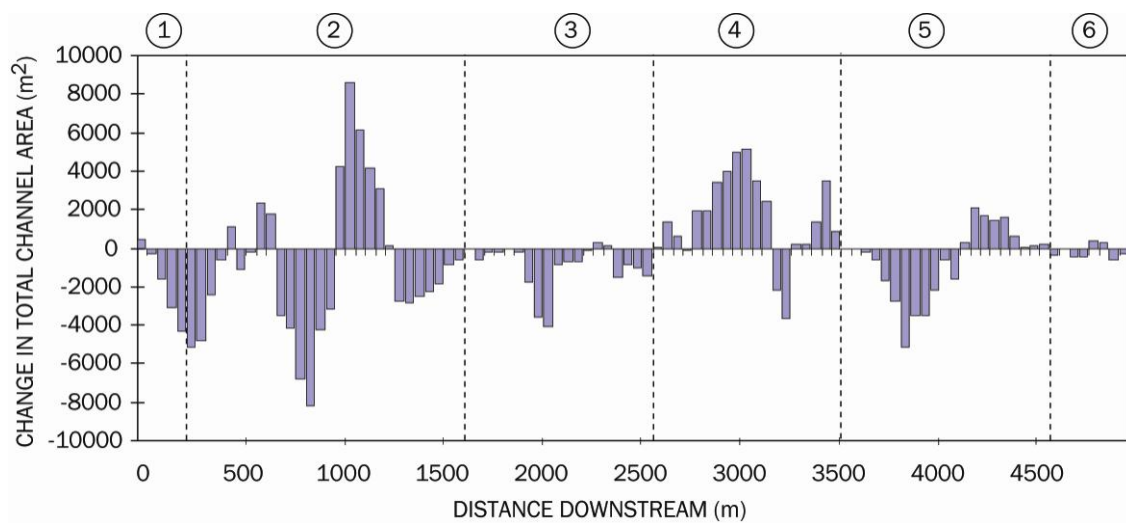


Figure 3.6. Change in channel segment areas (m²), 1948 – 2006. Dashed vertical lines indicate present-day zone boundaries. Numbers in circles on top x axis indicate zone.

Channel constriction can be explained in part by lateral encroachment of riparian vegetation. Encroachment has occurred predominantly along the left bank of the reach, with only limited amounts along the right bank in the upper and lower parts of the reach. Mid-reach encroachment has occurred only along the left bank. The overall extent of vegetation encroachment is illustrated in figure 3.7A where the 2006 total channel is shown within an envelope defined by the maximum extent of the channel boundaries during the study period (figure 3.7A). Former channels and different bands of vegetation can be seen through the forest canopy within this envelope. They can also be seen in the width of riparian forest outside of this envelope and illustrate that channel constriction and vegetation encroachment are ongoing processes that were occurring prior to 1948.

The position of the 2006 channel within this boundary also indicates that limited lateral shift has occurred. Rather than migrate across the floodplain, the channel has narrowed and straightened within its envelope. The maximum outer boundary is close to the right side of the 2006 channel but there is an average buffer of approximately 40 m that increases to approximately 100 m in places between the former limits and the present-day channel.

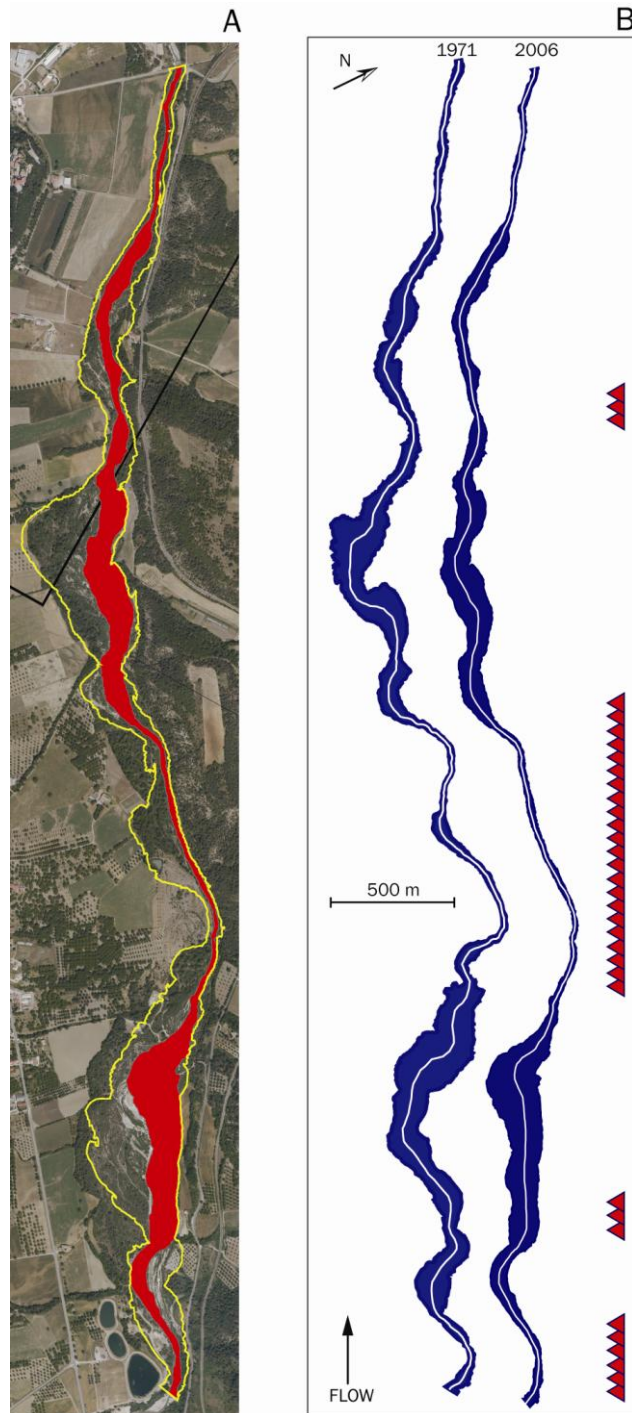


Figure 3.7 (A) Channel envelope (the maximum extent of the total channel boundary during the study period, solid yellow line) and the 2006 total channel area (red polygon) illustrating overall extent of vegetation encroachment. (B) Channel straightening between 1971 and 2006 (follow white channel centrelines) and locations where incision has exposed bedrock in the channel bed and banks (triangles with red fill). Scale, north arrow and flow direction applies to both A and B.

3.4.1.2. Channel straightening

Following an increase in sinuosity during the early part of the study period (1948-1971), the channel became substantially straighter (figure 3.8). This reduction in sinuosity may explain a proportion of the overall reduction in total channel area because, between the fixed ends of the reach, a more sinuous channel will occupy a greater total area. However, there is no clear relationship between changes in channel area and sinuosity during the study period ($r = 0.11$). For example, between 1971 and 1981 substantial reach-scale channel straightening occurred with sinuosity declining from approximately 1.16 to 1.10, but there was insignificant change in channel area during the same epoch (figure 3.4).

Parts of the reach where channel straightening has been most apparent also tend to exhibit channel incision that has exposed bedrock in both the channel bed and banks (figure 3.7B). There may then be some association between channel incision to bedrock and straightening.

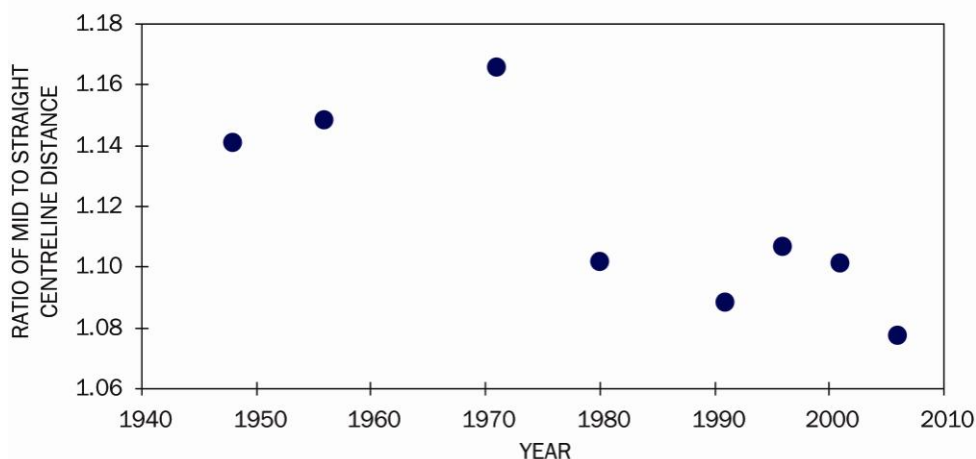


Figure 3.8. Channel sinuosity, 1948–2006.

3.4.1.3. Channel incision

Between 1928 and 2005 the reach was characterised by average channel incision of -0.8 m, although the amount and direction of change in bed elevation varied substantially along the reach (figure 3.9A). Four sub-reaches that have undergone considerable incision (≥ 1.2 m) are separated by abrupt transitions where incision is reduced, and which generally correspond with present-day zone boundaries (figure 3.9A). The uneven topography of underlying bedrock, relative to the surface of the overlying alluvial fill, may be one control on this sawtooth pattern. Bedrock has been exposed along the length of zone 3 (figure 3.7B) but similar amounts of incision in up and downstream locations have *not* revealed bedrock, suggesting that the base level may be elevated through the mid-reach. A uneven depth of alluvial channel cover may have also exacerbated the pattern of channel incision, with bedload protecting against incision in locations where sediment is available, and by acting as an

abrasive 'tool' over bedrock where bedload is limited (Sklar and Dietrich 2001, Turowski *et al.* 2007). Alternatively, the discontinuous sawtooth pattern of incision could reflect an uneven alluvial cover over bedrock as the downstream translation and dispersal of sediment 'macropulses' (Hoey 1992) 'slugs' (Nicholas *et al.* 1995) or 'waves' (Wathen and Hoey 1998, Lisle *et al.* 2001) is mediated by local variation in the storage and transfer of sediment.

Overall incision is interrupted at the transition between zone 3 and zone 4, approximately 2.6 km downstream (figure 3.9A, arrow Y). Since 1928 there has been a small amount of aggradation at this point (average 7 cm over 100 m). There has also been virtually no net change in elevation at the transition between zone 2 and 3, approximately 1.3 km upstream (figure 3.9A, arrow X). The maximum extent of incision (-2.1 m) occurred between these two points, in zone 3, suggesting that they may be structural controls on the long-term reach-scale pattern of channel incision.

Short-term changes in elevation through this mid-reach section are revealed in the surveyed profiles of 2003 and 2005. It is evident in the field that the bed topography of zone 3 is highly variable, with deep scour holes interspersed with bedrock steps and alluvial runs. The spatial variability of change in the profile, which indicates small pockets of aggradation (figure 3.9B) further suggests that changes in bed topography are relatively dynamic in time. Downstream changes in grain size (figure 3.10A) and sorting (figure 3.10B) (S. Rice, *unpublished data*) show that bedload is well-sorted at individual locations within zone 3, but that there are larger than average differences in grain size between the individual positions. This local size-sorting and apparent 'filtering' of coarse grains in zone 3 may reflect differences in the local storage and transfer of sediment that is caused by the heterogeneous bed topography (Lisle 2008). These pockets of aggradation further indicate that sediment transport is moderated by the bed structure of zone 3. In the field, coarser sediment was observed in the lee of protruding bedrock hummocks, in bedrock potholes and in fluting depressions (figure 3.11), suggesting that they promote size fractionation, by creating areas of flow separation where sediment is deposited and sheltered from entrainment. The observation that bedrock is an important control on downstream dispersal of bedload is consistent with the identification of bedrock structures as 'barriers' (Fryirs *et al.* 2007) to the longitudinal conveyance of sediment in other work (Werrity 1992, Hoey 1994, Kasai *et al.* 2004, Kasai 2006).

It is also notable that grain size in zone 4 is generally finer than in zones 2 and 3, suggesting that zone 3 tends to retain coarser bed materials and convey finer materials. These observations may indicate the scour or winnowing of fine gravels and the persistence of a coarser surface armour, which is consistent a long-term pattern of incision and reduction in sediment supply (Dietrich *et al.* 1989, Lisle *et al.* 1993).

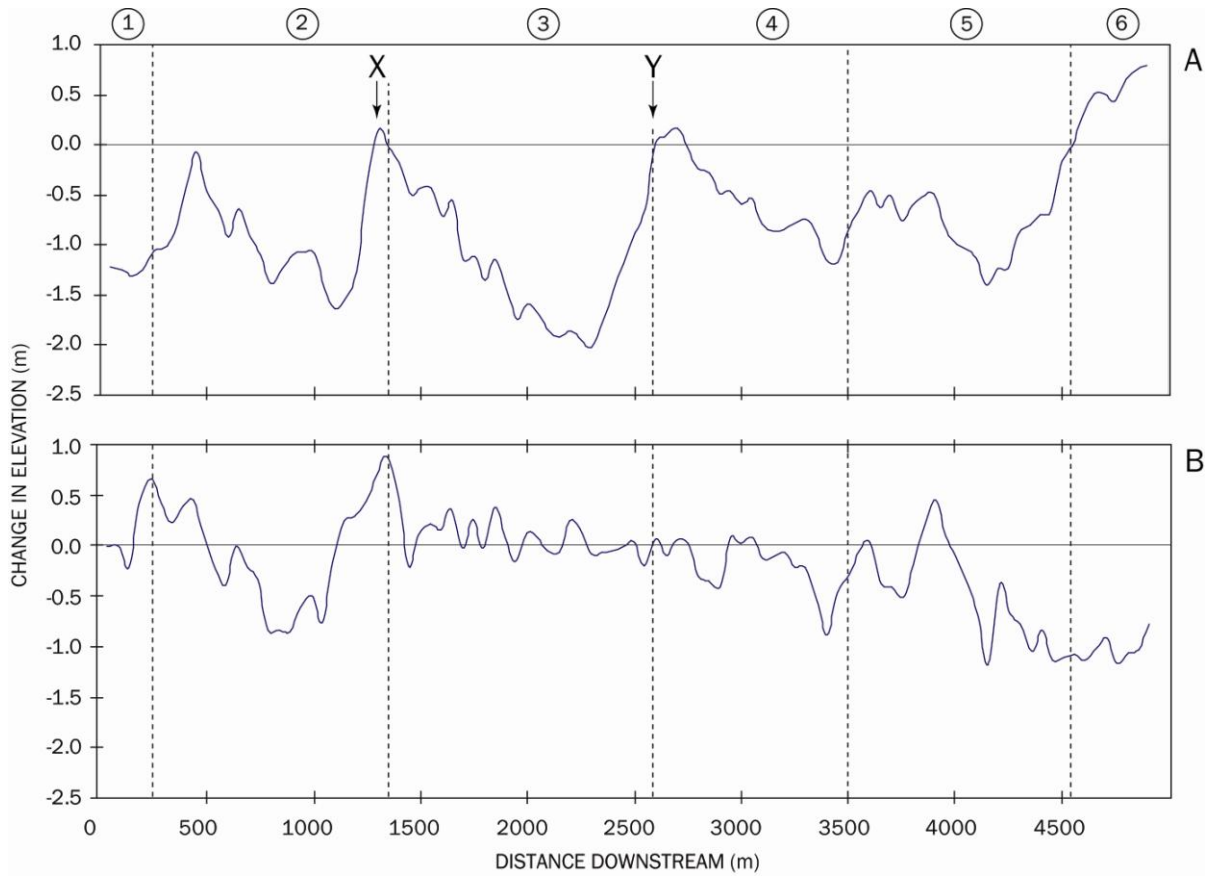


Figure 3.9. Overall changes in elevation (A) 1928–2005 and (B) 2003–2005. Dashed vertical lines indicate zone boundaries and numbers in circles refer to zones.

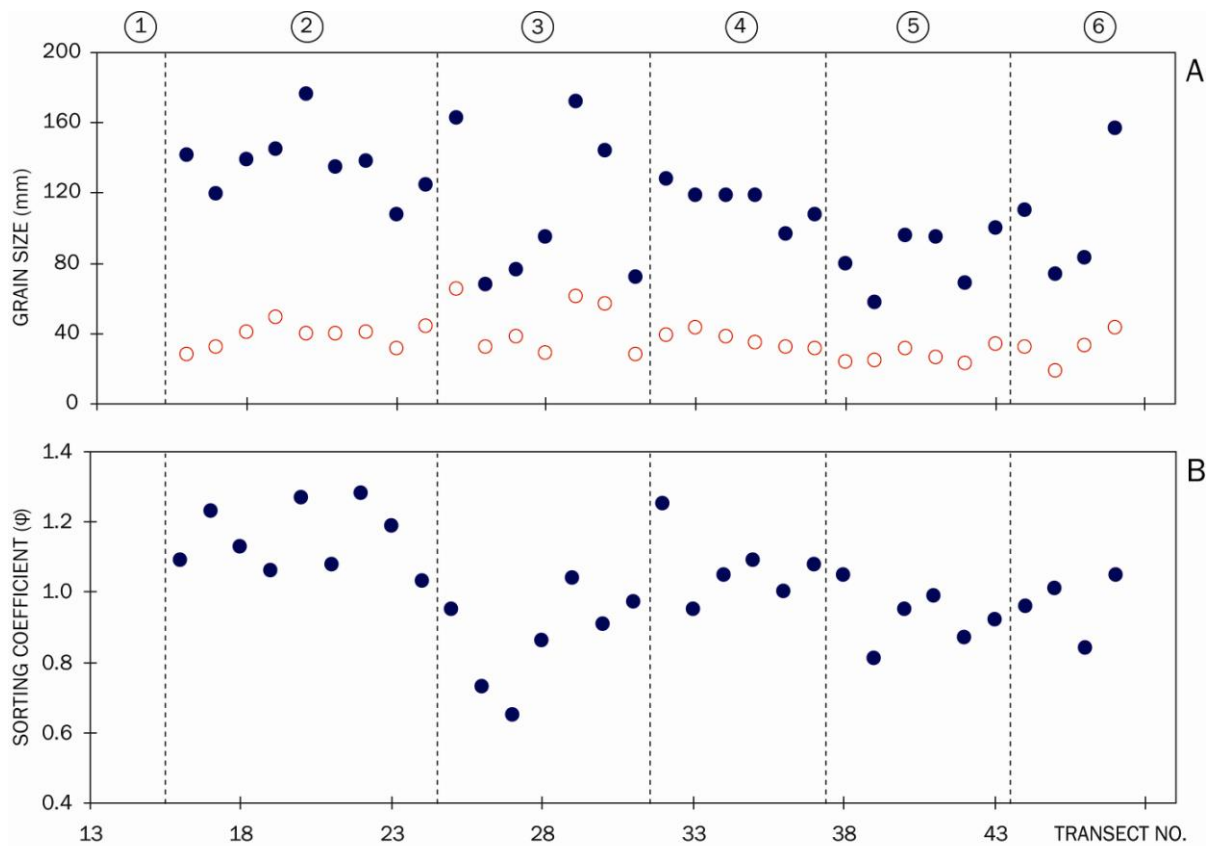


Figure 3.10. Downstream changes in (A) median (circles no fill) and maximum (solid circles) bed material grain size, and (B) sorting. Dashed vertical lines indicate zone boundaries and numbers in circles refer to zone. Transects are not evenly spaced. X axis does not represent distance downstream.



Figure 3.11. Gravel deposits in an unsubmerged bedrock pothole, zone 3.

Short-term changes in channel elevation between 2003 and 2005 also show that sections of aggradation are mainly restricted to the upstream part of the reach, above zone 3 (figure 3.9B). This upstream accumulation of sediment may reflect sediment input to the reach, possibly associated with the 1 in 44 year flood of December 2003, that has not yet been redistributed downstream. Between 2003 and 2005 incision was also greater in the downstream part of the reach, compared to upstream, which further supports the possibility that zone 3 acts as a control on the longitudinal conveyance of bedload along the reach.

It is apparent that sub-reach patterns of channel incision (figure 3.9A) show some association with sub-reach patterns of channel constriction (figure 3.6). However, the relationship between channel incision and channel constriction is not simple, and there is no overall correlation between segment-scale changes in channel elevation and channel area. It is clear, however, that channel incision is a dominant characteristic of reach-scale adjustment, with incision occurring in the majority of channel segments, irrespective of whether area increased or decreased (figure 3.12).

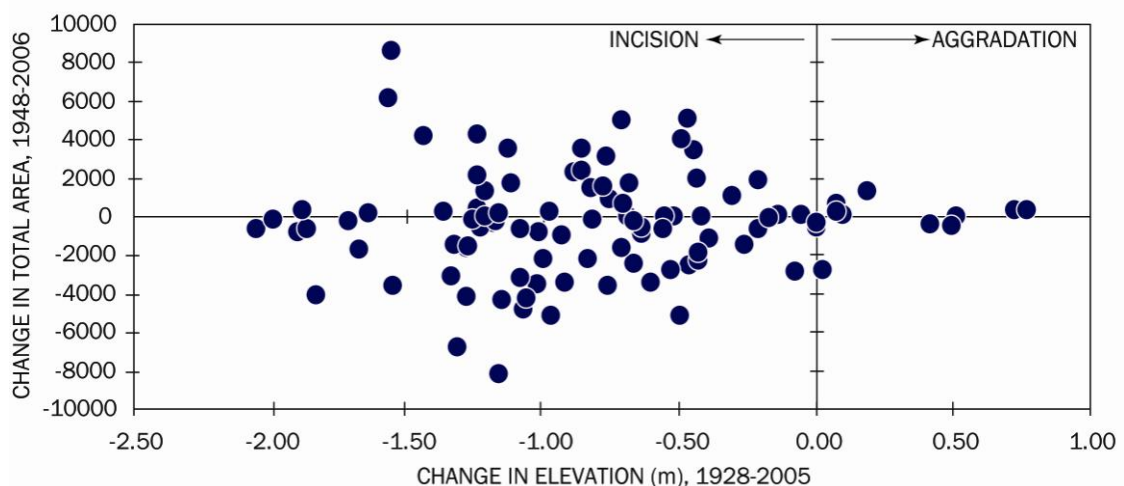


Figure 3.12. Segment-scale changes in elevation (1928–2005) and active channel area (1948–2006).

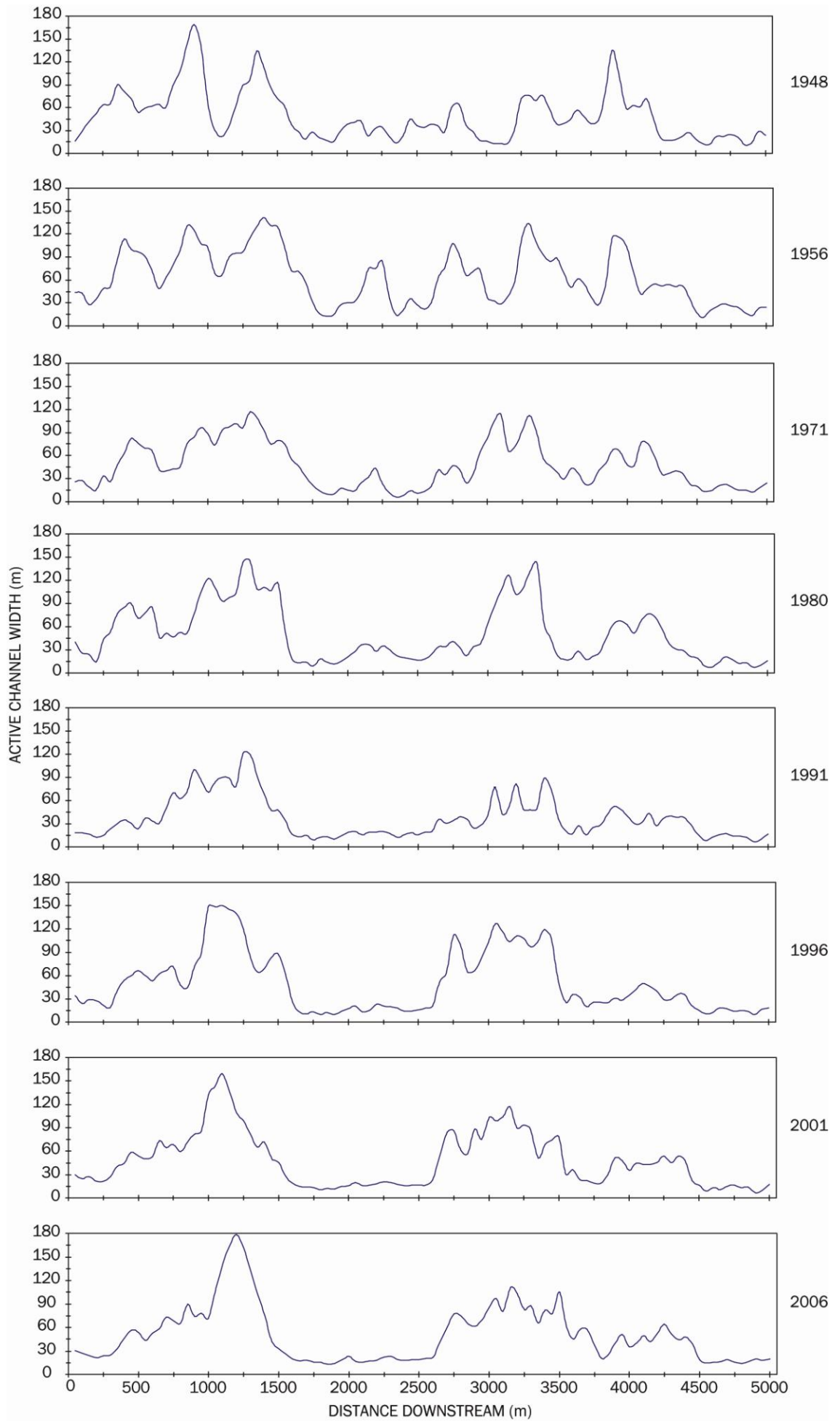
3.4.2. Sub-Reach Changes in Channel Morphology and the Development of Present-Day Channel Zonation

3.4.2.1. Sub-reach patterns of channel narrowing

Downstream sequences of active channel width for each epoch (figure 3.13) show that reach-scale variation in channel width has decreased and that a systematic pattern of wider and narrower sub-reaches has developed through time. In 1948, there is frequent variation in active channel width and transitions between sub-reaches are relatively gradual. Through time, reach-scale variation in channel width decreases and transitions between wider and narrower sub-reaches become increasingly abrupt. Between 1948 and 2006, the development of sub-reach homogeneity is indicated by a decrease in the average difference in active channel width measured every 10 m downstream ($n = 500$) (figure 3.14).

By 1980, a narrow mid-reach 'corridor' is particularly evident and links two wide upstream and downstream sub-reaches, centred at approximately 1.0 km and 3.0 km (figure 3.13). There is little subsequent change to this reach-scale pattern, which is framed by two narrow sub-reaches along the uppermost and lowermost 500 m of the channel, indicating that the importance of the mid-reach, as a control on vertical channel behaviour, extends to sub-reach patterns of lateral channel adjustment. Between 1980 and 2006 the stability of this pattern and the transitions between narrower and wider sub-reaches indicates that local trajectories of channel adjustment have been maintained between stable sub-reach boundaries. This may suggest that controls on channel form inherited by 1980, particularly the mid-reach corridor, have influenced the subsequent development of present-day channel zonation.

Figure 3.13 (following page) *Downstream changes in active channel width, 1948-2006.*



It is notable that in 1956, 1981, 1991 and 2006, there are short-term increases in the difference in active channel width between successive measurements 10 m apart (figure 3.14) because large flood events occurred shortly prior to these dates. This indicates that flood events may be responsible for increasing sub-reach variation in channel width, and are thus an important influence on the development of the present-day channel zones. It is also apparent that there is minor fluctuation in reach-scale variation in width between 1991 and 2006 (± 0.7 m, figure 3.14) illustrating that the stable, reach-scale channel pattern of wider and narrower sub-reaches inherited by 1980 (figure 3.13) has been maintained during this latter part of the study period.

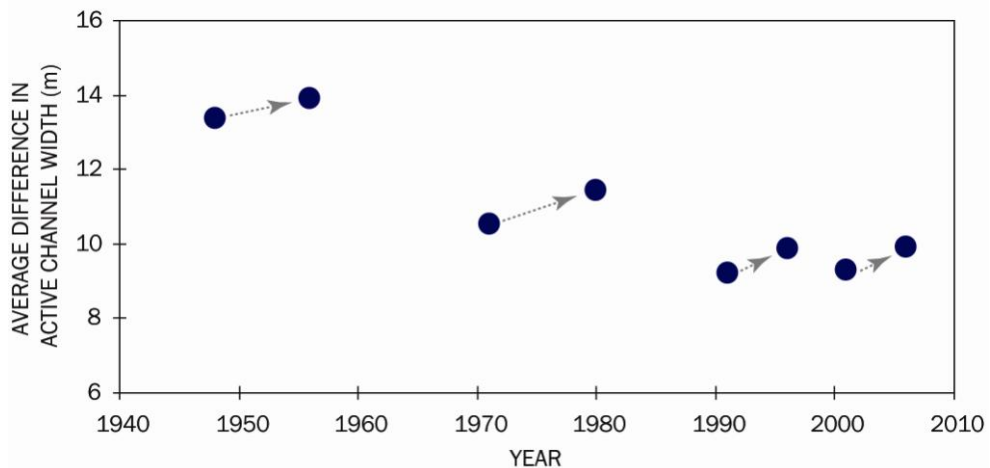


Figure 3.14. Average difference in active channel width between successive measurements 10 m apart, 1948-2006

3.4.2.2. Objective evaluation of channel zonation

In 2006, abrupt transitions between wider and narrower sub-reaches (figure 3.13) correspond with the zone boundaries assessed by field observation. At larger and more detailed scales, statistical boundaries in river corridor widths have been shown to indicate important physical boundaries in landscape evolution (Gangodagamage *et al.* 2007), and, given the association between changes in active width and present-day zone boundaries, changes in active channel width were chosen as a basis from which to identify zone boundaries in the historical record, and thereby understand the development of zonation through time.

To this end, the non-parametric Pettit test (Pettit 1979) was applied to downstream sequences of active channel width for each epoch. The Pettit test is based on the Mann Whitney test and identifies significant thresholds in a sequence of measurements by evaluating the null hypothesis of an absence of change (Pettit 1979). It has been successfully applied in other work seeking to identify longitudinal structure in sequences of data (e.g. Rollet 2007, Lassetre *et al.* 2008).

To first evaluate the use of changes in channel width as a robust basis from which to delineate zones, the test was used to identify significant (α 0.05) downstream changes in active channel width of the 2006 channel (figure 3.15). There is good general agreement between thresholds identified for the 2006 sequence of active width and the zone boundaries identified by ground observation (figure 3.15), especially in the middle and lower parts of the reach. These results are sufficient to confirm that the Pettit analysis can provide an objective means of identifying morphological zone boundaries in the earlier photo sets, for which no ground truthing is available. It was therefore applied to sequences of active channel width extracted from each photo set, providing a consistent possible indication of how present-day channel zonation has developed through time.

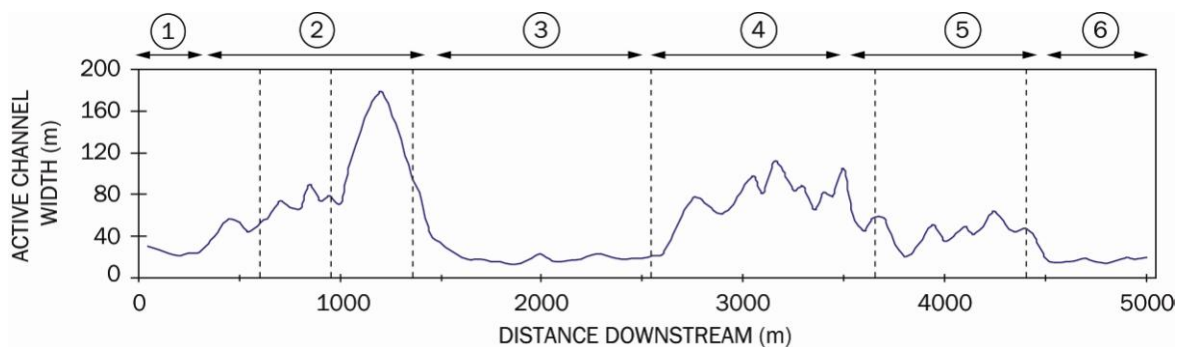


Figure 3.15. Significant (α 0.05, Pettit test) downstream changes (dashed vertical lines) in active channel width, 2006. Arrows and numbers in circles indicate zones assessed by field observation.

3.4.2.3. Spatio-temporal changes in zone boundaries

The significant downstream changes in active width identified by the Pettit test confirm the spatio-temporal persistence of the current zone boundaries through time. There have been only minor changes in the total number of zones along the reach as sub-reach patterns of channel narrowing have developed within these boundary settings (figure 3.16).

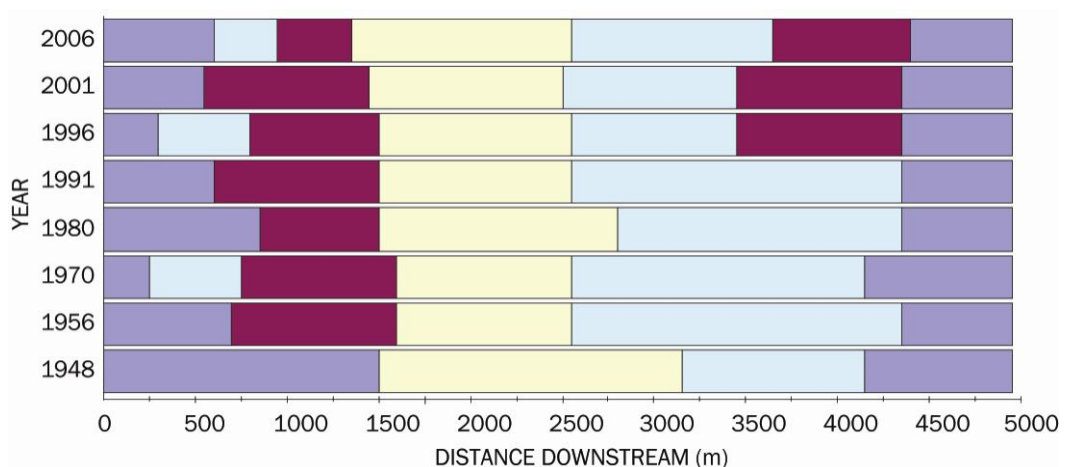


Figure 3.16. Significant (α 0.05, Pettit test) downstream changes in active channel width, 1948-2006.

Along the downstream part of the reach, boundaries identified by the Pettit test are relatively stable throughout the study period (figures 3.16 and 3.17). Zone 6 is evident in each epoch. There has been little change in channel width along this final 500 m section of the channel through time (figure 3.17, arrow D) probably because it has been constrained by a left bank dike and the weir at its downstream end, at Recoubeau. Boundaries identified by the Pettit test reveal that zone 3 has also been present throughout the study period (figure 3.17, arrow B). In 1948 this narrow section extended further downstream, but by 1956 channel widening along the downstream part of the channel has moved the boundary upstream. There has been virtually no subsequent change in the position of this downstream boundary through time.

Between 1948 and 1991 a wide zone was present between zone 3 and the downstream constrained zone 6 (figure 3.17, arrow C). There is no statistical difference in active width along this section of the channel until 1996, when it subdivided into zones 4 and 5 (figure 3.17, arrows C and F).

Between 1956 and 1971, a narrow zone was created at the upstream end of the reach, as mid-channel vegetation on the left and right banks joined the floodplain (figure 3.17, arrow E). At the present day, the narrow upstream zone is a bedrock channel that can be clearly identified and delineated by an abrupt downstream transition to a wide, alluvial zone. The Pettit test identifies the boundary in channel width in 1971 and 1996 only. Between 1956 and 2006 the transition in width is apparent in each channel planform, despite that it is not statistically present in sequences of active width. The narrow upstream zone is zone 1 (figure 3.17, arrow E) and the wide downstream zone is zone 2 (figure 3.17, arrow A).

Compared to the relative stability of downstream zone boundaries, upstream zonation has been variable during the study period (figure 3.17, arrow A). Between 1948 and 2006 boundaries identified by the Pettit test organise the upper part of the reach between one and three zones. Some of this variability may be due in part to patterns of lateral vegetation encroachment and considerable channel straightening, which have caused frequent variability in channel width along the upper part of the channel.

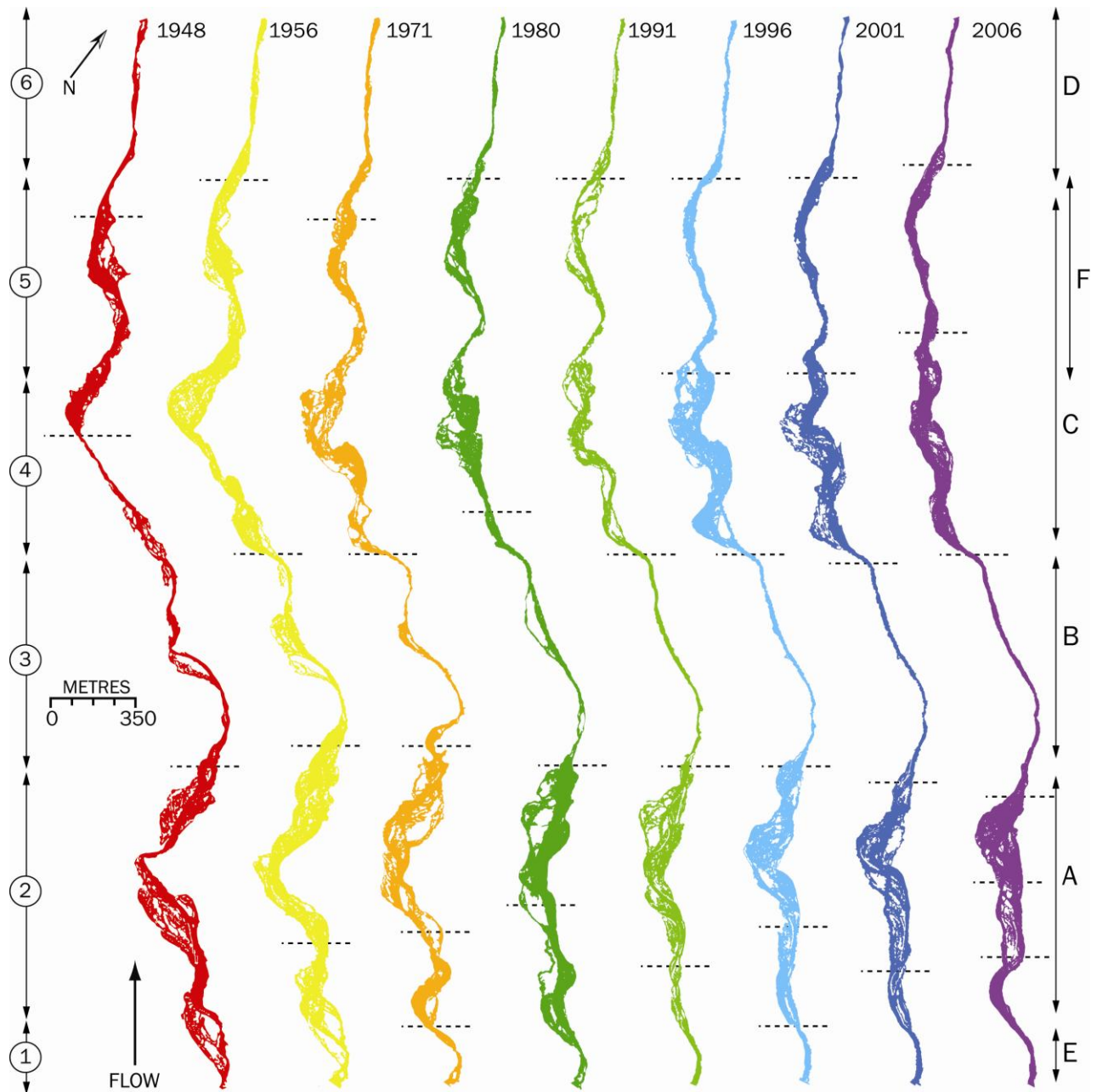


Figure 3.17. Significant (α 0.05, Pettit test) changes in active channel width (dashed horizontal lines), 1948-2006. Arrows on the left indicate present-day zone boundaries (numbered, in circle). Arrows on the right are referred to in the text and indicate the development of present-day channel zonation.

3.4.2.4. Spatio-temporal patterns of downstream change

Consistent zone-scale patterns of change in active channel width are apparent during each photo epoch (figure 3.18). There is marked similarity in the overall amounts and downstream patterns of change in active width that occur between the present day zone boundaries. This consistency suggests that the zones are variably susceptible to adjustment, particularly flood-induced processes of vegetation establishment and removal. Large floods occurred during photo epochs that exhibit overall, reach-scale increases in active channel width (1948-1956, 1971-1980, 1991-1996 and 2001-2006). Three photo epochs

undisturbed by flood activity show overall narrowing of the active channel (1956-1971, 1980-1991 and 1996-2001). It is also apparent that there has been a temporal change in these spatial patterns, with greater overall amounts of change during earlier epochs, and smaller amounts in later epochs.

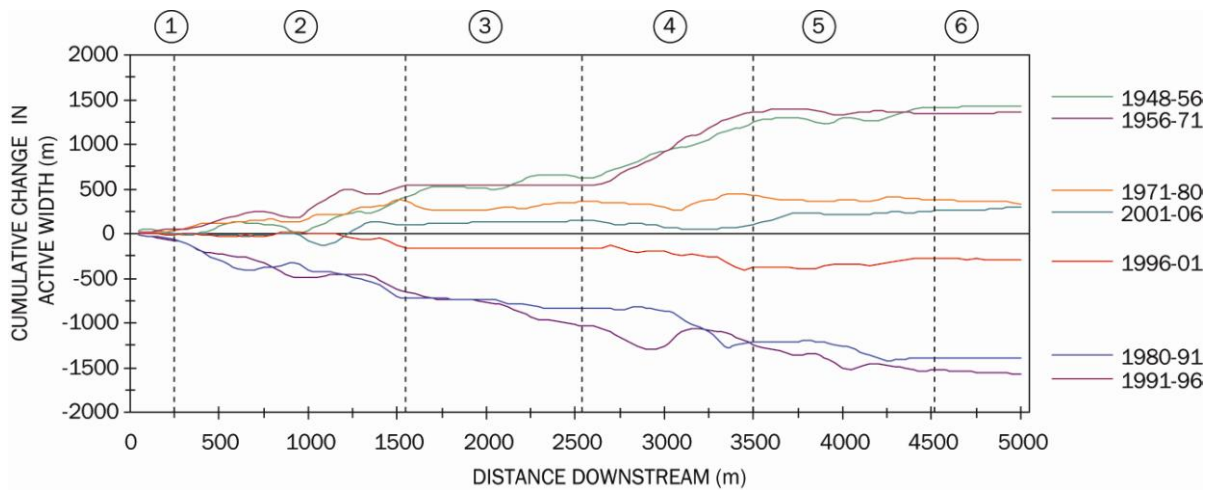


Figure 3.18. Cumulative downstream changes in active channel width, for each epoch. Dashed vertical lines indicate zone boundaries. Numbers in circles refer to zone.

Zones 2 and 4 in particular have shown consistent overall amounts and patterns of widening and narrowing within each epoch. These areas of lateral instability are bordered by a wide riparian buffer and their floodplains are unconstrained (figure 3.7A), suggesting that processes of lateral vegetation encroachment, and removal, are important controls on the development and maintenance of their wide and braided characteristics. In contrast, the narrow mid-reach zone 3 has shown little or no change in active width through time (figure 3.18). The present-day channel through the mid-reach is confined within a deep, rectangular bedrock ‘slot’ and, given the lateral stability of this section of the channel between 1980 and 2006, and the stability of the reach-scale channel pattern seen between the same dates (section 3.4.2.1, figure 3.13), it is possible that the present-day lateral constraint through the mid-reach had been inherited by 1980. Zones 1 and 6 have also been relatively stable and record small or no changes in active width through time. Zone 5 is more dynamic than these uppermost and lowermost zones, but has also demonstrated relatively little change in channel width between epochs.

It is also apparent that changes in active width in zone 2 are more spatially variable compared to those in zone 4 (figure 3.18). This relative difference in variability in active width between these unconfined channel areas may reveal that they undergo different flood-induced processes of lateral vegetation establishment and removal. In addition to the differential variability in width, different overall amounts of change that occur between zone 2 (maximum changes +459 m, -604 m) and zone 4 (maximum changes +827 m, -368 m) may also reveal that there is an important difference in the flood-induced redistribution of gravel between these zones, and thus that they possess different regimes of bedload yield and transfer.

3.4.3. Summary of Results

- Between 1948 and 2006, the reach has undergone modest overall constriction (-14 % in total channel area) and modest overall narrowing (-5 m in average total channel width). These trends are interrupted only by two short-term increases in channel area and width seen by 1956 and 1996.
- Since 1980 there has been considerable reach-scale straightening, which is associated with substantial incision and bedrock exposure.
- These overall, reach-scale trends are characterised by distinct spatial discontinuity. Abrupt downstream transitions occur between sub-reaches that have undergone different overall directions and amounts of morphological change, and these transitions are coincident with present-day zone boundaries.
- There has been little change to the present-day pattern of wider and narrower sub-reaches since 1980, suggesting that present-day zonation has developed between, and been controlled by, relatively stable boundaries established by 1980.
- Within each epoch, different patterns of change in channel width have occurred between the present-day zones. In zones 2 and 4, the active channel has widened in response to large flood events, and narrowed in the absence of large flood events. Other zones have shown little or no overall change in response to flood activity. The differences in width changes between the zones, and the consistent patterns of change within each zone, demonstrates their variable capacity and sensitivity to change.
- In addition to patterns of spatial variation, there has been temporal variation in the nature of channel adjustment. Greater overall amounts of change during earlier epochs, and smaller overall amounts of change in more recent epochs may indicate a temporal change in channel behaviour, perhaps as the channel adjusts to changes in sediment supply and flood activity.

3.5. Discussion

In light of these observations, overall reach-scale changes in channel morphology, and the historical development of present-day zonation will now be discussed. Particular consideration will be given to the role of individual flood events and their relative timing against changes in bedload supply and flood frequency, and changes in sediment transfer and storage along the reach through time. This section will also consider temporal trajectories of change in channel morphology, and prospects for future changes.

3.5.1. Flood Induced Channel Adjustments

The short-term interruptions to long-term, overall channel constriction seen by 1956 and 1996 (figures 4.4 and 4.5) most likely reflect lateral channel expansion in response to two of the four large flood events (defined as twice the magnitude of the mean annual flood, $61.2 \text{ m}^3 \text{ s}^{-1}$) that occurred during the study period, in 1951 and 1994 (table 3.4). This highlights the importance of large flood events for causing changes in channel morphology along the reach. However, flood-induced channel change has not been consistent through time and it is clear that during the study period the response of the channel to individual flood events has been different.

A small increase in the proportion of active channel (exposed gravel and bedrock) between 1948 and 1956 must be due to channel bank expansion, because the increase is matched by an increase in total channel area, and also a small increase in the area of mid-channel vegetation (table 3.3A). This is in contrast to the impact of subsequent flood events. Small increases in the proportion of active channel area seen by 1980, 1996 and 2006 were, instead, caused by decreases in the area of mid-channel vegetation, of -7 %, -42 % and -58 % respectively, without any appreciable change in the total channel area (figures 4.4 and 4.5). This pattern indicates that since 1980 there has been a shift in the way that the channel expends its energy, away from the erosion of channel margins and channel bank expansion, towards the removal of mid-channel vegetation.

YEAR	MAXIMUM AVERAGE DAILY Q ($\text{m}^3 \text{ s}^{-1}$)	ESTIMATED RECURRENCE (YEARS)	EXCEEDENCE PROBABILITY (%)	SERIES RANK (1948-2006)	SERIES RANK (1907-2006)
1951	63.0	16.36	6.11	4	9
1978	64.3	17.38	5.75	3	8
1994	108.0	99.80	1.00	1	3
2003	86.8	44.78	2.23	2	4

Table 3.4. The four largest flood events during the study period, with recurrence intervals estimated using the maximum series of daily average discharge between 1948 and 2006.

It is most likely that this temporal change in channel response to flood events has been controlled by the timing of changes in flood frequency (section 2.5) and upstream sediment supply to the reach (section 2.3), relative to channel conditions at the time of impact (e.g. Lane *et al.* 1996, Lane and Richards 1997, Brewer and Lewin 1998). In 1978, the third largest flood of the study period occurred at a time when channel conditions were particularly sensitive to change. This flood event is hypothesised to hold particular significance in the history of channel evolution between Luc and Recoubeau, by inducing substantial reach-scale morphological changes that have controlled the subsequent development of sub-reach channel morphology.

3.5.1.1. Changes in zone 3, 1971-1981 and the 1978 flood

Between 1971 and 1980 the most noticeable changes in channel morphology were a dramatic reduction in channel sinuosity (figure 3.8) and the creation of a new, straight channel through the right bank in zone 3 (figures 4.3 and 4.19). At present, this mid-reach section of the channel is constrained in a relatively deep and incised rectangular slot, characterised by substantial outcrops of bedrock in the bed and in the valley walls (figure 2.8). It is apparent that the position of this 'corridor' has remained notably stable since 1980 (figures 4.3 and 4.13), and that there has also been little change to the reach-scale pattern of wider and narrower sub-reaches that has developed between stable spatial boundaries, since its creation (section 3.4.2.3, figure 3.17). This has led to the hypothesis that the development of present-day zonation has been controlled by structural constraint on the channel which has been inherited from the catastrophic scouring of the channel, and the narrow and deep mid-reach corridor, during the 1978 flood.

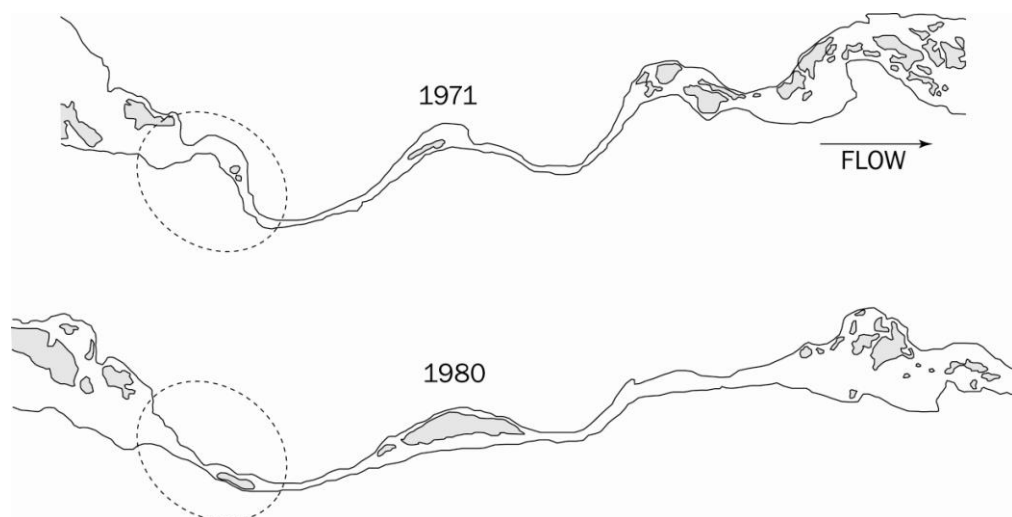


Figure 3.19. Changes in channel planform through the mid-reach, 1971–1980. The creation of a new, mid-straight and narrow channel is hypothesised to have occurred by avulsion where the channel narrows to a bottleneck (dashed ellipse) in response to the long-term accumulation of sediment. Grey shaded areas within the channel are vegetated islands.

Alluvial, or floodplain stripping is a term used to describe the flood-induced removal of floodplain sediment during channel avulsion. It is considered that a similar process of stripping may have scoured the narrow mid-reach channel through the right bank floodplain of zone 3. Stripping has been observed in other mixed bedrock-alluvial channels (Heritage *et al.* 1999) to depths in excess of 2 metres (Bourke 1994). It has also been observed in channels that are slow to adjust to changes in flow regime, and/or where there the floodplain is narrow (Nanson 1986, Warner 1997, Largo *et al.* 2006).

The mid-reach avulsion that occurred in 1978 started at the downstream end of zone 2 where the channel narrows to a bottleneck (figure 3.19, dotted ellipse) and the floodplain is narrow. At present, the left bank is also bedrock, resistant to flood-induced erosion, and constrains lateral channel adjustment into the left bank floodplain. The accumulation of sediment at the bottleneck during the entire study period indicates that it is also a long-term constraint on the downstream transfer of sediment. This is evident on all aerial photography, in the abrupt interruption to overall incision between 1928 and 2005 (figure 3.9A, arrow X), and short-term aggradation between 2003 and 2005 (figure 3.9B, arrow X). It is hypothesised that the long-term accumulation of bedload at this point caused the channel to avulse during the 1978 flood, circumnavigating the bottleneck and sculpting the new channel through the right bank (figure 3.19). It is likely that the avulsion into the right bank was facilitated by the resistance of the left bank, and was channelled within a narrow corridor when it came into contact with the reciprocal resistance of the right bank valley walls.

The avulsion may have been primed by a substantial decrease in sediment supply and flood activity to which the channel had been slow to adjust. By the start of the study period there had been a substantial reduction in the dominant sediment supply to the reach, following widespread afforestation and the installation of small flood defence infrastructure in the Béoux sub-catchment (section 2.3). This gradual decline was further compounded by the construction of the Trescherènes dam in the upper part of the Béoux sub-catchment in 1965. It has been estimated that this dam can impound a volume of sediment seventy-one times greater than the annual bedload yield of the Béoux ($565 \text{ m}^3 \text{ yr}^{-1}$) (Liébault and Beullens 1997) and most likely caused a dramatic and sudden decrease in bedload supplied to the reach by the 1970s. The reduction in sediment supply was also accompanied by a reduction in the number of days on which the mean annual flood was exceeded: from 13 days between 1956 and 1971 (approximately once per year) to 6 days between 1971 and 1980 (approximately once every two years) (section 2.5). By the time the flood occurred in 1978, fifty-three years had also passed since the occurrence of a flood of greater magnitude ($68 \text{ m}^3\text{s}^{-1}$ in 1925) and this period of conditioning to supply-limited conditions and infrequent flood activity may have rendered the reach as a whole particularly sensitive to change. The less frequent redistribution of a reduced sediment supply may have also led to an impoverished but also heterogeneous alluvial cover both across and along the channel (Nelson *et al.* 2009) and thus the 1978 flood

feasibly also occurred at a time when the reach was sensitive to spatially variable flood-induced erosion. Sub-reaches with a thin alluvial cover, such as where the underlying bedrock is elevated relative to the depth of overlying alluvium, likely underwent substantial scour and incision during the flood. Other sub-reaches were possibly protected by their relative depth of alluvial cover (e.g. Sklar and Dietrich 2001) and so the 1978 flood may have further exacerbated the already heterogeneous alluvial cover of the channel bed.

It is possible that during the 1978 flood, avulsion in zone 3 was further facilitated by anthropogenic routing of the active channel. Unauthorised sites of gravel extraction in the downstream part of zone 2 can be interpreted on the photograph of 1971 (section 2.4, figure 2.2) and it is possible that artificial gravel embankments were created along the left side of the channel to prevent the inundation of extraction sites at the channel margin.

At the upstream entrance to the mid-reach corridor there is evidence that the floodplain was stripped, where the right bank has been eroded to bedrock around a relatively resistant piece of the floodplain (figure 3.20A). This remnant has been isolated as an island since 1980 (figure 3.20B). It thus resisted removal during the 1978 avulsion, and subsequent flood-induced erosion. The resistant island is also coincident with the upstream location of two points at which there has been insignificant net change in bed elevation (figure 3.9A, arrow X) and suggests that it may be a long-term structural control on channel adjustment to changes in sediment and flow regimes. In addition to the mid-reach corridor, the isolation of this island during the 1978 avulsion, and its persistence since 1980, provides some evidence that present-day constraint on the channel was inherited from the 1978 flood. It is also apparent that subsequent channel adjustments, and the evolution of present-day zonation have not only been controlled by this constraint but by flood-induced incision along the length of the reach.

3.5.1.2. Subsequent reach-scale channel adjustment, 1980–2006

In addition to the creation of the mid-reach corridor, another particularly important effect of the 1978 flood was the routing of the channel along the right side of the channel boundary. Relatively large and dense mid-reach vegetated islands establishing on the left side of the channel boundary, particularly in zones 2 and 4, were not removed and left undisturbed by the flood (figure 3.3). This reach-scale straightening and associated incision, and the fixing of the channel mid-reach within its bedrock 'slot' appears to have influenced subsequent channel evolution by initiating a disconnection between the active channel and the floodplain. It is evident on 1980 aerial photography that the channel is incised beneath the floodplain terrace, particularly in zones 2 and 3, and it is likely that this lateral disconnection limited or even precluded subsequent overbank inundation of the floodplain. Between 1980 and 1991 there were also no large floods and, because the routing of the 1978 flood along the right side of the channel did not disturb large areas of vegetation establishing along the left side of the channel, the majority of mid-channel vegetation had been establishing since at least 1971. By

1991, this long period of undisturbed establishment can explain in part the substantial reach-scale narrowing between 1980 and 1991, when the average active channel width reduced by 27 % (table 3.3B). The succession of mid-channel vegetation during this time is also seen in the temporal increase of the cumulative area, which reached a maximum between 1980 and 1991 (figure 3.21).

The disconnection between the channel and the floodplain initiated by incision during the 1978 flood was probably reinforced by vegetation that established during this long, undisturbed period, by increasing the resistance of the channel banks, particularly along the left side of the channel, to subsequent flood-induced erosion (e.g. Simon and Collinson 2002, Pollen *et al.* 2004). In doing so, the encroachment of vegetation along the channel margins acted to accelerate reach-scale narrowing, incision, and the disconnection between the channel and the floodplain. The subsequent routing of flow within a narrower, straighter and incised channel feasibly caused a relative increase in stream power and an evident change in the way in which stream energy was expended between 1980 and 2006. Between 1991 and 2006 there is a significant reduction in the cumulative area of mid-channel vegetation (figure 3.21) and in the proportion of mid-channel vegetation within the total channel boundary (figure 3.22), and this is most likely because the relative increase in stream power removed mid-channel establishments rather than eroding the by now resistant channel banks. The hypothesis that flood events are a dominant control on the establishment and removal of mid-channel vegetation is supported by the small increase in the proportion of mid-channel vegetation, in the absence of a large flood event between 1996 and 2001 (figure 3.22).

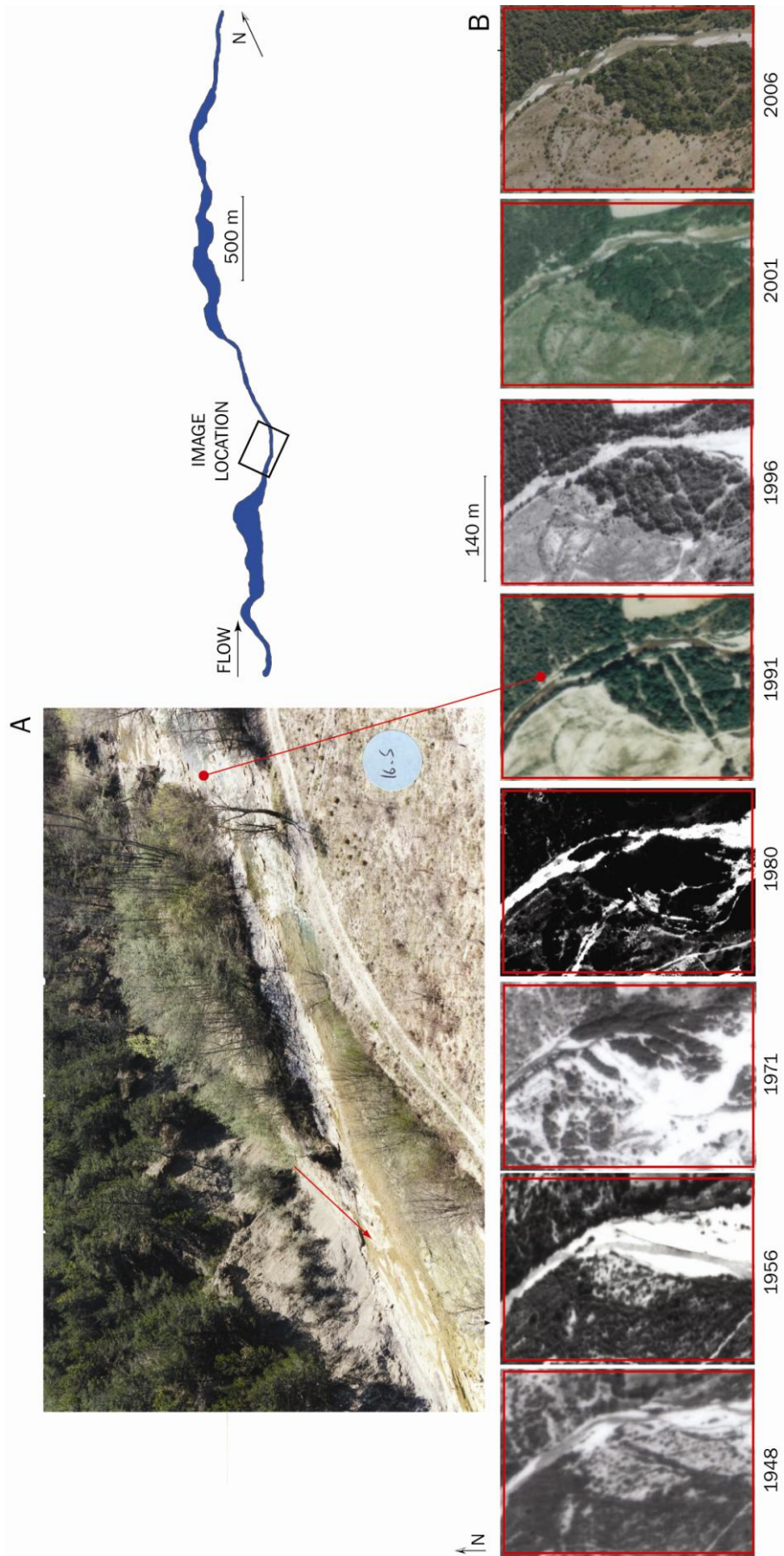


Figure 3.20 A remnant of floodplain, seen in (A) 1995, that is hypothesised to have been isolated as an island during the 1978 flood. This island first appears to be isolated in 1980 and has since been resistant to erosion (B).

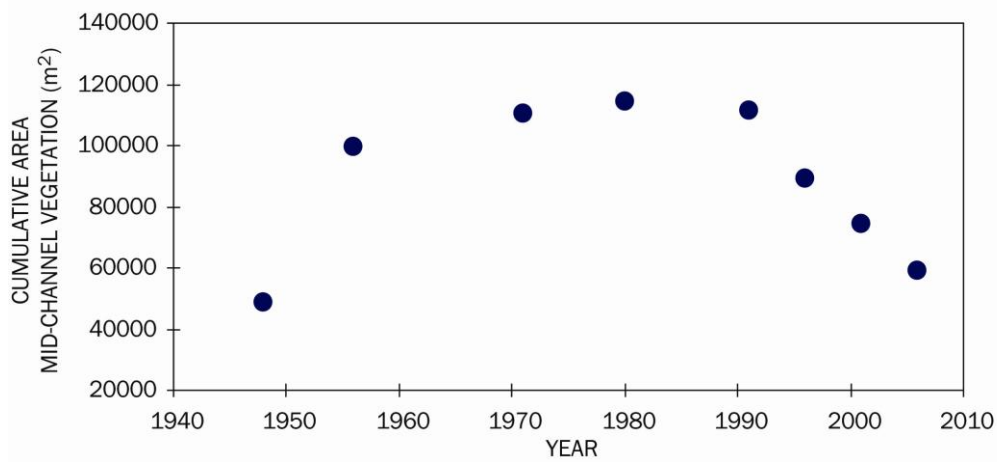


Figure 3.21. Cumulative area of mid-channel vegetation, 1948 – 2006.

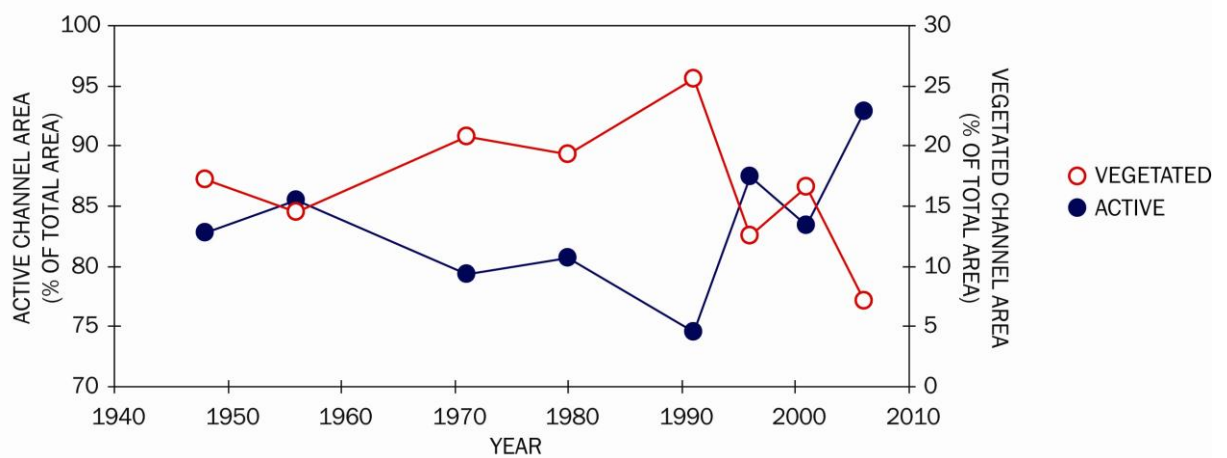


Figure 3.132. Active and vegetated proportions of the total channel area, 1948 – 2006.

Thus, the incision accomplished by the 1978 flood caused an initial reach-scale disconnection between the channel and the floodplain, and by routing the channel along the right bank, also permitted a long, uninterrupted period of vegetation establishment. Between 1980 and 1991 the reach-scale disconnection between the channel and the floodplain was further accelerated by the establishment of vegetation along the channel margins, facilitated by a long period of flood inactivity, which strengthened channel banks to further flood-induced erosion.

The flood that then occurred in 1994 was the largest of the study period, and the third largest during the historical record (since 1907). In response to this event there was only a relatively small amount of channel expansion (figure 3.4) and a small increase in sinuosity (figure 3.8). These reach-scale morphological changes were relatively modest compared to the substantial adjustments caused by the 1956 and 1978 floods, even though the 1994 flood was 58 % and 69 % larger, respectively, than these two previous events. The relative lack of lateral channel expansion in response to such a high magnitude flood highlights the

importance of lateral constraint on channel adjustment that developed and reinforced after 1978.

The small impact of the 1994 flood also suggests that it did not introduce much bedload to the reach. Shortly prior to 1991, the construction of a small weir at the upstream end of zone 1 virtually disconnected the reach from the already very limited supply of sediment, and so the 1994 flood probably redistributed locally available channel bedload. Between 1991 and 1996 the total channel areas of zones 2 and 4 expanded by 10 % and 73 %, respectively (with little or insignificant change in other channel zones) and this relative difference provides some evidence of the local sourcing of sediment, particularly from the upper part of the reach for redistribution downstream.

Given the substantial and sudden reduction in sediment supply, associated with the weir, and the likely patchy availability of bedload, it is also feasible that the downstream redistribution of sediment during the 1994 flood also incurred substantial scour of the channel bed, particularly in zones 1 and 3, where the underlying bedrock appears to be elevated relative to the surface of overlying alluvium, and the depth of overlying alluvium is generally thin, and inadequate as a protective cover. Between Luc and Recoubeau bedrock is marly and quite friable (figure 3.23) and thus where bedload was available for scour it is likely to have undergone substantial abrasion. The exposure of a greater area of bedrock likely exacerbated local discontinuity in transport rate and storage capacity (e.g. Lisle and Church 2002), further contributing to the uneven redistribution of bedload along the reach.



Figure 3.23. *Bedrock in zone 3 exhibits how the lithology is friable and easily eroded.*

The final large flood of the study period occurred nearly ten years later, in December 2003. Total channel expansion did not occur, and the general tendency toward constriction and channel straightening was again observed, indicating that by 2003 the former channel areas of zones 2 and 4 were resistant to erosion and not 'reactivated' by channel bank expansion. By 2006, incision has been reinforced as a long-term, reach-scale trend. The reach-scale disconnection between the channel and the floodplain is clear in the contrasting effects

of the 1994 and 2003 floods (figure 3.24). In 1994 some locations experience channel expansion, but undergo constriction in 2003.

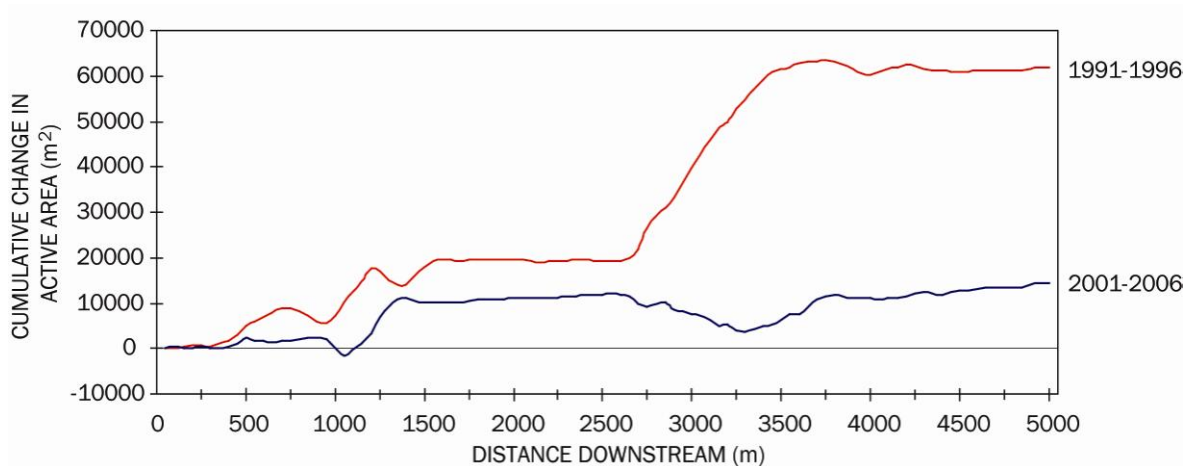


Figure 3.24. Cumulative downstream changes in active channel area, 1991-1996 and 2001-2006.

3.5.2. Patterns of Sediment Storage and Connectivity

It is apparent that the 1 in 64 year flood of 1978 has caused long-term, reach-scale channel narrowing, straightening and incision, yet the much larger 1 in 99 year flood of 1994 caused only short-term and localised corrections to these overall trajectories. By fixing the channel within its mid-reach bedrock corridor, and imposing lateral and vertical constraint on channel adjustment, the 1978 flood has created discontinuity in the propensity and the capacity of the channel to adjust, particularly in response to subsequent large flood events. Zones 2 and 4 have undergone consistent patterns of channel expansion and constriction (section 3.4.2.4, figure 3.18) while zone 3 appears to be more dynamic in terms of change in elevation (section 3.4.1.3, figure 3.9B). This appears to have controlled differences in the storage and transport of sediment along the reach and thus the behaviour of the zones is an important control on how changes in flood activity and sediment load are propagated downstream.

3.5.2.1. Sub-reach connectivity through time

It is hypothesised that the mid-reach zone 3 corridor has been the most important control on the evolution of channel zonation. The transfer of bedload from zones 1 and 2 to downstream zones 4 and 5 appears to have been facilitated by the relative competence of this narrow bedrock channel. This dynamic suggests a pattern of sub-reach sediment connectivity between zones 2, 3 and 4, which have acted as source, transfer and accumulation zones, respectively (figure 3.25).

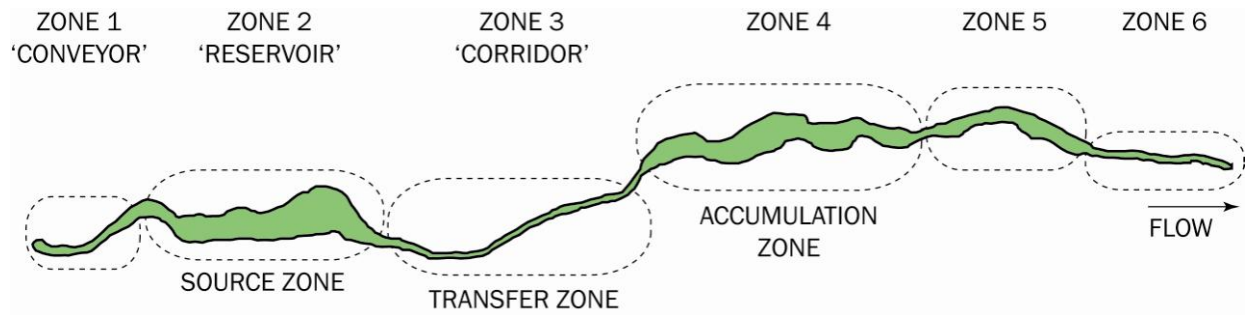


Figure 3.25. Hypothesised sediment connectivity between Luc and Recoubeau.

Between **1948** and **2001**, the accumulation of sediment in zone 4 is indicated by channel expansion (a 61 % increase in total channel area) and a clear increase in sinuosity through time (figure 3.3). The increase in total channel area of zone 4 is matched by a 75 % increase in active channel area, alongside a substantial increase in the area of mid-channel vegetation (figure 3.3). There is further field evidence of sedimentation in unit bars and a wide range of surface grain sizes across the zone (figure 2.9C). During the same epoch, a 19 % reduction in the total channel area of zone 2, in addition to channel incision (maximum -1.6 m, figure 3.9A) and channel straightening (figure 3.3) suggests that sediment was being sourced from this upstream part of the channel for redistribution downstream.

Upstream of zone 2, the channel in zone 1 is bedrock, with patches of alluvial cover. There are no storage areas for bedload like those in zone 3, however. When sediment is supplied to the reach, it appears to be readily conveyed downstream to zone 2. The supply of sediment to zone 2, and stocking of this upstream reservoir is thus dependent on the external, upstream supply to the reach. Since the channel in zone 1 incised to bedrock, it is likely that this situation has changed relatively little. Pettit tests were used to identify zone boundaries in antecedent years for which no ground observation is available (section 3.4.2.2). The test first identified a significant boundary between present-day zones 1 and 2 in 1971 (figure 3.18, section 3.4.2.3), and there has been little change in planform since then. It is also feasible that the 1978 flood caused substantial scour of the channel in zone 1, exposing bedrock, and that incision in zone 1 rapidly increased following the construction of the upstream weir shortly before 1991, and during the flood of 1994. In light of these observations it is reasonable to suppose that zone 1 has been efficiently conveying bedload into the zone 2 reservoir at least since 1971.

It can be seen that the configuration of sediment source, transfer and accumulation between zones 2, 3 and 4 facilitates zones 2 and 4 to be 'well-coupled' (Harvey 2002, Hooke 2003) and so any changes that occur in the upstream part of the reach, specifically changes in bedload supply, will be effectively propagated downstream, and seen in the behaviour of the channel zones.

3.5.2.2. Recent changes in sub-reach connectivity, 2001 – 2006.

Channel adjustments seen between **2001** and **2006** suggest that the nature of connectivity, in terms of the dynamics of bedload redistribution between the zones, has changed. Zone-scale adjustments in planform indicate that the upstream supply of sediment had become so scarce that by 2001 the channel was availability-limited (*sensu* Ferguson 2008). It appears that the transfer and storage of sediment along the reach is no longer operating at the zone scale, with bedload being locally sourced from wherever it is available.

Between 2001 and 2006, zone 4 constricted by -18 % and the channel in zone 5 underwent expansion (14 %). Within this period, between 2003 and 2005, incision through zone 4 approached -1 m, and localised aggradation occurred in zone 5 (average +0.25 m) (figure 3.9B). It is possible that channel incision and constriction in zone 4, and aggradation and expansion in zone 5 reflects the sourcing of sediment from zone 4, particularly within the upper part, and downstream redistribution in zone 5 (figures 4.3 and 4.9B). It is hypothesised that this has been caused in response to an insufficient supply of sediment from the zone 2 reservoir, as the substantial decrease in sediment supply has reduced volumes available for downstream redistribution. There has also been substantial incision in zone 2. In 2003, the second largest flood of the study period did not reactivate the wide left bar in zone 2, and instead the channel narrowed and straightened. This indicates the resistance of the left bank to flood-induced removal, and further suggests that the channel had incised beneath the bar, which was becoming part of the floodplain. The long-term transport of sediment is dominated by the availability of floodplain sediments (Ham and Church 2000) and the disconnection between the channel and the floodplain in zone 2 has rendered the sediment stored in the wide, alluvial zone 2 reservoir inaccessible for distribution downstream to zone 4 (Madej *et al.* 2009).

The routing of the 1978 flood along the right side of the channel boundary appears to have initiated incision and the disconnection between the channel and the left bank in zone 2. It is also apparent that this has controlled channel narrowing and constriction of the channel boundary in zone 2, by permitting vegetation to establish on the left bank and join the floodplain. Vegetation encroachment has also increased the resistance of the left bank to flood-induced erosion. This process can be seen in distinctive age bands of vegetation bordering zone 2, within the envelope delineating the maximum channel boundary (figure 3.7B). In 2008, the outer band of forest is older than 60 years (Gagnage 2008), suggesting it was established prior to 1948 and has been undisturbed since. The youngest forest bordering the channel is less than 5 years old (*idem*) and has thus become established since 2003. The age of the riparian forest therefore increases systematically with distance from the wetted channel, and this progressive encroachment suggests that the channel has been incising below the riparian terrace through time. The reciprocal resistance of the right bank has also contributed to incision and straightening in zone 2, by funnelling the channel into a chute

along the right bank (figure 2.7B). It is apparent that the channel was locked into this chute by 2001 (figure 3.3).

Between 2001 and 2006, a small section the right bank was eroded, and likely caused by the relative stream power of the incised chute, during the 2003 flood (figure 3.26, arrow A and grey shaded area). It is apparent that by 2003 the competence of the chute has increased, because the section of channel bank removed by the 2003 flood was unaffected by the 1 in 99 year flood of 1994. The local avulsion of the right bank provides further evidence of the type of flood-induced erosion hypothesised to have sculpted the mid-reach corridor (section 3.5.1.1). It is unlikely that that it was caused by the upstream regression of incision from zone 3. In degrading Tuscan rivers the upstream migration of degradation was prevented by alternating bedrock-controlled and alluvial reaches (Rinaldi 2003) and similar structural constraint is imposed by bedrock at the transition between zones 2 and 3.

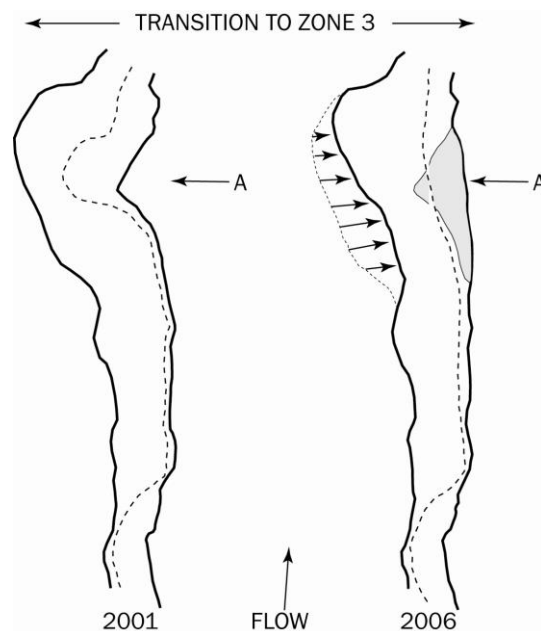


Figure 3.26. Change in the total channel boundary (solid outline) of zone 2, 2001-2006. Vertical, dashed centreline indicates course of low-flow active channel. Dotted line and arrows on left of 2006 sketch indicate change in total channel boundary and extent of vegetation encroachment. Spatial position of arrow A is the same on both sketches to indicate the extent of channel bank removed (grey shaded area) between 2001 and 2006.

In response to the 2003 flood, the constriction of the left bank channel boundary provides further evidence that vegetation encroachment and establishment is an important mechanism that causes channel incision, by stabilising bar surfaces and increasing channel bank resistance to flood-induced removal (figure 3.26, dashed arrows and dotted area) (Gregory and Gurnell 1988, Friedman *et al.* 1996, Pollen *et al.* 2004). Once initiated, channel incision then appears to control channel narrowing, by increasing the relative elevation between the channel and bar and bank tops and thus disconnecting the channel from formerly active channel areas, which in turn causes less frequent overbank inundation, permitting

undisturbed vegetation establishment and eventually channel constriction as successions join the riparian floodplain.

This process can be seen in the different variability in active width, and different overall amounts of change in active width that occurred between zone 2 and zone 4, until 2001 (section 3.4.2.4, figure 3.18). Incision in zone 2 has disconnected the active channel from former channel and floodplain areas, enabling progressive vegetation encroachment, channel constriction and straightening. In contrast, patterns of channel narrowing and expansion in zone 4 have been less systematic through time. There is no clear temporal pattern of vegetation establishment in zone 4 suggesting that the accumulation of sediment in zone 4 and frequent disturbance of lateral channel areas has maintained a connection between the channel and the floodplain for a greater length of time. Until 2001, the more frequent reworking of lateral bars has precluded the encroachment of vegetation and limited incision. However, between 2001 and 2006, in response to the reduced availability of bedload from the zone 2 reservoir, and the sourcing of sediment from the upper part of zone 4, this former zone of accumulation has undergone incision and channel constriction. During the latter part of this period, there was remarkable field evidence of how a reduction in sediment yield and flood activity permits vegetation establishment. Between October 2005 and May 2006 bankfull discharge ($Q_{1.5}$ 1948-2006, $19.9 \text{ m}^3 \text{ s}^{-1}$) was not attained on any given day, and in twenty months the rapid succession of mid-channel vegetation on a mid-channel bar in zone 4 was clear (figure 3.27).

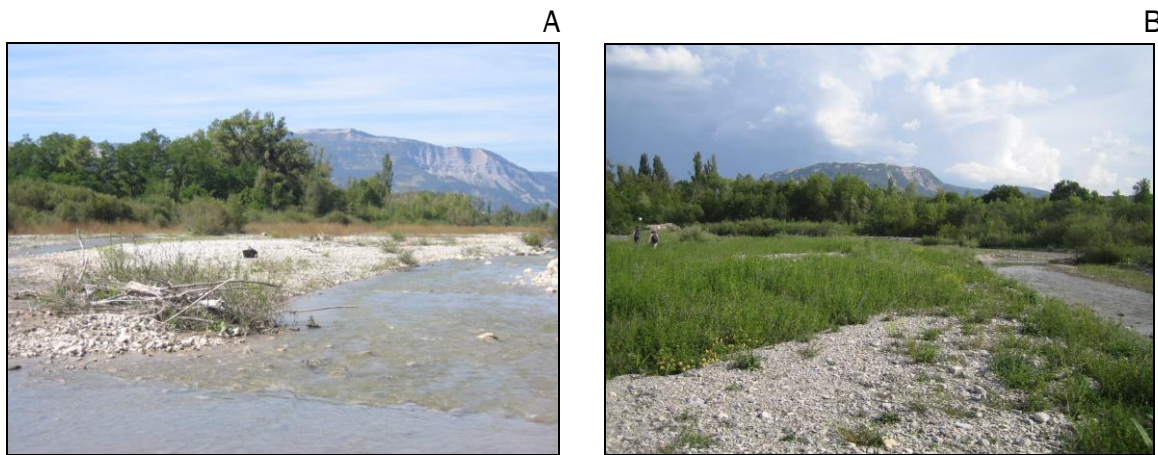


Figure 3.27. Rapid vegetation establishment in zone 4. The same mid-channel bar seen from (A) upstream in September 2005 and (B) downstream in May 2006.

3.5.3. Potential Trajectories of Future Change

By 2006 it appears that trajectories of channel narrowing, straightening and incision that were initiated by the 1978 flood have been further reinforced, and progressed to become ongoing, reach-scale trends. The overall reduction in sinuosity from 1.17 in 1971 to 1.07 in 2006 appears modest (figure 3.8), but the contrast in channel planform between 1971 and

2006 is clear (figure 3.7B). While the different channel zones are distinct at the present time, ongoing, reach-scale channel incision continues to disconnect the channel from the floodplain in zones 2 to 5, . This has encouraged the encroachment of vegetation on lateral channel areas, and caused channel constriction and straightening in zones 2 and 4. Between 2001 and 2006, the right bank avulsion (figure 3.26) and left bank constriction account for the narrowing and straightening of the channel downstream in zone 2, which, together with narrowing and straightening in zone 4, and widening in zone 5, give the impression that the mid-reach is elongating. It appears that there has been a reduction in the distinctiveness of the channel zones, and that ongoing channel incision and narrowing will generate a tripartite channel structure of upstream, mid-reach and downstream sub-reaches (figure 3.28).

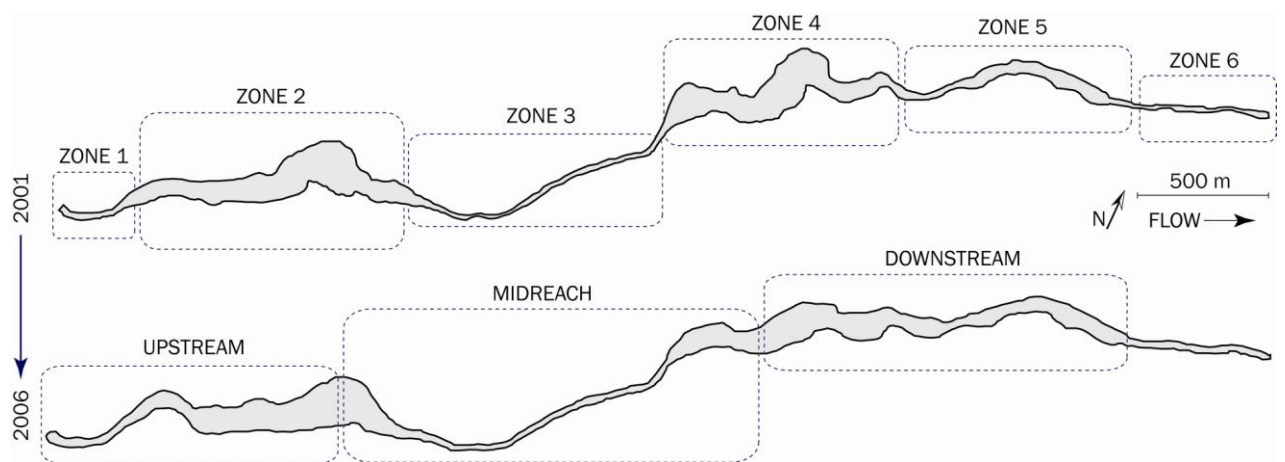


Figure 3.28. Between 2001 and 2006 zone-scale changes in planform appear to have reduced the distinction of the channel zones, such that a tripartite structure of upstream, mid-reach and downstream sub-reaches is apparent.

At present, the diverse channel morphology of the reach creates an ecotone between the upper and lower Drôme. During the next five years, if the channel undergoes the same reduction in sinuosity that occurred between 2001 and 2006, then by 2011 the reach would undergo the same amount of reach-scale straightening seen between 1971 and 1980. An associated reach-scale reduction in the diversity of channel hydromorphology would have critical implications for in-stream ecology, both along the reach between Luc and Recoubeau, and in downstream reaches of the Drôme. The historical development of channel zonation between Luc and Recoubeau could thus be interpreted as a succession of stages along a trajectory of overall degradation, as the reach tends to a straight, narrow and incised conduit, linking upstream and downstream reaches of the Drôme. However, this interpretation does not allow for the critical importance of variability in channel constraint and channel structure, which causes variable sub-reach adjustments.

Overall reach-scale changes affirm the generalised trends of channel constriction, narrowing and incision documented both within the Drôme and in other catchments, in response to a bedload deficit caused by afforestation and check dam installation (Landon 1999, Lach and Wyzga 2002, Liébault and Piégay 2002, Liébault 2003, Keesstra *et al.* 2005, Vanacker *et al.* 2005, Boix-Fayos *et al.* 2007) and gravel mining (Rinaldi *et al.* 2005, Rovira *et al.* 2005, Wishart *et al.* 2008). Between Luc-en-Diois and Recoubeau, the relative importance of these independent causes is difficult to isolate. Each has contributed to the observed changes in channel planform but it is clear that they have not had a uniform effect. In response to these influences channel adjustments cannot be generalised at the reach scale. Without accounting for local controls on change in channel form, observations of overall constriction and incision may obscure important sub-reach processes that are fundamental to reach-scale channel evolution.

The development of channel zonation has also been contingent on the relative timing and sequence of larger-scale changes operating externally to the reach, and the sensitivity of the channel at the time of flood impact. This also highlights the importance of the connection between the study reach and the Béoix sub-catchment, specifically in terms of sediment supply, and thus the importance of long-term and larger-scale controls on change in patterns of bedload redistribution and channel connectivity through time. This perspective of channel evolution permits an understanding of present-day channel form and process and provides a robust basis from which to project future channel adjustments. This will be undertaken in chapter 5.

3.5.4. Summary: Channel Evolution between Luc and Recoubeau, 1948-2006

Between 1948 and 2006, reach-scale changes between Luc and Recoubeau can be summarised by three main phases, which centre around a threshold hypothesised to have been crossed in 1978, in response to substantial flood-induced avulsion and incision (figure 3.29).

Photo epoch 1948 – 1980

Between 1948 and 1980, the reach underwent channel constriction and a substantial decrease in the proportion of active channel area, that by 1971 can be explained by establishment of mid-channel vegetation. During this period, a substantial reduction in sediment supply to the reach and relatively frequent bankfull flows (a maximum of 37 days between 1956 and 1971) likely produced a much reduced and heterogeneous alluvial cover, as locally available sediment was redistributed within the reach. Sediment was likely sourced from upstream zones for redistribution in downstream zones, but it is apparent that this reach-scale transfer was impeded by a mid-reach channel bottleneck. It is also possible that there were local, unauthorised gravel extractions from the upstream part of the channel during this

time. In addition to local variation in sediment availability, local variation in the relative elevation of underlying bedrock may have contributed to an uneven pattern of channel sensitivity to change. The combination of these internal and external influences appears to have primed the channel for substantial erosion during the 1978 flood event.

Photo epoch 1980 – 2001

Between 1971 and 1980 a straight and narrow channel had developed through the right bank floodplain in zone 3. It is hypothesised that it was sculpted by avulsion during the flood event of 1978. This mid-reach corridor appears to have mediated the subsequent evolution of the channel, by controlling the downstream redistribution of sediment. It is hypothesised that present-day zonation reflects the dynamics of sediment source, transfer and accumulation, between zones 2, 3 and 4. It is apparent that the 1978 flood also caused reach-scale straightening and narrowing, and incised the active channel along the right side of the channel boundary. This has also had an important long-term effect on subsequent channel evolution, by initiating a disconnection between the channel and the left bank. It is also apparent that this permitted a lengthy period of undisturbed vegetation encroachment along the left side of the channel boundary, which can account for the considerable channel constriction seen between 1980 and 1991. This further strengthened bank resistance to erosion, promoting further channel incision. By 1991 bedload supply to the channel had been further reduced by the construction of a weir immediately upstream of the reach, and the channel had undergone a substantial reduction in flood activity. Between 1991 and 2001 a rapid decrease in the area of mid-channel vegetation is considered to reflect an increase in stream power in the increasingly incised channel. During the large flood of 1994 it is considered that the reach may have undergone substantial incision where bedrock was exposed and sediment was locally available to scour the channel bed. Some lateral channel areas were reactivated by the flood, maintaining the distinction between wider and narrower zones.

Photo epoch 2001 – 2006

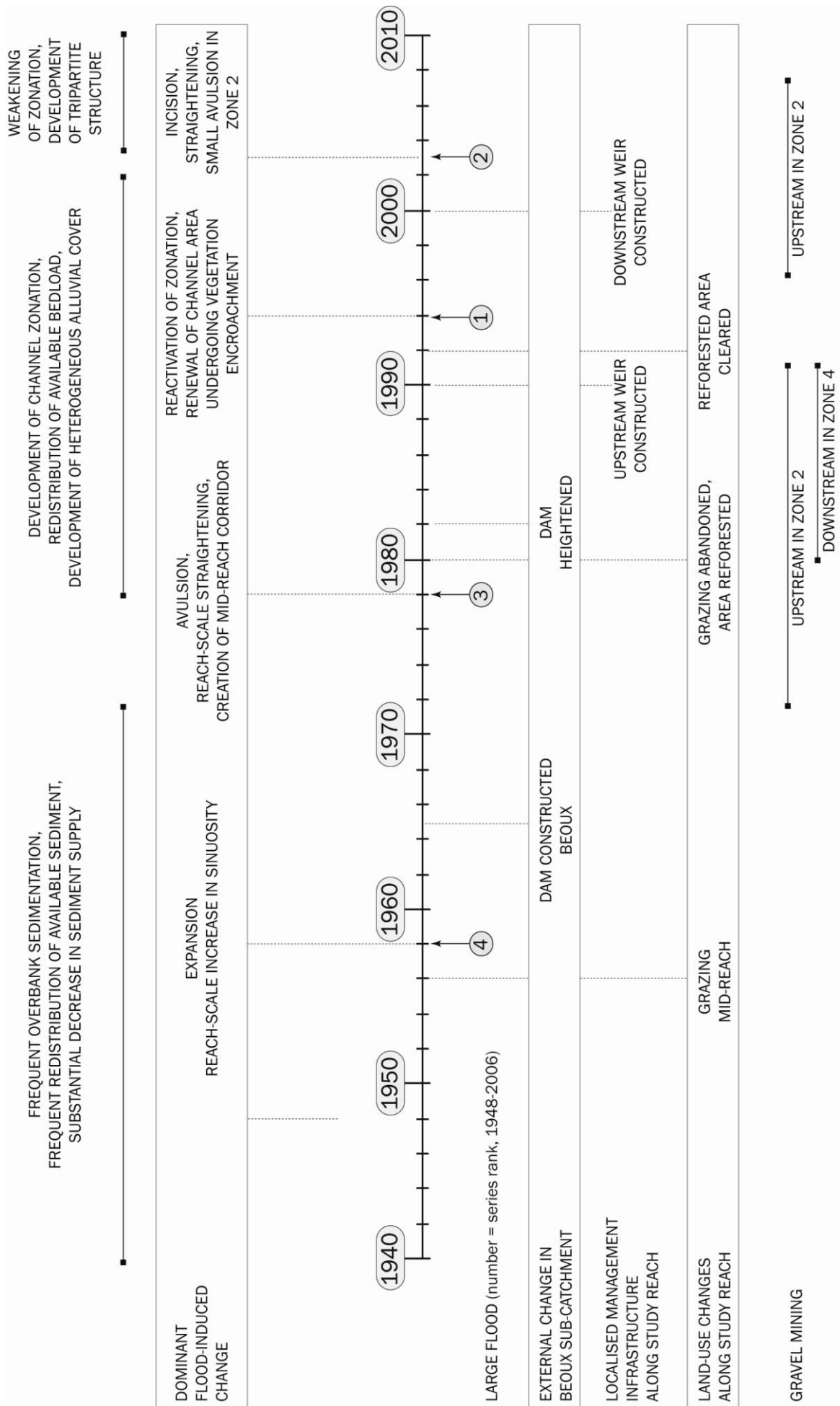
By 2001 there was very limited bedload supply to the reach. During the latter five years of the study period substantial incision and constriction in zone 2 indicates that the channel has disconnected from the alluvial floodplain stores of this upstream reservoir. Channel narrowing and incision through the upstream part of zone 4 and expansion and aggradation in zone 5 suggests that zone 4 is no longer an accumulation zone but is providing bedload for downstream redistribution. These changes in channel planform in zones 2, 4 and 5 has reduced the distinctiveness of the channel zones and in response to reach-scale trajectories of straightening and incision the channel appears to be developing a tripartite structure of sub-reaches.

3.6. Chapter Conclusions

In response to the chapter aims outlined in section 3.2, this chapter has established:

- Between 1948 and 2006 there has been distinct spatio-temporal variability within overall trends of channel constriction, narrowing and straightening. Abrupt downstream transitions occur between channel zones that have undergone different overall directions and amounts of morphological change.
- It is hypothesised that the 1978 flood was the catalyst of present-day pattern of channel zonation, by causing substantial reach-scale incision and straightening and sculpting a narrow channel through the right bank of the mid-reach. This transfer zone has since controlled the distribution of bedload along the reach.
- The evolution of zonation has been further shaped by substantial reductions in sediment supply and flood frequency, in response to long-term land use changes in the B  oux sub-catchment.
- Between 2001 and 2006 reach-scale straightening and incision appears to be reducing the distinction between channel zones (especially through the central part of the reach in zones 2, 3 and 4) and suggests that the reach may be developing a tripartite structure of sub-reaches.

Figure 3.29 (following page) *Summary timeline of dominant controls on morphological evolution between Luc and Recoubeau, 1948-2006.*



4. Present-Day Macroinvertebrate Community Organisation between Luc-en-Diois and Recoubeau-Jansac

4.1. Introduction

The overall aims of this chapter are to characterise present-day in-stream macroinvertebrate community organisation along the study reach, and identify whether present-day morphological zonation that characterises the channel (chapter 2) is reflected in the distribution of macroinvertebrate taxa. In the context of management plans to reactivate the dominant supply of bedload to the channel, it is of particular interest as to whether the zones are characterised by distinctive macroinvertebrate communities, because the introduction of sediment will involve changes in channel morphology, and also the in-stream macroinvertebrate community. It is not yet clear how this management intervention may impact the in-stream macroinvertebrate community because the present-day organisation of macroinvertebrate taxa is currently unknown.

The present-day morphological zonation has developed through time as a function of local discontinuity in the capacity of the channel to adjust, and the redistribution of bedload between zones of sediment source, transfer and accumulation (chapter 3). More recent changes in channel planform, of reach-scale straightening and narrowing (section 3.5.3) indicate a change in these dynamics. The distinction between the zones appears to be declining, such that the reach is tending toward a tripartite pattern of upstream, mid-reach and downstream sub-reaches. This sub-reach structure is also of particular interest because it may indicate that the channel is already in transition, thereby adding to the importance of understanding how the present-day macroinvertebrate community is organised along the reach. Combined with the insight of historical and present-day channel behaviour, an understanding of macroinvertebrate community organisation gained in this chapter will enable predictions to be made on the likely future trajectories of morphological and ecological change (chapter 5).

One likely explanation for any spatial structure in macroinvertebrate community organisation is spatial variation in physical characteristics of the reach. Morphological zonation has been visually assessed on account of abrupt changes in planform style and substrate (chapter 2), although it is not clear whether there are significant differences in physical channel characteristics within and between these spatial boundaries. Notwithstanding the main aim of investigating spatial patterns of macroinvertebrate community organisation, this chapter will first examine downstream changes in a range of physical variables (section 4.4.1) to determine whether the two spatial structures of particular interest (zones and sub-reaches) can be differentiated on account of their physical characteristics. This will provide a physical context for the interpretation of how macroinvertebrate communities are organised along the

reach (section 4.4.2), before possible associations between physical channel characteristics and macroinvertebrate community organisation are investigated (section 4.4.3).

4.2. Aims and Objectives

In order to examine the reach-scale organisation of macroinvertebrate taxa between Luc and Recoubeau, and possible associations with physical channel characteristics, this chapter aims to establish:

- Spatial patterns in physical channel characteristics
- Spatial patterns of macroinvertebrate community organisation
- Associations between physical characteristics and the distribution of macroinvertebrate taxa.

4.3. Methodology

To examine reach-scale variation in both physical channel characteristics and macroinvertebrate community organisation, a range of variables were sampled under low flow conditions during August and September 2006 (figure 4.1, table 4.1). The relative stability of low flow conditions optimises the ability to identify distinct habitat units, and so sample the macroinvertebrate communities associated with them.

To remain consistent with the overall objective of understanding spatial variation in macroinvertebrate community organisation, and to avoid confounding patterns by the introduction of temporal variation, macroinvertebrate samples were collected at one time of year over a relatively short period. When identifying spatial patterns of macroinvertebrate organisation, it has been argued that seasonal changes are less important than flow-related variables (Suren and Jowett 2006) and also that temporal variability in hydrological regime is reflected in a spatial dimension of river zonation (Thoms and Parsons 2003). By consistently sampling similar hydraulic environments, the snapshot provided by one season of sampling is considered to represent a 'reference condition' of the present-day reach-scale macroinvertebrate community between Luc and Recoubeau.

With the exception of the possibility of unauthorised gravel extraction, five out of the six morphological zones have been unaffected by anthropogenic disturbances, and have shown dynamic channel adjustments through time (section 3.4.2.3, figure 3.18). However, zone 6, the final 500 m of the reach, has been constrained by a left bank dike and shown little overall change in channel planform during the period of morphological changes examined in chapter 3. Zone 6 has been further impacted by the construction of a small weir at the downstream end of the reach, sometime after 1995. Furthermore, the channel is easily accessible from the road and during the summer months it is frequently disturbed by people that paddle and bathe in it, and create small artificial dams using channel bed materials. The

hydromorphology of the channel along zone 6 is unlike that of the upstream undisturbed channel, and does not exhibit riffle and pool habitats typical of those in zones 1 to 5. As a result, the macroinvertebrate community of zone 6 was not considered to be comparable with that of zones 1 to 5 and has not been examined as part of this study.

Two sites were sampled in each of the five geomorphic zones along the reach, producing a total of ten sites from which to observe both reach-scale and sub-reach variability in both physical variables and macroinvertebrate community structure (figure 4.1).

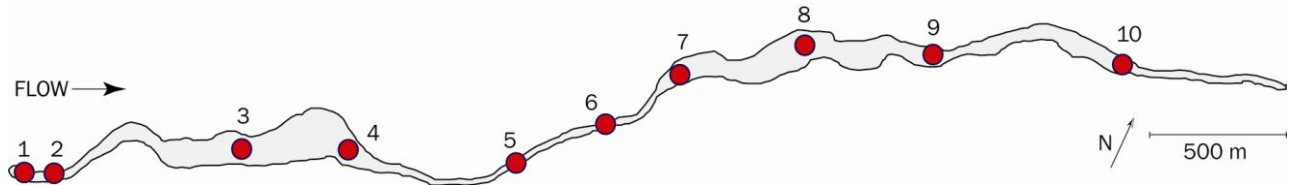


Figure 4.1 Location of the ten sites sampled (numbered).

VARIABLES SAMPLED	<i>n</i> replicates
Macroinvertebrate Surber samples	15
Particulate Organic Matter (POM)	15
Temperature	15
pH	15
Conductivity	15
Benthic Velocity	15
Mean Velocity	15
Surface grain size	1
Subsurface grain size	1

Table 4.1. Variables sampled at each of the ten sites.

4.3.1. Macroinvertebrate Sampling

In order to minimise variation in the physical environment as a possible explanation for spatial variation in macroinvertebrate community organisation, a single habitat type was examined along the reach. Macroinvertebrate communities are commonly recognised to be most abundant and/or diverse in alluvial riffles (e.g. Brown and Brussock 1991, Parsons and Norris 1996, Principe 2008). It has also been identified that in piedmont streams, there are minor differences in bioassessment indices between riffle and other habitat types, suggesting that riffles represent the macroinvertebrate community of a given channel reach (Blocksom *et al.* 2008). In light of these observations, sites characteristic of riffles were chosen over other habitat types commonly recognised in alluvial channels (such as a pools or glides).

In zone 1, samples were collected from patches of gravel lining shallow depressions within the relatively flat, smooth bedrock channel bed. These alluvial patches share common

characteristics with riffles, specifically high Froude numbers and relatively coarse, unconsolidated sediments, but it is apparent that their behaviour and their hyporheic environment is different. The ten sampling locations examined in this study are therefore best described as 'high Froude number sites' (hereafter referred to as sites) rather than riffles, because criteria that are commonly understood to describe riffles do not accurately describe the alluvium sampled over bedrock.

Within each site, fifteen Surber samples (replicates) were collected (Surber area 0.5 m², mesh size 250 µm), producing a total of 150 alluvial samples along the reach. Sampling locations were distributed randomly within each site but progressed systematically from downstream to upstream, to prevent disturbing unsampled areas. Surber sampling is a standard quantitative method used to characterise macroinvertebrate community composition at a given site and, compared to the qualitative method of kick sampling, is more efficient in capturing community richness over a heterogeneous substrate (Storey *et al.* 1991).

The surface layer of bed sediment (a depth of approximately 50 mm) was disturbed by hand and gently cleaned for any attached aquatic invertebrates. All surface grains within the surber frame were removed and retained separately for grain-size measurements. All macroinvertebrates and particulate organic matter collected were retained, filtered into specimen tubes and preserved in 70 % industrial methylated spirit. On return to the laboratory, samples were processed by sorting macroinvertebrates in a standard white tray. All sample particulate matter collected was retained, dried at 60 °C and ashed at 550 °C to determine both organic and inorganic content. Macroinvertebrates were identified under a dissecting microscope to family level, with the exception of Oligochaeta, Hyrundinea, Hydracarina, and early instars (first or second) of Trichoptera, which were identified as such.

The appropriate taxonomic level to which macroinvertebrate communities should be identified has been widely discussed (e.g. Wright *et al.* 1995, Bowman and Bailey 1997, Hewlett 2000, Kitchin 2005). It is generally determined by the spatial scale of interest (Marchant *et al.* 1995, Jacobsen 2004), and the effort permitted by timescales of the study. Biological traits can be accurately described at both genus and family level (Dolédéc *et al.* 2000, Gayraud *et al.* 2003) and so additional biological detail gained by a higher level of resolution may not balance the time cost involved with the 'taxonomic effort' of species level identification (Bailey *et al.* 2001). There is evidence to suggest that significant spatial differences in community structure can be detected using family level data, at larger spatial scales (Bournaud *et al.* 1996), and at smaller scales, in response to gradients of 'sandiness' and conductivity (Metzeling *et al.* 2006), and variation in substrate texture (Downes *et al.* 2000). Other studies have shown that identification to family level can discriminate the degree of anthropogenic impact between sites (Arscott *et al.* 2006) and is adequate to inform reference condition models of community structure (Reece *et al.* 2001). In light of these arguments and because species-specific behavioural information is not required to interpret spatial patterns of community structure, family-level identification is appropriate. Furthermore,

many small sized individuals were collected and it was not possible to accurately identify them beyond family level, so the use of family level reduced the possibility of misidentification and the introduction of ambiguity in to the data set.

Forty macroinvertebrate taxa were identified in 150 samples along the reach (appendix VI). Thirteen rare taxa, with abundance counts ≤ 2 individuals, occurred in $<1\%$ of samples. To reduce noise within the data they were excluded from subsequent analyses (Gauch 1982), reducing the total number of taxa to twenty six.

4.3.2. Hydraulic Variables

At each Surber sample location, flow velocity measurements were recorded in the centre of the sampled area immediately after the collection of macroinvertebrates, using a Sensa RC-2 electromagnetic current meter (ECM). Readings were scanned every ten seconds and averaged from three readings over thirty seconds. To assess the immediate hydraulic environment of the macroinvertebrates collected, *benthic* velocity was recorded as close to the channel bed as possible (probe depth, <0.02 m). In addition, *mean* flow velocity was estimated as that at $0.4 \times$ stage height from the channel bed ($0.6 \times$ depth from the water surface) (Gordon *et al.* 2004) and measured in the same location. Conductivity, pH and water temperature were recorded in the centre of the Surber area after the velocity measurements had been taken, using handheld instruments (Hanna HI-98303 Dist 3 and Hanna HI-98128, accurate to 0.01 pH and $0-1999 \mu\text{S cm}^{-1}$). This data set totalled fifteen measurements of benthic velocity, mean velocity, temperature, pH and conductivity, per sampling site.

4.3.3. Sediment Sampling

To describe the immediate living environment from which macroinvertebrates were collected, all surface grains within the Surber frame were retained from each sample, and pooled to generate a single sample of surface sediment at each site. The average number of grains extracted from the 15 Surber frames varied between sites (average 332 grains, range 143–514 grains). They were then passed through a Wolman template and a single grain-size distribution was calculated for each site.

When the macroinvertebrate sampling was complete, each site was revisited to sample the subsurface sediment using a McNeil sampler (Bunte and Abt 2001). Bulk volumes (average 31 kg) of subsurface sediment were extracted by driving a cylindrical core into the stream bed, and excavating all sediment within this cylinder by hand. A plunger within the cylinder, fitted with a valve that opened as the plunger was depressed and which closed at the bottom of the stroke was used to extract all fine bed sediment suspended in the water contained by the cylinder. Three cores of subsurface sediment were extracted at random locations from each site, and then pooled to generate one large sample of subsurface

sediment. The total mass of sediment extracted at each site was variable as a function of the depth to which the cylinder penetrated the bed (range 22.5–41.3 kg), however grain-size fractions were expressed as a ratio of the total mass extracted. All sediment was sieved into Wentworth fractions and down to 16 mm in the field. All remaining sediment finer than 16 mm was well mixed and a sub-sample of the total mass was taken for precise sieving into smaller fractions and down to silt ($< 63 \mu\text{m}$) on return to the laboratory. Fractions sieved in the laboratory were scaled to those obtained in the field using the ratio of the sub-sample to full sample ($< 16 \text{ mm}$) weight. A single subsurface grain-size distribution was calculated for each site. Variation in both surface and subsurface sediment distributions at each site was described by sorting coefficients calculated using Folk's (1980) inclusive graphic standard deviation.

4.4. Results

Given the three main objectives of evaluating reach-scale spatial patterns in physical variables, ecological variables, and then possible associations between the two (section 4.2), the following results section is organised into three main parts. The first part examines spatial structure in physical variables sampled along the reach (section 4.4.1), the second part examines spatial structure in macroinvertebrate community organisation (section 4.4.2) and associations between the physical variables and macroinvertebrate community structure are examined in the third and final part (section 4.4.3). In their respective sub-sections, longitudinal patterns in physical variables and indices of macroinvertebrate community structure will be individually evaluated for the presence of zonation and/or a tripartite sub-reach structure (figure 4.2). Any differences observed between the five geomorphological zones or the three sub-reaches will be tested for significance using appropriate univariate analysis. To further explore spatial structure using multivariate data sets, and confirm the presence of spatial structures identified in the univariate data, appropriate ordination analyses are also undertaken within each sub-section.

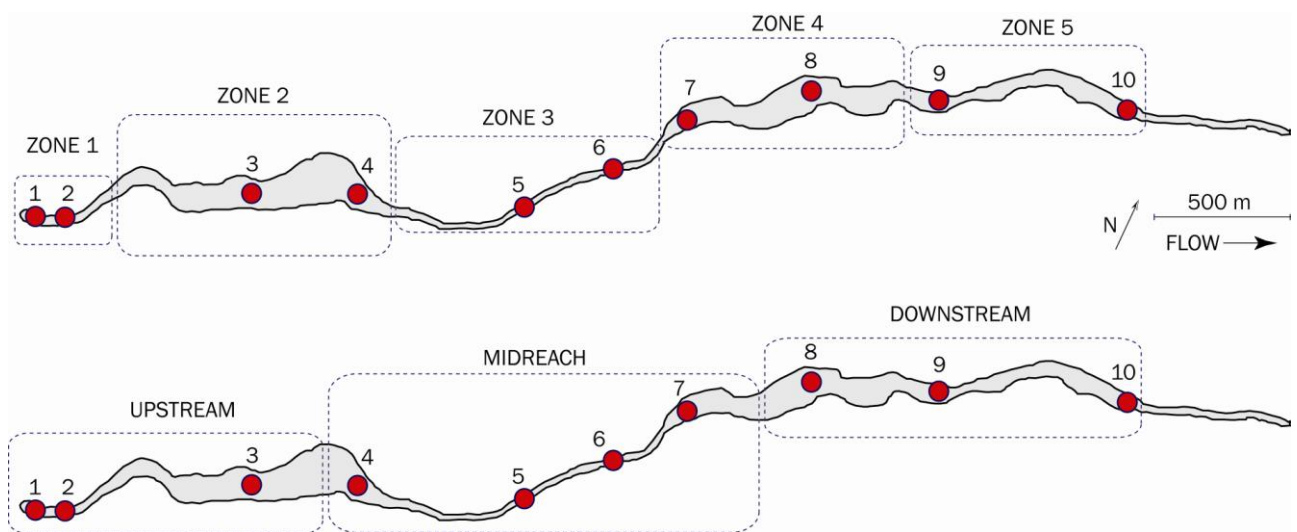


Figure 4.2. The two spatial structures of interest in the data: (A) zonation and (B) sub-reaches. Dashed lines indicate boundaries between the zones and sub-reaches. Numbers indicate sampling site.

4.4.1. Spatial Structure in Physical Variables

Six physical variables were measured at every Surber sample location along the reach ($n = 150$) (table 4.1), of which two (pH and temperature) were excluded from the final analysis. Abnormally high measurements of pH were recorded within and between sites 3 and 6 (figure 4.3), and considered to be erroneous due to equipment failure. There is otherwise no downstream variation in pH and an average measurement of 8.2 was taken to characterise this variable at the reach scale. During the sampling campaign, downstream sites recorded considerably warmer water temperatures than upstream sites, with an average difference of 5.3 °C between sites 1-6 and 7-10 (figure 4.4). Maximum air temperatures attained in the region were considerably higher on days when water temperature was measured at sites 7-10 (figure 4.5) (accessed at <http://climexp.knmi.nl/data/xgdcn61569029001.dat>) and it is therefore most likely that the downstream contrast in water temperature reflects ambient air temperatures rather than some other physical explanation. To avoid distorting subsequent analyses by incorporating this longitudinal difference, temperature was not considered any further.

By excluding pH and temperature, the number of variables for which sample measurements ($n = 150$) are available is reduced to four: POM, benthic and mean velocity, and conductivity (appendix VII). Longitudinal trends in these variables were assessed by using the averages of all fifteen samples collected within a site (appendix VIIIA). Of the entire range of grain-size percentiles calculated for each site, the median and extreme grain sizes of both surface and subsurface distributions were also considered (D_{50} , D_5 , and D_{95}) in addition to the sorting coefficients of both surface and subsurface sediment distributions (appendix VIIIB and C), generating a data set of twelve physical variables (table 4.2). Downstream changes in these twelve physical variables are first examined by observing their individual patterns (section 4.4.1.1).

Benthic velocity
Mean velocity
Conductivity
Particulate Organic Matter (POM)
Surface grain size percentiles (D_5 , D_{50} , D_{95})
Surface sorting coefficient
Sub-surface grain size percentiles (D_5 , D_{50} , D_{95})
Sub-surface sorting coefficient

Table 4.2. Summary of the twelve physical variables examined in the analysis.

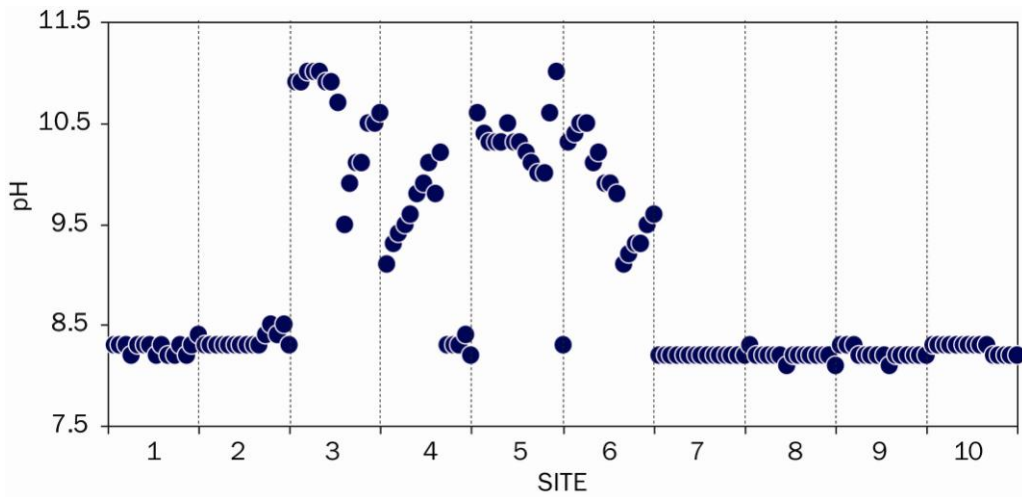


Figure 4.3. Within-site, sample variation in pH. Dashed vertical lines indicate site boundaries.

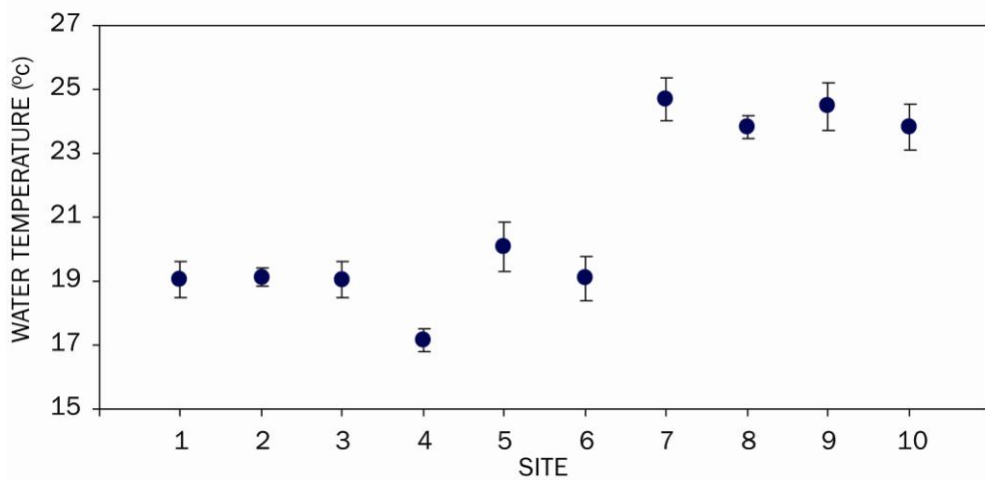


Figure 4.4. Downstream changes in water temperature between sites 1-10. Centrepoint = average, error bars = ± 1 standard error. X axis does not represent distance, but sites are ordered longitudinally.

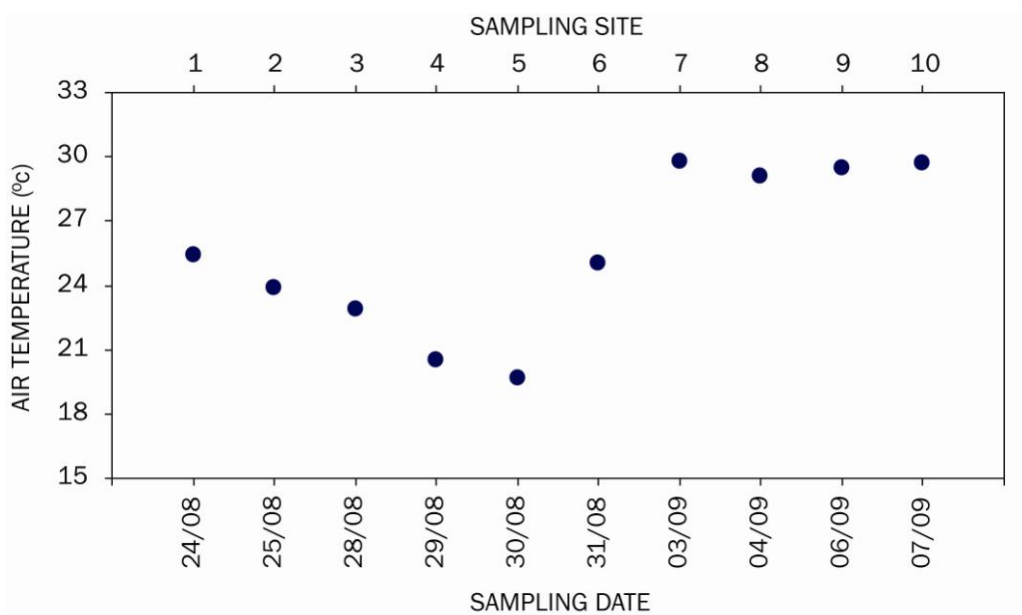


Figure 4.5. Maximum air temperatures recorded at Bron, Lyon, 24 August – 07 September 2006

4.4.1.1. Univariate patterns in physical variables

There is a clear downstream reduction in the average *benthic* velocity recorded at a site, in addition to a downstream reduction in within-site variability of benthic velocity (figure 4.6A). There is greater upstream variation in average benthic velocity recorded between sites 1 and 4, and relatively small variation between sites 5–10. Between sites 1 and 7 there is also an overall reduction in average *mean* velocity (figure 4.6B). This downstream trend is punctuated by small increases between sites, followed by a substantial downstream increase at site 8. The slowest average mean velocity was recorded at sites 5 and 7 and the fastest average mean velocity was measured at sites 2 and 8.

In contrast, a gradual downstream increase in conductivity is seen between sites 1 and 10 (figure 4.6C), albeit with an anomalously high value at site 2. Relatively high variation in conductivity was recorded within upstream sites 1 and 2, mid-reach sites 5 and 6, and at downstream site 9.

There is substantial variation in the amount of POM collected in all 150 Surber samples along the reach (minimum 0.16 g, maximum 3.16 g), with a mass ≥ 1 g retained in only nine percent of samples, however there is an overall downstream reduction in the average mass collected at each site (figure 4.6D). Sites 1 and 3, in particular, yielded high masses of POM (approximately 0.8 and 1.1 g, respectively) and with the exception of a notable increase at site 8, masses at the remaining sites are quite consistent, averaging approximately 0.4 g. Within-site variability tends to be high at those sites with high mean values.

There is little overall downstream change in *surface* grain-size percentiles and sorting between sites 1 and 10 (figure 4.7 A–C). However, downstream changes in these coefficients are characterised by ‘sawtooth’ patterns that may reflect sub-reach processes of sediment transfer and storage along the reach (figure 3.25). This is most apparent for D_{95} which increases between sites 1 and 4, declines systematically through the mid-reach and increases between sites 7 and 10. This pattern is largely consistent with downstream changes in the surface sorting coefficient, D_5 and D_{50} . In particular, the mid reach (sites 4–7) is characterised by a marked decline in grain size and an improvement in sorting.

There is little downstream variation in *subsurface* D_5 , D_{95} or sorting (figure 4.8), although site 6 exhibits relatively poorly sorted sediment and site 8 exhibits relatively well sorted material. There is also an abrupt increase in the subsurface D_5 at site 8. In contrast, there is an overall downstream reduction in subsurface D_{50} that is disturbed through the mid-reach: there is downstream fining between sites 1–4, wide variation between sites 5 and 7, before systematic downstream fining recommences between sites 7–10.

Downstream changes in the twelve physical variables sampled along the reach show some weak longitudinal gradients between the ten sites. It is clear by observing figures 4.6–4.8 that site pairs within each of the five zones are not characterised by similar average values, and that the data does not reflect a pattern of zonation. However, certain variables appear to be structured by a pattern of upstream (sites 1–3), mid-reach (sites 4–7) and

downstream (sites 8–10) sub-reaches. Rather than indicate differences in physical characteristics of the zones, therefore, the data appears to reflect a differentiation in channel planform between upstream, mid-reach and downstream sub-reaches that has developed more recently (sections 3.5.2.2 and 3.5.3). Differences in all twelve physical variables were tested for significance between the three sub-reaches, using a weighted parametric test (Welch’s ANOVA), to conform to the heteroscedasticity of the data.

Welch’s ANOVA (in all instances, $\alpha = 0.05$) indicated that overall differences in POM, benthic velocity and mean velocity are significant between upstream, mid-reach and downstream sub-reaches. There are no significant differences in conductivity between the sub-reaches (table 4.3). Dunnett’s T3 post-hoc tests (in all instances, $\alpha = 0.05$) indicated that sample masses of POM are significantly higher in the upstream sub-reach than in the mid-reach. There are no significant differences in POM between the mid-reach and downstream sub-reach. The difference in mean sample masses of POM between upstream and downstream sub-reaches is large, but not significant ($p = 0.058$) (table 4.4A). The upstream sub-reach recorded significantly faster benthic velocity than the mid-reach and downstream sub-reach. There is no significant difference in benthic velocity between mid-reach and downstream sub-reaches (table 4.4B). Although Welch’s ANOVA indicated that overall differences in mean velocity between the sub-reaches are significant, Dunnett’s T3 post-hoc tests did not reveal any further significant differences when pairwise tests between individual sub-reaches were made. Welch’s ANOVA indicated that there are no overall significant differences in either surface or subsurface grain-size characteristics between the upstream, mid-reach and downstream sub-reaches.

INDEX	p VALUE
POM	0.001
Benthic Velocity	0.000
Mean Velocity	0.046
Conductivity	0.591

Table 4.3. Significance scores (Welch’s ANOVA, $\alpha 0.05$) of differences in the mean sample values of POM, benthic velocity, mean velocity and conductivity, between upstream, mid-reach and downstream sub-reaches.

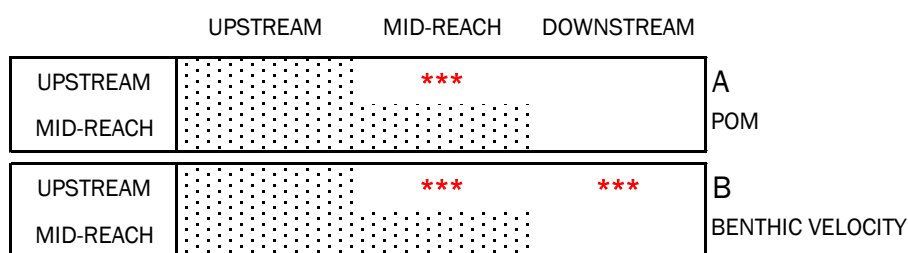


Table 4.4. Three asterisks (***) indicate a significant (Dunnett’s T3 post-hoc tests, $\alpha 0.05$) difference in the mean values of (A) POM and (B) benthic velocity between upstream, mid-reach and downstream sub-reaches.

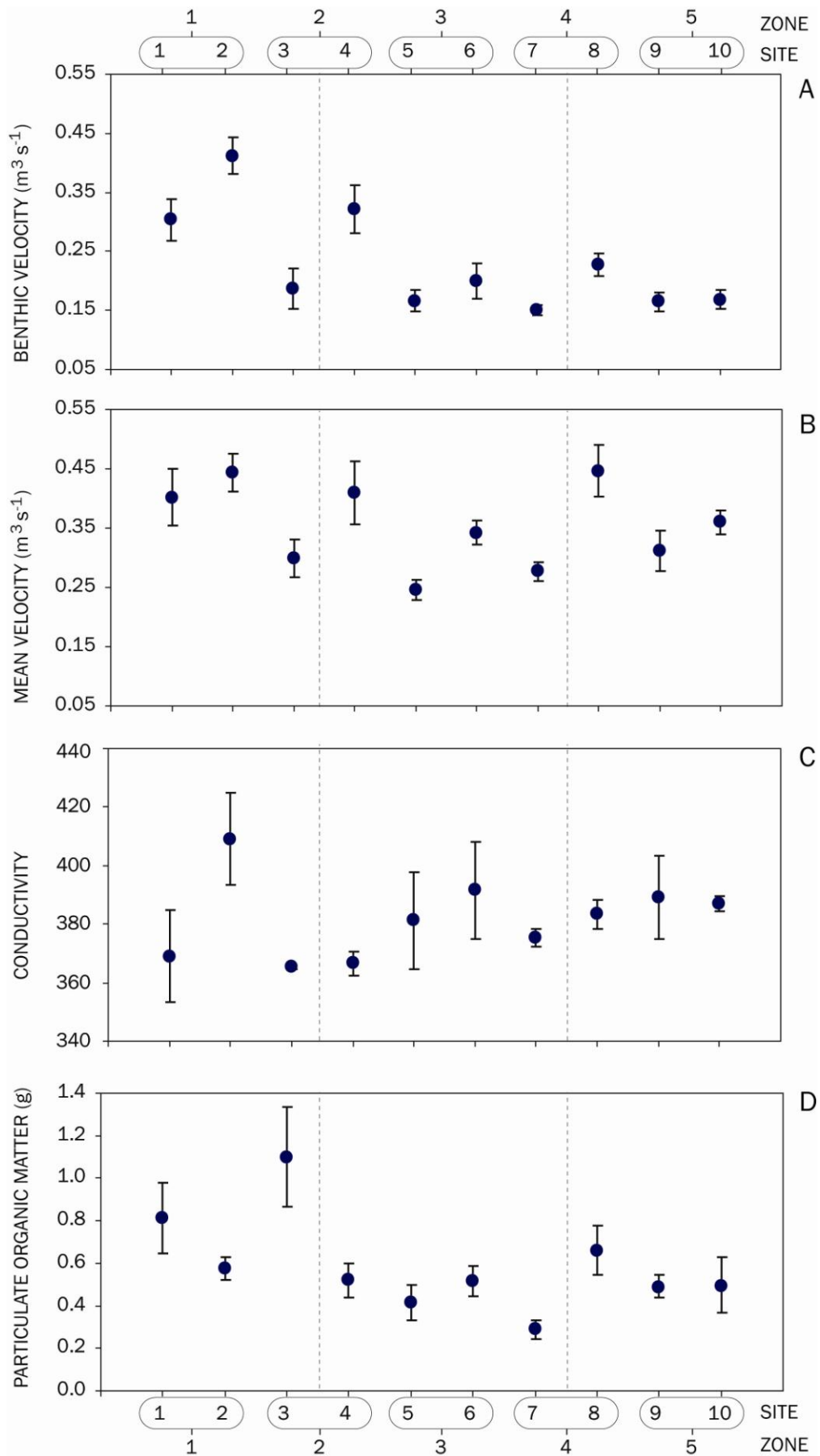


Figure 4.6. Downstream changes in (A) benthic velocity, (B) mean velocity, (C) conductivity and (D) sample organic mass between all ten sites. Centrepoin = average, error bars ± 1 standard error. Zones are indicated and the dashed vertical lines indicate sub-reach boundaries.

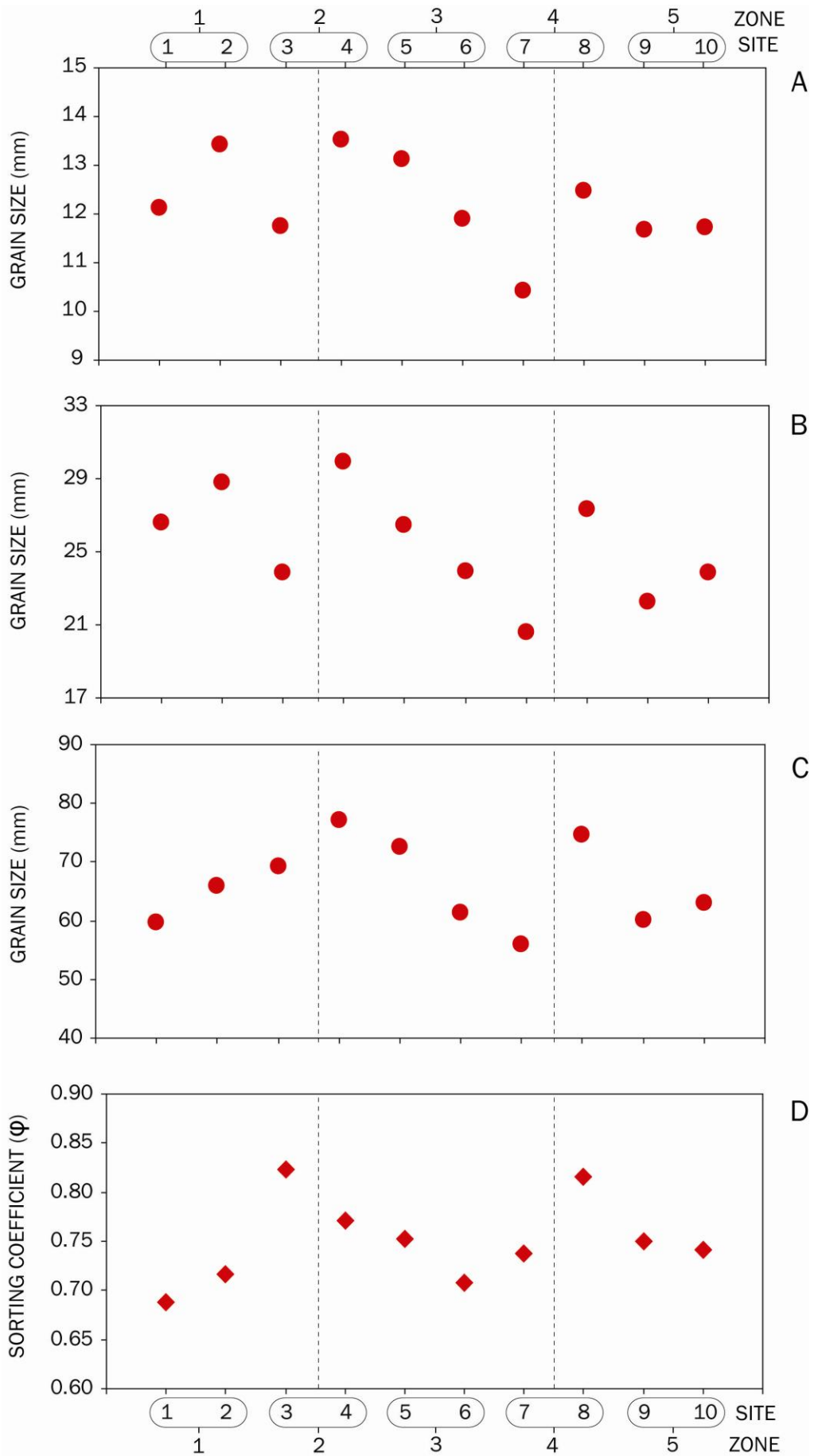


Figure 4.7. Downstream changes in **surface** sediment percentiles (A) D_5 , (B) D_{50} , (C) D_{95} and (D) Folk's sorting coefficient between all ten sites. Zones are indicated and the dashed vertical lines indicate sub-reach boundaries.

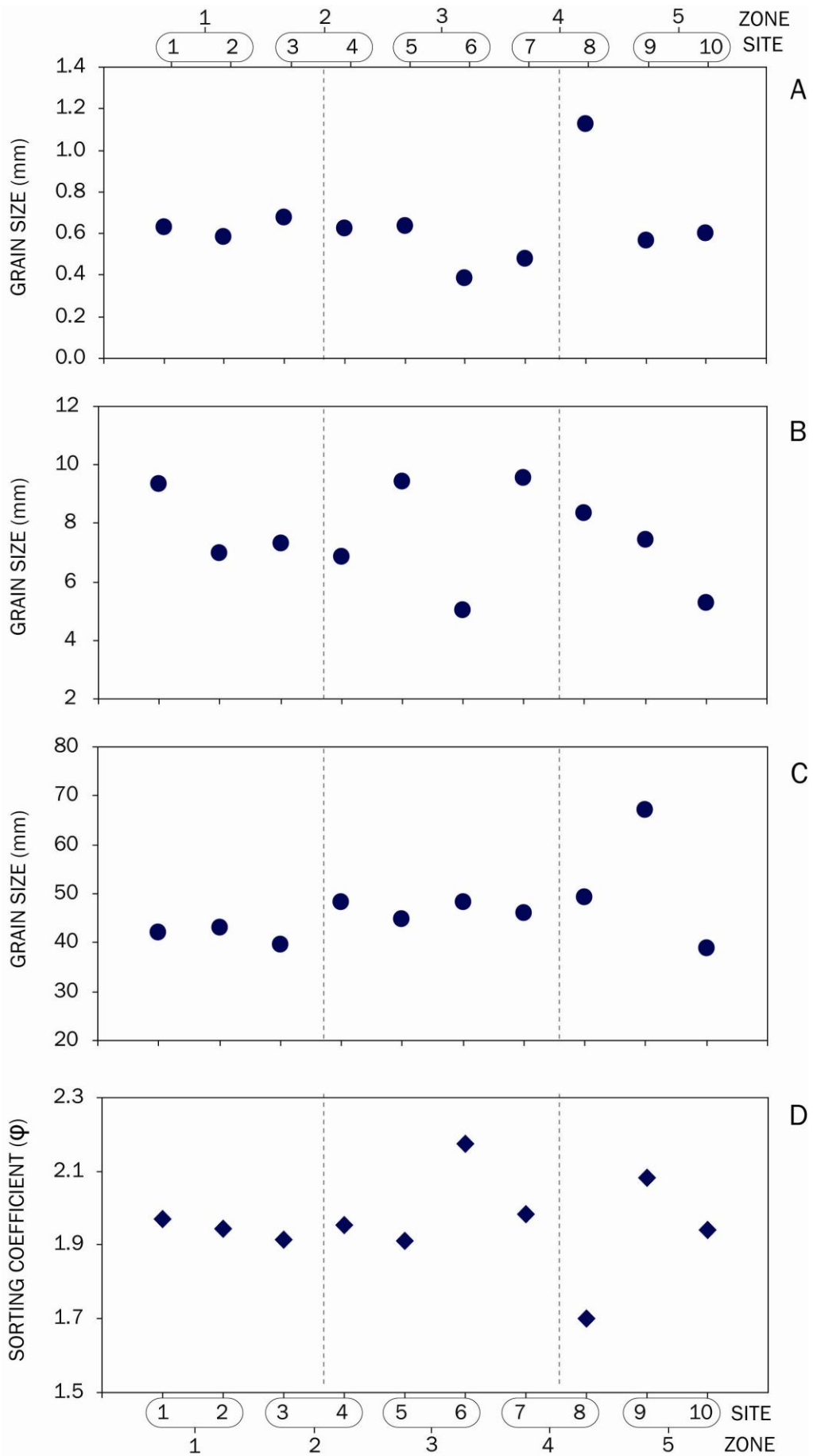


Figure 4.8 Downstream changes in **subsurface** sediment percentiles (A) D_5 , (B) D_{50} , (C) D_{95} and (D) Folk's sorting coefficient between all ten sites. Zones are indicated and the dashed vertical lines indicate sub-reach boundaries.

To identify any reach-scale gradients using the combination of all physical variables, and confirm the sub-reach patterns apparent in the univariate data, two separate sets of Principal Components Analysis (PCA) were undertaken. Section 4.4.1.2 first examines spatial structure using the four variables for which sample data ($n = 150$) is available (POM, benthic velocity, mean velocity, and conductivity). Section 4.4.1.3 examines spatial structure in site-scale data, using site averages of the same four variables, in addition to grain-size characteristics (table 4.2).

4.4.1.2. Multivariate gradients in physical variables using all sample data

When PCA was undertaken using the four variables for which sample data is available ($n = 150$), the output did not indicate any clear spatial structure associated with sites, zones or sub-reaches. The majority of samples overlap each other around the centre of the axes, indicating that they have relatively similar physical characteristics, and confirming that all Surber sample locations from which macroinvertebrates were collected were very similar. Certain samples were separated from this central cluster, however, on account of their variation in benthic velocity and POM (figure 4.9). The differentiation of these samples along axes 1 and 2 can explain 85 % of the variation in the data (table 4.5). Regardless of their longitudinal position along the reach, samples with unusually high sample masses of POM (> 2 g, figure 4.6D) are scattered along axis 1. A number of upstream samples from sites 1 and 2 are also separated from the main sample cluster along axis 2, on account of faster benthic flows (figure 4.6A).

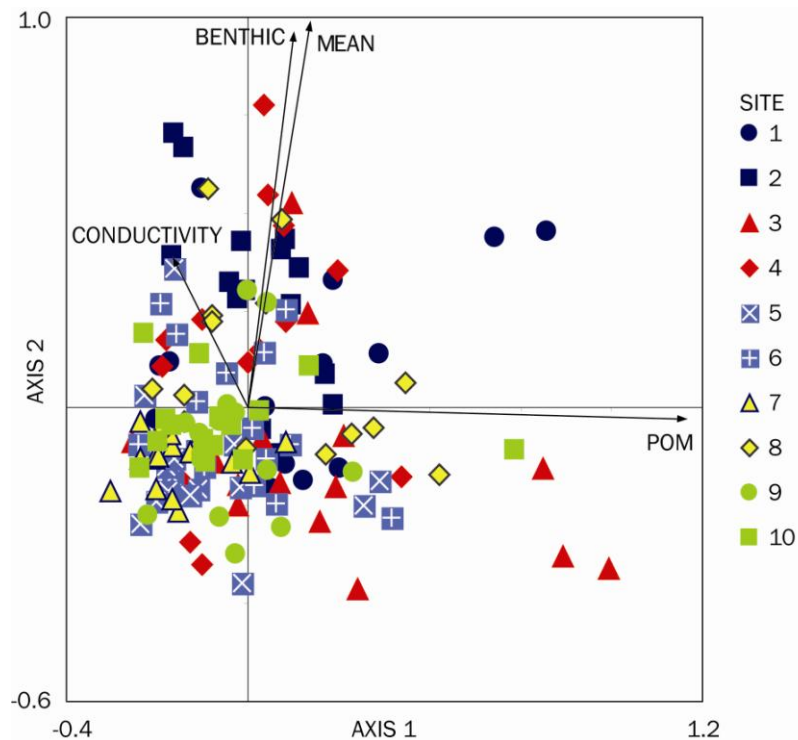


Figure 4.9 PCA using all sample data ($n = 150$).

AXIS	1	2	3	4
EIGENVALUES	0.67	0.19	0.11	0.04
CUMULATIVE VARIANCE OF DATA (%)	66.7	85.2	96.0	100.0

Table 4.5. Axes scores of variation in the sample distribution established by PCA using all sample data.

4.4.1.3. Multivariate gradients in physical variables using site-scale data

When PCA was undertaken using site-scale data, there was also no clear longitudinal pattern in the output, or any spatial structure associated with zones or sub-reaches (figure 4.10). Sites were associated with physical gradients on account of their atypical physical characteristics. Sites 6 and 10, and sites 1 and 5 plot as two separate pairs at opposite ends of axis 1. The association of these two separate groups with the *subsurface* D_{50} gradient reflects the smallest and the coarsest median subsurface grain sizes along the reach, respectively. Sites 2, 3 and 4 plot together as a group on axis 2 and are associated with surface sediment percentiles D_5 , D_{50} and D_{95} , site-averaged masses of POM, and site averaged measurements of benthic velocity and mean velocity. This organisation reflects the relatively coarse D_5 and D_{50} surface grain sizes sampled at sites 2 and 4 (figure 4.7A and B), and the highest average mass of POM sampled at site 3 (figure 4.6D). Site 4 is characterised by the coarsest surface D_{95} along the reach. The association of site 8 with a gradient of subsurface D_5 and subsurface sorting reflects the coarsest D_5 percentile and an atypical, well sorted subsurface distribution at this site (figure 4.8A and D). The smallest median *surface* grain sizes sampled at sites 7 and 9 are reflected in the position of these downstream sites along a gradient of surface D_{50} . Site 9 is associated with the subsurface D_{95} and this relates to the coarsest grain size of this percentile sampled along the reach (figure 4.7B). The distribution of sites along axes 1 and 2 explains 62 % of variation in the data (table 4.6), which, as indicated by the longer gradients of both surface and subsurface grain-size characteristics, is greater in these variables than in POM, benthic and mean velocity and conductivity.

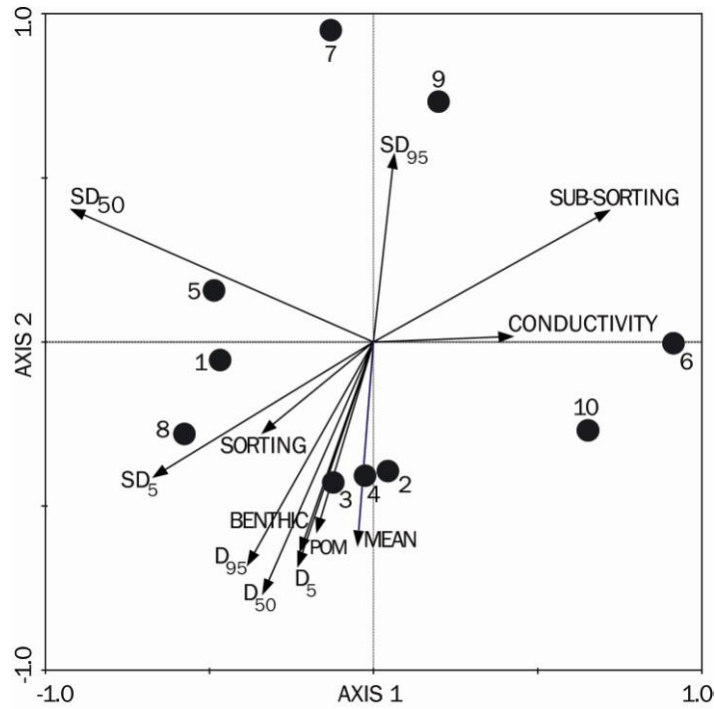


Figure 4.10. PCA using site-scale data ($n = 10$). Grain-size percentiles prefixed with ‘S’ indicate a subsurface percentile. ‘Mean’ and ‘benthic’ refer to velocity, POM = particulate organic matter. ‘Sorting’ and ‘sub-sorting’ refer to surface and subsurface sorting coefficients, respectively.

AXIS	1	2	3	4
EIGENVALUES	0.32	0.30	0.17	0.10
CUMULATIVE VARIANCE OF DATA (%)	32.2	61.8	78.8	89.0

Table 4.6. Axes scores of variation in the sample distribution established by PCA using site-scale data.

The PCA has confirmed that macroinvertebrates were collected from very similar ‘high Froude number’ sites and that zonal differences in channel planform and substrate cannot be differentiated by the physical variables examined in the analysis. The PCA has also indicated that reach-scale gradients cannot be generalised in the data, and this is likely because sub-reach variation in the twelve physical variables, seen in figures 4.6–4.8, is not simple. Sub-reaches are evident in figure 4.6 on account of average site measurements, which, for the variables of POM and benthic velocity, are significantly different. Sub-reaches are also clear in downstream patterns of surface grain-size characteristics (figure 4.7), and the sub-surface D_{50} (figure 4.8B) although this is not detected by the analysis. This section has determined that the physical character of the reach between Luc and Recoubeau can be structured by sub-reaches, rather than zones.

4.4.2. Spatial Structure in Macroinvertebrate Community Organisation

Excluding rare taxa (section 4.3.1), three of the twenty six taxa identified between Luc and Recoubeau dominate the reach-scale macroinvertebrate community. Hydropsychidae, Baetidae, and Chironomidae comprise 34 %, 20 % and 14 % of the total abundance count, respectively, and 68 % collectively (figure 4.11). Twenty three taxa comprise the remaining 32 % of the reach-scale community, of which fifteen taxa account for ≤ 1 %.

Although the reach-scale community is highly dominated, it is well represented in over half of all 150 samples, and the majority of macroinvertebrate taxa occur at every site along the reach (appendix IXA). Fourteen taxa occur in more than 50 % of all samples, and only 6 taxa occur in less than 10 % of all samples (figure 4.12). The most frequently occurring taxa are Chironomidae, Baetidae, Hydropsychidae and Leuctridae, within 99 %, 98 %, 91 % and 81 % of samples, respectively. Only five taxa are absent from one or more sites. These few absences are not systematic or consistent to specific sites, and because of the reach-scale omnipresence of nearly all taxa, it is not possible to discriminate 'indicator taxa' that occur exclusively between or within individual sites.

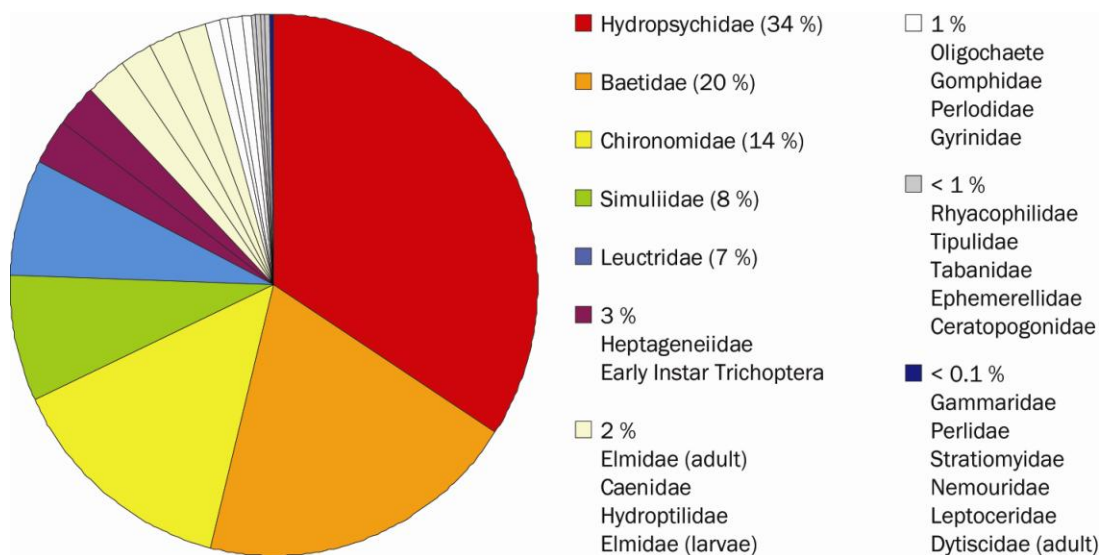


Figure 4.11 Proportional composition of the reach-scale macroinvertebrate community.

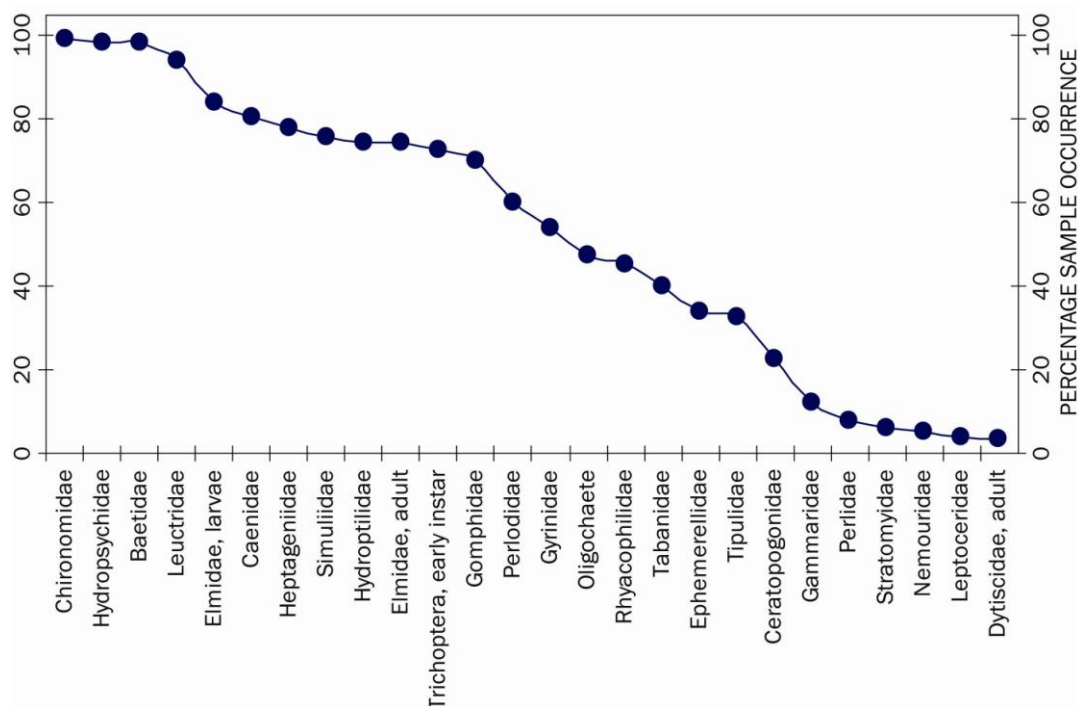


Figure 4.12 The percentage of samples in which each of the twenty six macroinvertebrate taxa occur along the study reach.

Five indices were calculated to describe macroinvertebrate community structure between Luc and Recoubeau. These indices were calculated for each sample ($n = 150$) and then expressed at the site-scale ($n = 10$) by using the average of the fifteen samples collected within a site (appendix IXB).

Abundance is a simple count of the number of individual macroinvertebrates collected. The number of different taxa within a sample was also counted, and this is otherwise referred to as sample *richness*. These two simple measures do not account for the relative abundances of each different taxon, however, and so three indices of alpha diversity will be explored to examine the relative density of different taxa at each sampling location. Simpson's index of *diversity* accounts for both the richness and proportion of each species within a community. An increase in this index indicates that the macroinvertebrate community is diverse in the sense it is populated by a comparatively greater number of taxa with greater abundances. The Berger Parker index of community *dominance* expresses the numerical importance of the most abundant species within a community. An increase in this index indicates that the macroinvertebrate community is dominated by a small number of taxa. Brillouin's index of *evenness* is a measure of the relative abundance of the different species, and thus indicates how similar the abundances of different taxa at a given site are. An increase in this index indicates that the taxa within the macroinvertebrate community occur in similar numbers. Subsequent discussion of macroinvertebrate diversity, dominance and evenness refers to these indices of Simpson diversity, Berger Parker dominance and Brillouin evenness. The next section examines spatial structure in macroinvertebrate community organisation by observing downstream changes in these five indices.

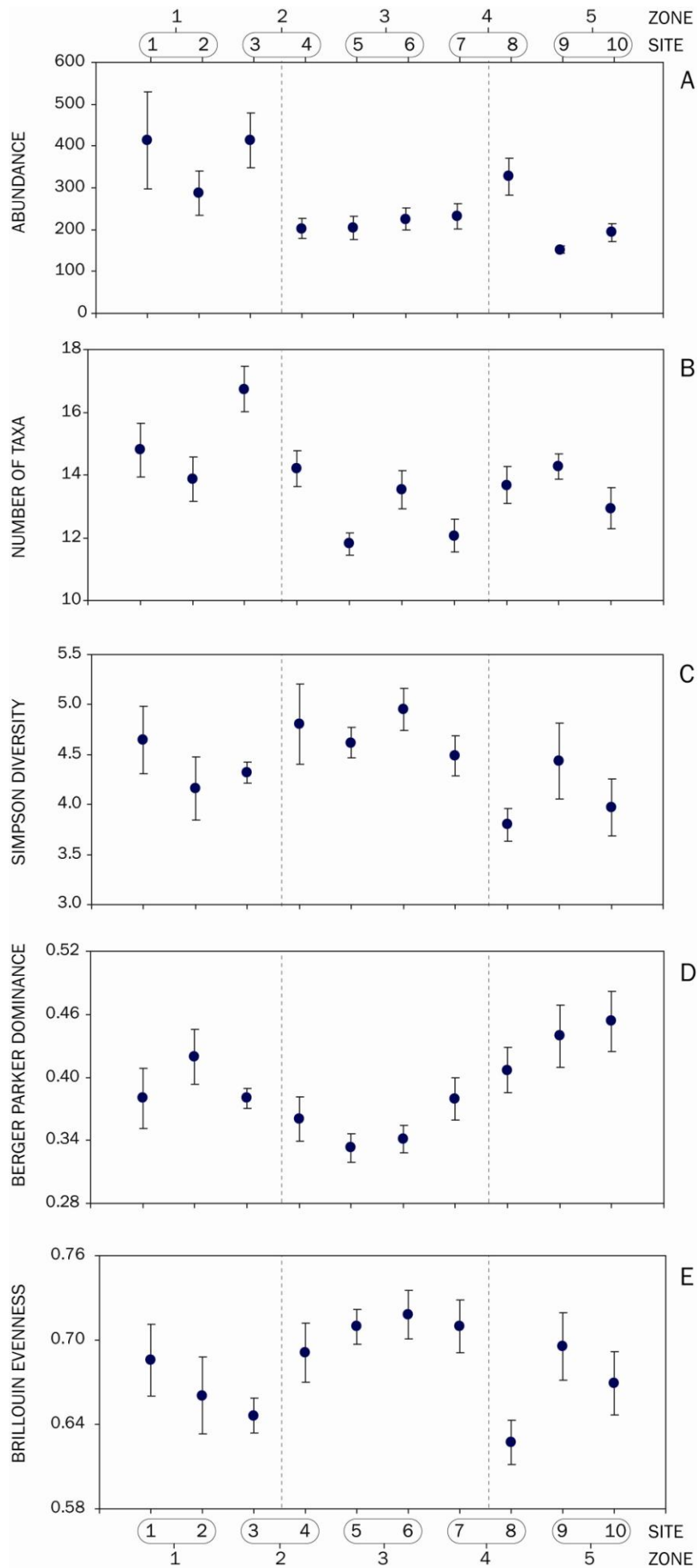
4.4.2.1. Univariate patterns of macroinvertebrate community structure

There is a strong downstream reduction in both absolute counts and the variance of sample abundance at each site (figure 4.13A). 73 % of taxa are most abundant at sites 1, 2 and 3, and there is greater within-site variation in sample abundance compared to downstream sites. Sites 4–7 show relatively similar average abundance counts, and similar variance. There is an increase in average abundance at site 8, very minor variation in sample abundance at site 9, and site 10 shows both reduced average and reduced variation compared to the sites upstream. There is notable similarity between this pattern and that exhibited by POM (figure 4.6D). Average sample richness also decreases downstream (figure 4.13B) with more taxa at sites 1 and 3 in comparison to sites 4 to 10.

There is an overall reduction in average community diversity (figure 4.13C), and some indication of sub-reach patterns in this trend: upstream sites 1–3 show relatively lower average diversity than mid-reach sites 4–7, and downstream sites 8 and 10 show the lowest average values of diversity. Downstream changes in macroinvertebrate community dominance are systematic along a clear U shaped gradient (figure 4.13D), with a decline in dominance between sites 1 and 5, and an increase in dominance between sites 5 and 10. Mid-reach communities are the least dominated. There is little overall change in Brillouin evenness between sites 1 and 10, but there are differences between upstream, mid-reach and downstream sites (figure 4.13E). Upstream sites 1–3 are relatively less even. Mid-reach sites 4–7 are relatively more even, with an abrupt reduction at site 8 and greater variation in average community evenness between the downstream sites.

It is apparent in this description that while there is some longitudinal structure in these macroinvertebrate community indices, there is also clear evidence of sub-reach structure. Site pairs within each of the five zones are not similar in terms of their community characteristics, and zones cannot be clearly distinguished in the data. However, the indices of abundance, diversity, dominance and evenness appear to be structured by a pattern of upstream (sites 1–3), mid-reach (sites 4–7) and downstream (sites 8–10) sub-reaches. This organisation is consistent with the spatial structure observed in the twelve physical variables (section 4.4.1.1) and recent observations of channel form described in chapter 3 (sections 3.5.2.2 and 3.5.3).

Figure 4.13 (following page) Downstream changes in (A) abundance, (B) richness, (C) Simpson diversity, (D) Berger Parker dominance and (E) Brillouin evenness between all ten sites. Centre point = average, error bars ± 1 standard error. Zones are indicated and the dashed vertical lines indicate sub-reach boundaries.



4.4.2.2. *Spatial structure in the distribution of macroinvertebrate taxa*

To explore spatial patterns in sample abundances of the twenty six macroinvertebrate taxa identified along the reach, Detrended Correspondence Analysis (DCA) was undertaken. There is no clear longitudinal pattern in the ordination output, but there are clear between-site differences when samples are coded by their site (figure 4.14A). Samples from sites 1–3 are clearly distinct from samples collected in downstream sites 4–10. This organisation accounts for 31 % of variation in the data (table 4.7), and reflects the uneven reach-scale pattern of macroinvertebrate abundance (figure 4.13A).

Site 3 samples are clustered and distinct as an individual group, close to samples from sites 1 and 2. The taxon biplot (figure 4.14B) indicates taxa that are most abundant at these three upstream sites are associated with samples from sites 1–3 (Tipulidae, Tabanidae, Gyrinidae, Rhyacophilidae, Ceratopogonidae, Simuliidae, Stratyomyiidae, Gammaridae, and adult Dytiscidae) (figure 4.14B) suggesting that the DCA output is representative of spatial variation in abundance.

Within the group of samples from sites 4 to 10, samples from site 4 are tightly clustered and can be distinguished as an individual cluster. Site 4 is the only site along the reach that is dominated by a taxon other than Hydropsychidae (Baetidae), and the separation of Perlidae from the main group of taxa, in a similar location in ordination space to site 4 samples (figure 4.14B) reflects that the majority of the total Perlidae population (55 %) occurs at this site. Samples from sites 5 and 6 scatter together as a group and overlap the group of samples from sites 7, 8, 9 and 10. Samples from sites 7 and 8 can be distinguished from samples collected at downstream sites 9 and 10, which group together. The distinction between samples from sites 7 and 8 may reflect large differences in the dominant taxa at these sites. At site 8, Hydropsychidae, Chironomidae and Leuctridae account for 41 %, 25 % and 3 % of the total site abundance, respectively, in contrast to equivalent values of 36 %, 6 % and 18 % at site 7. Site 8 is also the least diverse and least even site of all ten sampled along the reach (figure 4.13D and E), but average sample abundances are relatively high compared to mid-reach and downstream sites (figure 4.13A). Between the two groups of samples from sites 1–3, and sites 7 and 8, a third group of samples from sites 9 and 10 overlap each other, suggesting that their characteristics are relatively similar.

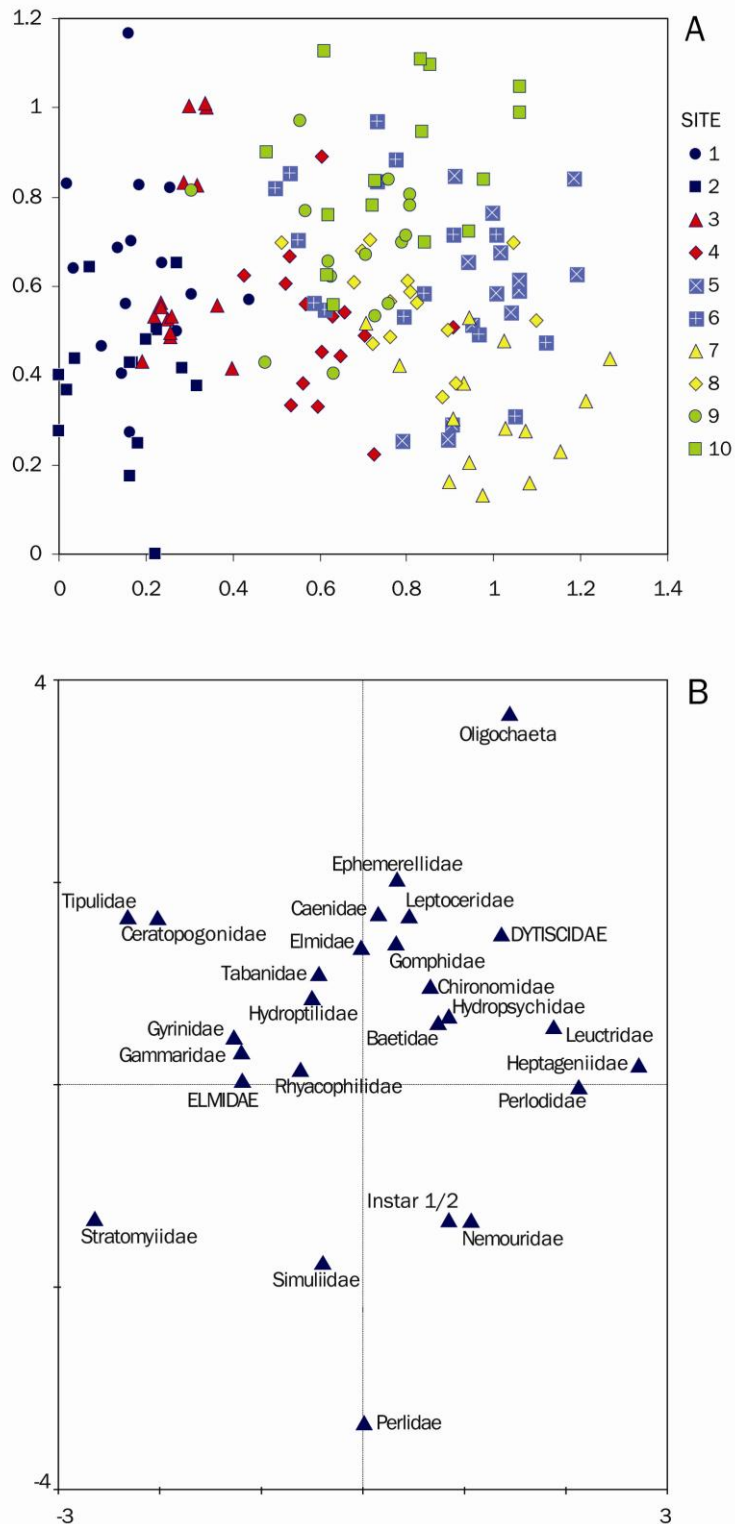


Figure 4.14. DCA biplots of (A) samples and (B) taxa using all sample data ($n = 150$). Taxa in capitals are adult, not larvae. Instar 1/2 denotes first and second instars of Trichoptera.

AXIS	1	2	3	4
EIGENVALUES	0.102	0.048	0.038	0.026
GRADIENT LENGTHS	1.268	1.165	1.270	0.928
CUMULATIVE VARIANCE OF SPECIES DATA (%)	20.9	30.9	38.8	44

Table 4.7 Axes scores of variation in the sample distribution established by DCA using all sample data.

It is apparent in this description of sample clusters that there is some zonal or sub-reach structure within the organisation of macroinvertebrate taxa. When samples are coded by their zone, rather than sampling site, four of the five zones can be clearly differentiated in the DCA biplot (figure 4.15A). Zone 1 is apparent in the distinctive cluster, formed by samples from sites 1 and 2. Zone 2 is less apparent in the biplot, because samples from sites in zone 2 (sites 3 and 4) are separated. Samples from the upstream site in zone 2 (site 3) plot with zone 1 samples. Samples from the downstream site in zone 2 (site 4) can be distinguished as a separate group. Zone 3 samples (sites 5 and 6) overlap samples from zones 4 and 5 indicating that macroinvertebrate communities in the mid-reach may share characteristics with those identified in downstream zones 4 and 5. When zone 3 samples are removed from the DCA biplot, the distinction of zones 4 and 5 is clear (figure 4.15B). Although sites 7 and 8 can be differentiated when samples are coded by sampling site, together they reflect zone 4, and zone 5 is represented by the scatter of samples from sites 9 and 10.

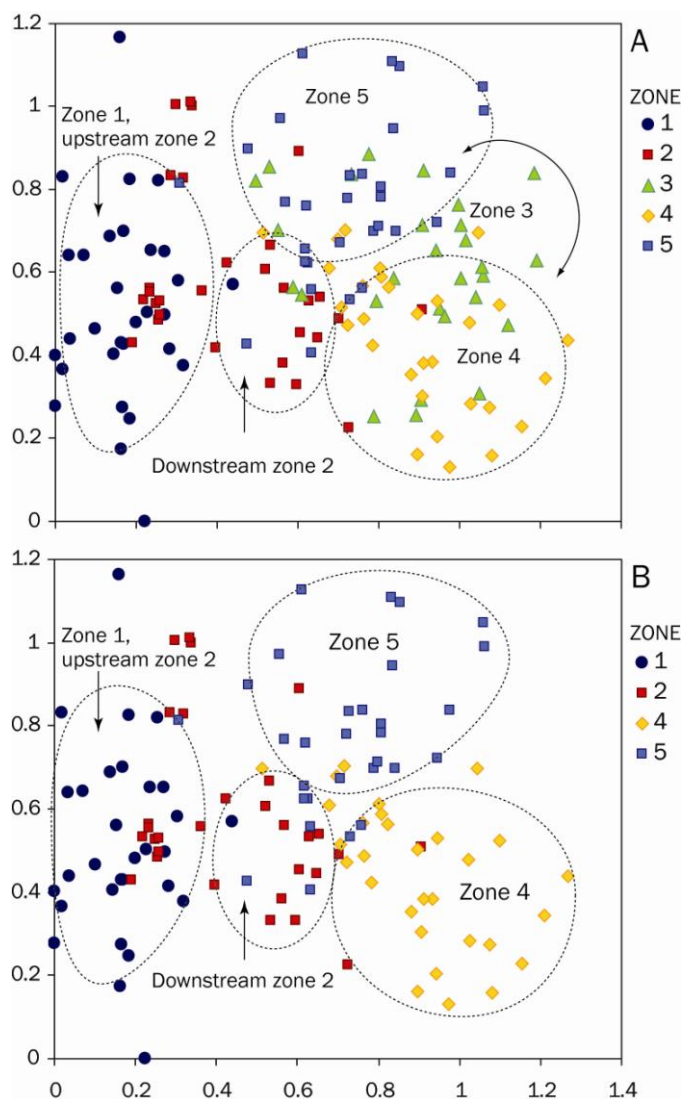


Figure 4.15. DCA sample biplot coded by zone. Four of the five zones are clearly visible (A). Samples in zone 3 overlap samples from zones 4 and 5 (B), indicating that mid-reach sites share characteristics of downstream sites.

To examine this zonal structure for significance, a non-parametric Kruskal Wallis test was used to identify differences in mean values of community structure between the five zones. Overall differences in abundance, richness, diversity and macroinvertebrate dominance are significant between all five zones ($\alpha = 0.05$), however differences in evenness are only significant at $\alpha = 0.10$ (table 4.8). Mann Whitney U post-hoc tests were used to examine differences in community structure between individual zones ($\alpha = 0.05$, table 4.9). Upstream zones 1 and 2 support significantly higher macroinvertebrate abundances than downstream zone 5. Mean abundance counts in zone 4 are also significantly higher than those in zone 5. For richness, sixty percent of the ten possible pair-wise comparisons showed that significantly different numbers of taxa were sampled between the zones. Zones 1 and 2, zones 1 and 5, zones 3 and 4, and zones 4 and 5 did *not* show significant differences in mean sample richness. For diversity, macroinvertebrate communities sampled in zone 3 are significantly more diverse than those sampled in zones 2, 4 and 5. Macroinvertebrate communities sampled in zone 3 are also significantly less dominant than those in zones 1, 4 and 5, and more even than those in zones 2 and 4. Downstream samples in zone 5 are significantly more dominated than those in zone 2.

INDEX	ASYMP. SIG.
Abundance	0.005
Richness (<i>n</i> taxa)	0.000
Simpson Diversity	0.045
Berger Parker Dominance	0.001
Brillouin Evenness	0.057

Table 4.8. Asymptotic scores of significance (Kruskal Wallis test, $\alpha 0.05$) in differences of the mean sample values of community structure between the five zones.

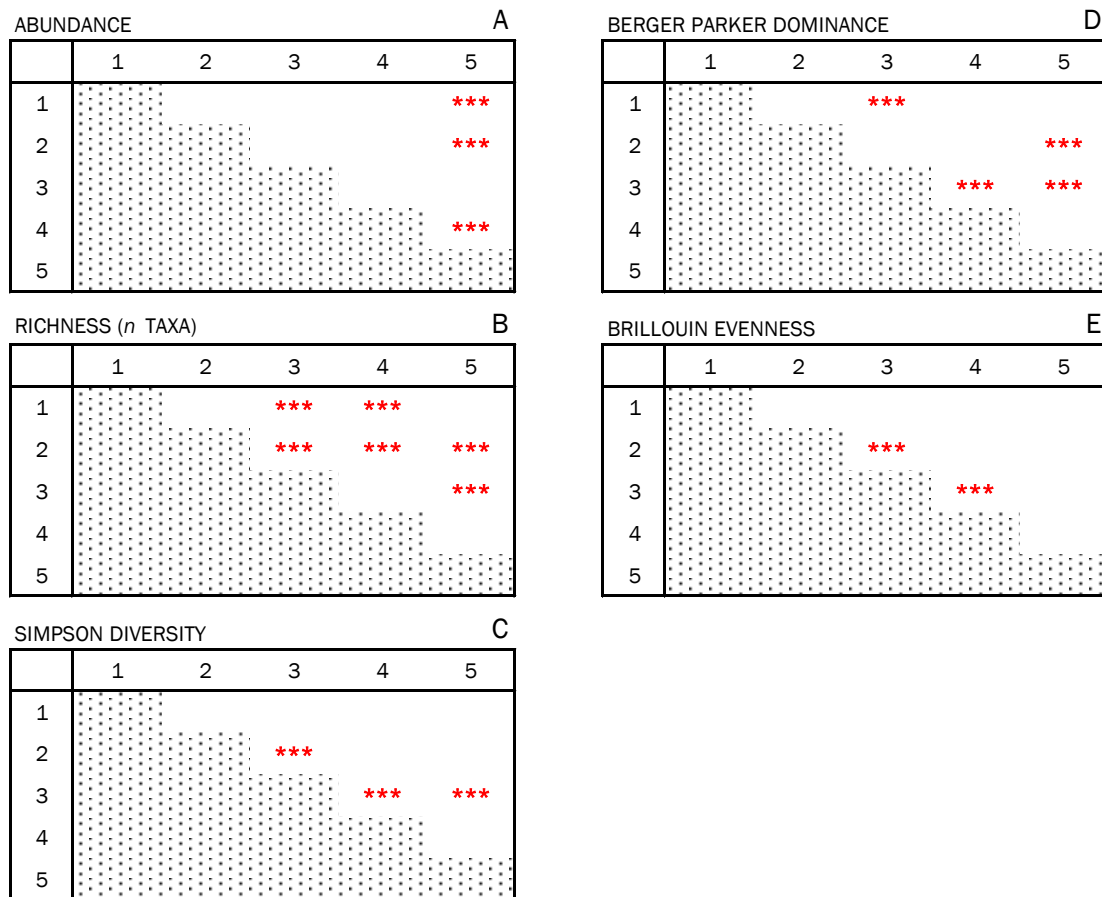


Table 4.9. Three asterisks (***) indicate significant asymptotic scores (Mann Whitney U tests, α 0.05) of difference in mean values of (A) abundance, (B) richness (the number of different taxa), (C) Simpson diversity, (D) Berger Parker dominance and (E) Brillouin evenness, between the five geomorphic zones (1 – 5).

The zonation identified in the DCA contrasts with the organisation of sub-reaches seen in the univariate plots of community structure, between upstream, mid-reach and downstream sites (section 4.4.2.1, figure 4.13). To explore whether the interpretation of zonation was the ‘best fit’ on the sample distribution, and whether sub-reach structure is apparent in the DCA, the output was also structured by coding samples according to their upstream, mid-reach or downstream sub-reach location (figure 4.16).

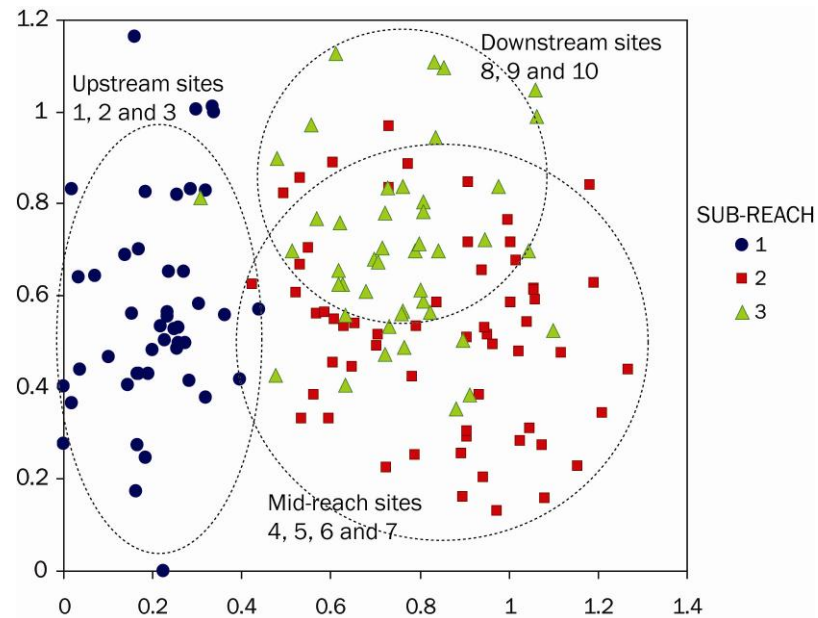


Figure 4.16. DCA sample biplot coded by sub-reaches.

Samples from sites 1–3 are clearly distinguished as the upstream sub-reach from two groups of mid-reach and downstream samples. However, there is considerable overlap between mid-reach and downstream samples which suggests that they cannot be clearly differentiated in terms of their macroinvertebrate community characteristics. Overall differences in the mean values of all macroinvertebrate community indices are, however, significant between all three sub-reaches (Kruskal Wallis test, α 0.05, table 4.10), confirming the observations of sub-reach structure in the univariate data (figure 4.13). Mann-Whitney U post-hoc tests (α 0.05) indicated that the upstream sub-reach is significantly more abundant than the mid-reach and downstream sub-reaches, however there is no significant difference in abundance between mid-reach and downstream sub-reaches (table 4.11A). There are significant differences in richness between all three sub-reaches (table 4.11B). The mid-reach supports significantly more diverse communities than both upstream and downstream sub-reaches, but there is no significant difference in macroinvertebrate diversity between upstream and downstream sub-reaches (table 4.11C). Macroinvertebrate communities within the mid-reach are significantly less dominated and more even than those upstream and downstream. There is no significant difference in macroinvertebrate community dominance or evenness between upstream and downstream sub-reaches (table 4.11D and E).

INDEX	ASYMP. SIG.
Abundance	0.011
Richness (<i>n</i> taxa)	0.000
Simpson Diversity	0.006
Berger Parker Dominance	0.000
Brillouin Evenness	0.010

Table 4.10 Asymptotic scores of significance (Kruskall Wallis test, α 0.05) in differences of the mean values of community structure between the three upstream, mid-reach and downstream sub-reaches.

	UPSTREAM	MID-REACH	DOWNSTREAM	
UPSTREAM		***	***	A ABUNDANCE
MID-REACH				
UPSTREAM		***	***	B RICHNESS (<i>n</i> TAXA)
MID-REACH			***	
UPSTREAM		***		C DIVERSITY
MID-REACH			***	
UPSTREAM		***		D DOMINANCE
MID-REACH			***	
UPSTREAM		***		E EVENNESS
MID-REACH			***	

Table 4.11. Three asterisks (***) indicate significant ($p \leq 0.05$) (Mann Whitney U tests, α 0.05) differences in mean values of (A) abundance, (B) richness (the number of taxa), (C) Simpson diversity, (D) Berger Parker dominance and (E) Brillouin evenness, between upstream, mid-reach and downstream sub-reaches.

So, there are two contrasting and significant spatial patterns that can be identified within the DCA: zonation and sub-reaches. When either sites, zones or sub-reaches are identified in the output, however, there is a consistent distinction of upstream sites 1–3, and so the ordination appears to indicate significant spatial differences in macroinvertebrate abundance. Upstream sites 1–3 account for almost half (42 %) of the reach-scale abundance count, and 74 % of all taxa are most abundant in this upstream sub-reach. There is a significant difference in abundance between upstream (sites 1–3) and mid-reach (sites 4–7) sub-reaches, and between upstream (sites 1–3) and downstream (sites 8–10) sub-reaches, but *not* between mid-reach and downstream samples (table 4.11A), and hence the overlap of these latter two groups in the DCA output (figure 4.16). Furthermore, when samples in the biplot are coded by zones, there is a clear distinction between samples from zone 1 and the upstream zone 2 site (site 3), the downstream zone 2 site (site 4), zone 4 and zone 5 (figure 4.15A). Upstream zones 1 and 2 support significantly higher macroinvertebrate abundances than downstream zone 5, and samples collected within zone 4 are significantly more abundant than those in zone 5 (table 4.9A). There are no clear differences in abundance between

samples within zones 3, 4 and 5 and this accounts for the overlap of zone 3 samples onto those from zones 4 and 5 (figure 4.15B).

It can be concluded that in terms of *abundance* there is a clear difference between upstream sites 1–3 and downstream sites 4–10. The DCA has also indicated zonal structure in macroinvertebrate abundance. However, spatial variation in macroinvertebrate community *diversity*, *dominance* and *evenness* is most significant between sub-reaches. A pattern of zonation in these three indices is not clear due to the within-zone, between-site differences (figure 4.13). Moreover, post-hoc tests revealed very few significant differences in diversity, dominance and evenness between individual zones (table 4.6). In contrast, there are consistent significant differences between individual upstream, mid-reach and downstream sub-reaches on account of diversity, dominance and evenness (table 4.7).

This section (5.4.2) has thus determined that the two spatial structures of zonation and sub-reaches are both important in understanding the organisation of the reach-scale macroinvertebrate community. This finding is significant in the context of future channel changes (chapter 5), because zonation reflects the present-day morphological character of the channel, as a relatively stable channel form, while sub-reach structure reflects a possible future change in channel form, in response to a change in the sub-reach dynamics of sediment transfer and storage along the reach (section 3.5.3.2).

4.4.3. Associations between Physical Variables and Macroinvertebrate Community Structure

The distinction of the mid-reach in terms of macroinvertebrate abundance, diversity, dominance and evenness, is coincident with the differentiation of the mid-reach on account of downstream fining and sorting of surface sediment, slower benthic velocity and smaller average sample masses of POM. The correspondence of these patterns suggests that the reach-scale organisation of macroinvertebrate taxa may be influenced by different physical environments within these sub-reaches. To examine whether the distribution of macroinvertebrate taxa is influenced by sub-reach gradients in the physical variables, two separate sets of Canonical Correspondence Analysis (CCA) were undertaken. Section 4.4.3.2 first examines whether the distribution of macroinvertebrate taxa is influenced by the four variables for which sample data ($n = 150$) is available (POM, benthic velocity, mean velocity, and conductivity). Section 4.4.3.3 examines correspondence between the distribution of macroinvertebrate taxa and site-scale data (table 4.2).

4.4.3.1. Multivariate relationships using all sample data

In the CCA using all sample data ($n = 150$) the association between the five physical variables and the organisation of macroinvertebrate taxa is low. The distribution of samples along axes 1 and 2 explains only 9 % of the variance in the data (table 4.12). Samples from all sites overlap each other around the centre of the axes (figure 4.17A). A number of samples are scattered separately from this cluster and their differentiation is significantly influenced by their faster benthic velocities and greater sample masses of POM (table 4.13). Macroinvertebrate taxa are densely clustered around the centre of the ordination axes indicating that their distributions are not strongly influenced by the physical gradients identified in the CCA. Stratiomyidae is the sole taxon outlying from this cluster and is associated with the gradient of benthic velocity (figure 4.16B).

There is no longitudinal structure in the sample distribution, nor a clear pattern of zonation or a sub-reach structure. Apart from the variation in benthic velocity and masses of POM, this confirms that the physical characteristics of all ten sampling sites are similar, and indicates that spatial variation in the distribution of macroinvertebrate taxa cannot be distinguished by the variables of benthic and mean velocity, conductivity, and sample masses of POM.

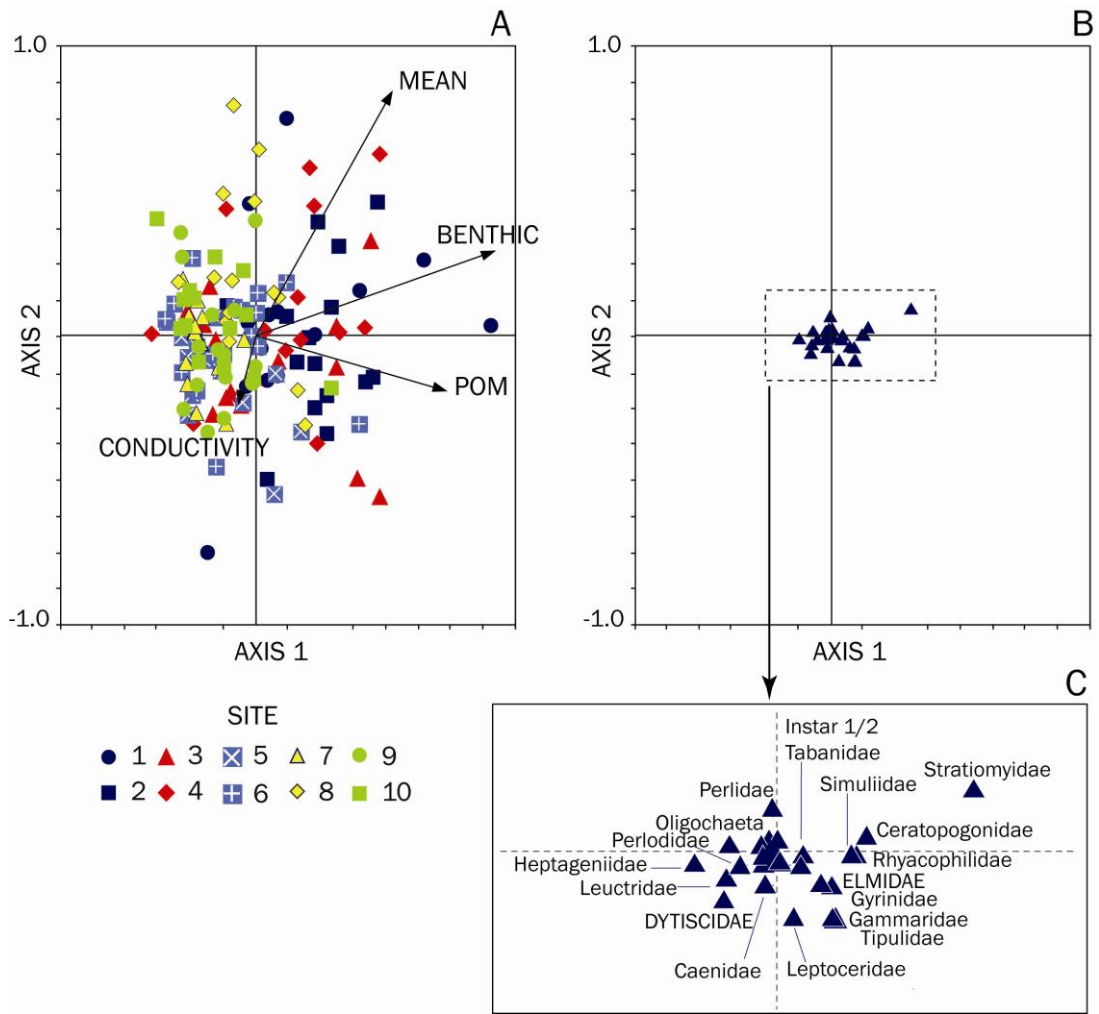


Figure 4.17. CCA biplots of (A) samples and (B) taxa using all sample data ($n = 150$). Taxa in capitals are adult, not larvae. Taxa clustered around the origin of the axes in (B) are enlarged in (C). Instar 1/2 denotes first and second instars of Trichoptera.

AXIS	1	2	3	4
EIGENVALUES	0.04	0.01	0.00	0.00
SPECIES-ENVIRONMENT CORRELATIONS	0.66	0.45	0.37	0.22
CUMULATIVE VARIANCE (%) OF SPECIES DATA	8.3	9.3	10.0	10.2
OF SPECIES-ENVIRONMENT RELATIONS	81.2	91.3	98.5	100.0

Table 4.12 Axes scores of variation in the sample distribution established by CCA using all sample data.

VARIABLE	p VALUE	F RATIO
BENTHIC VELOCITY	0.001	8.76
POM	0.001	5.38

Table 4.13 Significance values of gradients established in the sample distribution by CCA using all sample data (Monte Carlo permutation tests, $n = 999$).

4.4.3.2. Multivariate relationships using site-scale data

When CCA was undertaken using site-scale data ($n = 10$), there is no clear longitudinal pattern in the output (figure 4.18A). Zonation is also not apparent, and there is no clear distinction between upstream, mid-reach and downstream sites. The organisation of the ten sites along axes 1 and 2 explains 60 % of variance in the data (table 4.14), which is significantly influenced by gradients of benthic velocity, POM and the surface D_{95} (table 4.15). These gradients are associated with sites 1 and 2, site 3, and site 4, respectively, and indicate atypical values in these variables. Along axis 1 the association of sites 1 and 2 with the gradient of benthic velocity reflects the relatively high upstream velocities and within-site variation in benthic velocity sampled at these sites (figure 4.6A). The association of site 3 with the gradient of POM indicates the significantly higher average sample mass and the greatest within-site variation of POM sampled at this site (figure 4.6D). Site 4 is associated with a gradient of surface D_{95} , reflecting the coarsest grain size of this percentile sampled along the reach (figure 4.7C).

The majority of all macroinvertebrate taxa are clustered around the centre of the axes, indicating that they are not strongly influenced by the physical gradients identified in the CCA (figure 4.18B). Certain taxa can be differentiated from this cluster, suggesting that their abundance patterns are influenced by the gradient with which they are associated. Nemouridae plots closely to a gradient of conductivity. This taxon occurs almost exclusively upstream at sites 1 and 2 where greater conductivity and wider variation in conductivity were recorded. Perlidae, Leptoceridae and Dytiscidae are associated with the gradients of surface D_{95} and sorting, and Gammaridae with the gradient of POM. Gammaridae is most abundant at site 3 where sample masses of POM are greatest. Ceratopogonidae, Tipulidae and Stratiomyidae are also separated from the central cluster of taxa, near to gradients of benthic velocity and mean velocity. These three taxa are most abundant at upstream sites 1, 2 and 3 and may prefer, or withstand, the faster and wider range of benthic flows recorded at these three upstream sites.

AXIS	1	2	3	4
EIGENVALUES	0.04	0.03	0.02	0.01
SPECIES-ENVIRONMENT CORRELATIONS	1.00	1.00	1.00	1.00
CUMULATIVE VARIANCE (%) OF SPECIES DATA	36.9	60.1	73.0	82.9
OF SPECIES-ENVIRONMENT RELATIONS	36.9	60.1	73.0	82.9

Table 4.14. Axes scores of variation in the sample distribution established by CCA using site-scale data.

VARIABLE	<i>p</i> VALUE	F RATIO
BENTHIC VELOCITY	0.019	2.79
SURFACE D95	0.037	2.03
POM	0.034	2.40

Table 4.15. Significance values of gradients established in the sample distribution by CCA using site-scale data (Monte Carlo permutation tests, $n = 999$).

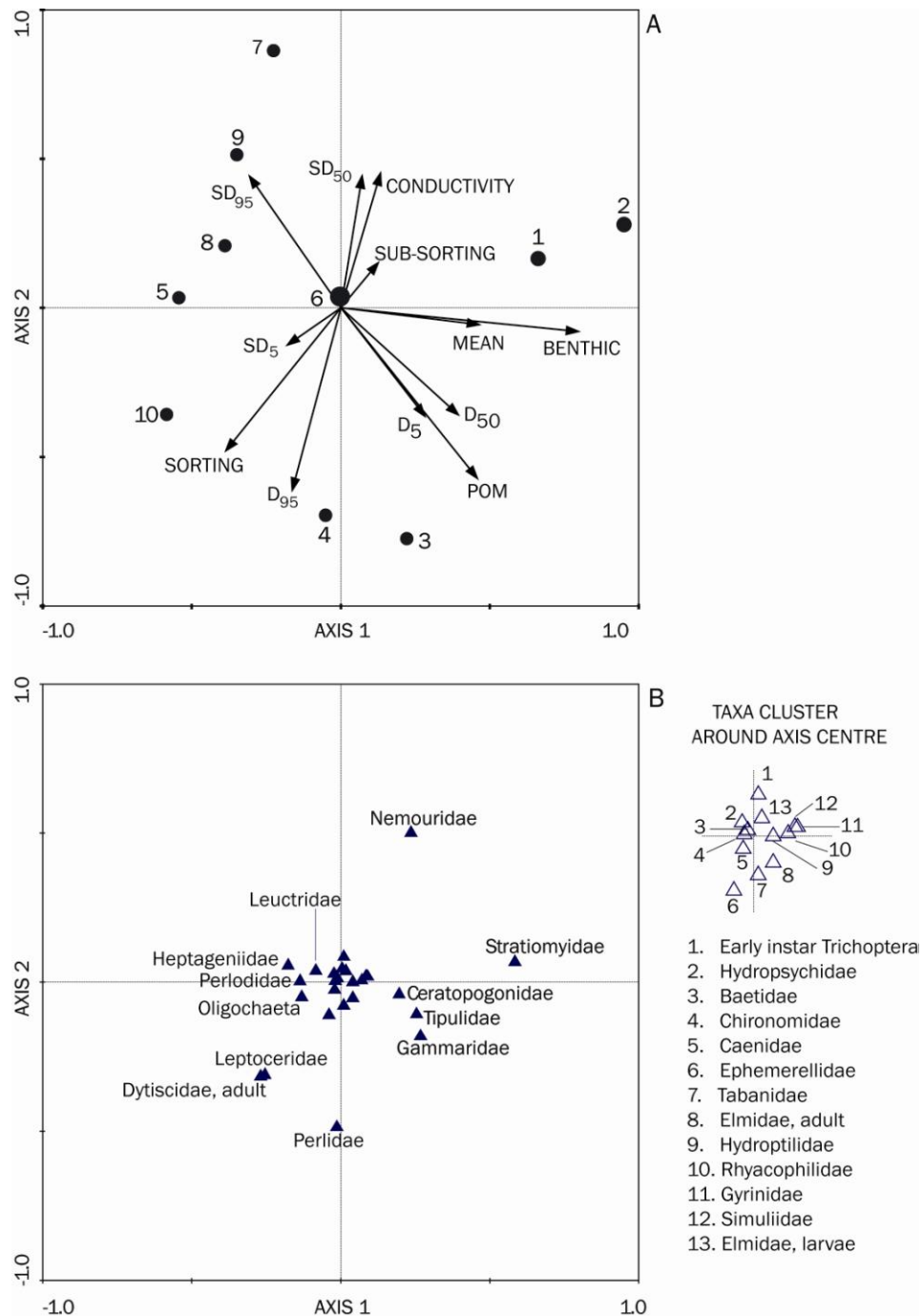


Figure 4.18. CCA biplots of (A) samples and (B) taxa, using site-scale data ($n = 10$).

CCA has indicated that reach-scale associations between physical and ecological variables cannot be generalised between Luc and Recoubeau. This was confirmed when Pearson correlation coefficients were determined using site-scale data. Every pairing of physical variables and community indices was tested, but only three associations are noteworthy. There is a significant relationship between average sample abundance and the average mass of POM collected at a site ($r = 0.84$, $\alpha = 0.01$), which is also reflected in the almost identical downstream patterns of abundance and POM (figures 4.6D and 4.13A). In addition, there is a moderate but insignificant negative relationship between macroinvertebrate diversity and the sorting coefficient of surface sediment between the ten sites ($r = -0.45$). Sites that support relatively diverse macroinvertebrate communities tend to show a relatively homogeneous distribution of surface grain sizes (figure 4.19). In contrast, there is a significant positive correlation between macroinvertebrate diversity and the subsurface sorting coefficient and ($r = 0.76$, $\alpha = 0.05$) indicating that macroinvertebrate community diversity increases in relatively poorly sorted, heterogeneous subsurface sediments.

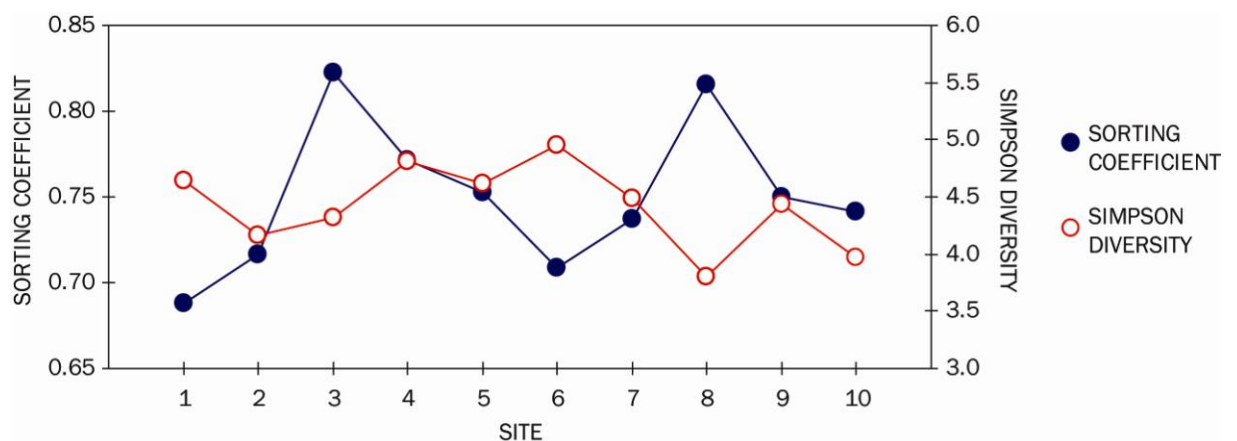


Figure 4.19 Surface sediment diversity and macroinvertebrate community diversity of all ten sites.

The CCA has confirmed that the spatial patterns of macroinvertebrate organisation clear in the DCA ordination (figures 4.14–4.16) cannot be related to general zonal or sub-reach variation in the twelve physical variables. This is likely because spatial variation in the twelve physical variables is not systematic (figures 4.6–4.8). As a result, there are very few simple reach-scale correlations between the physical variables and indices of macroinvertebrate community structure. The CCA indicated that higher upstream abundances of certain taxa at sites 1–3 are associated with variation in benthic velocity and POM. At the reach scale, POM is a significant influence on macroinvertebrate abundance and richness, and macroinvertebrate diversity is significantly related to subsurface grain-size diversity.

4.4.4. Summary of Results

Spatial Structure in Physical Variables

- When longitudinal patterns in the twelve physical variables are observed, zonation is not apparent in the data. The physical characteristics of the reach, particularly surface grain-size characteristics, are structured by sub-reaches. Differences in POM and benthic velocity between upstream, mid-reach and downstream sub-reaches are significant. Upstream sites 1, 2 and 3 are characterised by significantly higher average values and greater variance in these variables.
- PCA did not reveal any clear spatial structure in both the sample and site-scale physical data, however a number of samples from sites 1, 2 and 3 were differentiated on account of their faster benthic velocities and higher masses of POM. With the exception of this upstream variation, the ordination thereby confirmed that samples were collected from locations with similar sample masses of POM, similar flow velocities and conductivity.

Spatial Structure in Macroinvertebrate Community Organisation

- When individual indices of macroinvertebrate community structure are observed, zonation is not apparent, but sites are clearly structured by sub-reaches. There are significant differences in abundance, richness, diversity, dominance and evenness between upstream, mid-reach and downstream sub-reaches.
- When macroinvertebrate sample abundance counts were examined using DCA, zonation could be interpreted in the output. Zone boundaries were not neatly defined, with a notable similarity between zone 1 sites 1 and 2, and the upstream zone 2 site 3. However, overall differences in macroinvertebrate community structure are significant, between all five zones.
- Sub-reach structure could also be identified in the DCA output. Mid-reach and downstream samples were not clearly differentiated, but there is a clear distinction between samples from the upstream sub-reach sites 1, 2 and 3, and the mid-reach and downstream sub-reaches combined. The differentiation of sites 1, 2 and 3, regardless of whether zones or sub-reaches are interpreted in the DCA, reflects the uneven reach-scale pattern of macroinvertebrate abundance: 73 % of all taxa are most abundant at sites 1, 2 and 3.
- Post-hoc tests indicate that sub-reach structure in the indices of diversity, dominance and evenness is more significant than zonal structure. In contrast, spatial variation in abundance is stronger between zones. Zonation and sub-reaches are therefore two significant spatial patterns in different aspects of macroinvertebrate community organisation. They may both provide important insight to the structure and functioning of macroinvertebrate communities between Luc and Recoubeau.

Associations between Physical Variables and Macroinvertebrate Community Structure

- Sub-reaches structure both physical variables and indices of macroinvertebrate community structure, but there are few simple reach-scale correlations between the data sets. There are only three noteworthy reach-scale biophysical associations: Macroinvertebrate sample abundance is significantly correlated with sample mass of POM. Site-averaged community diversity is related to the diversity of surface grain size at a site, and is significantly correlated with the diversity of subsurface grain size at a site.
- CCA differentiated samples from sites 1, 2 and 3 on account of faster benthic velocities and higher masses of POM, and greater sample abundances were associated with this variation.
- Otherwise, reach-scale associations between physical variables and the organisation of macroinvertebrate taxa could not be generalised, because of different sub-reach patterns in the physical variables examined, and the reach-scale omnipresence of nearly all macroinvertebrate taxa.

4.5. Discussion

The different sets of univariate and multivariate analysis have not led to any simple conclusions, partly because they have examined different elements of the data sets, and different spatial scales. Nonetheless, there are four key observations that have emerged from the results.

First, the physical characteristics of the reach can be differentiated by upstream, mid-reach and downstream sub-reaches. In addition to surface grain-size characteristics, this distinction is clear in the variables of benthic velocity and POM. **Second**, it is clear that the significantly faster benthic flows and greater sample masses of POM within the upstream sub-reach are associated with significantly higher sample abundance counts. The diversity of surface and subsurface grain size was also shown to be associated with macroinvertebrate community diversity at the reach scale.

Third, different aspects of community structure appear to be manifest in different spatial ways. The reach-scale pattern of macroinvertebrate abundance is highly uneven between sites 1–3 and 4–10, and also appears to be structured by zones. In contrast, indices of community diversity, dominance and evenness are structured by sub-reaches. It is possible that both spatial structures are important in understanding the reach-scale organisation of macroinvertebrate taxa between Luc and Recoubeau.

Finally, the sub-reach patterns in surface grain-size characteristics may reflect sub-reach dynamics of sediment storage and transfer (section 3.5.2.3, figure 3.25), and thereby sub-reach environments of variable flow and substrate disturbance. Local patterns of flow and substrate disturbance are an important control on macroinvertebrate community structure and may explain in part the spatial variation in macroinvertebrate community organisation. It follows that while zonation reflects a spatial pattern of disturbance *history* (figure 3.18), sub-reach organisation indicates *present-day* morphological dynamics, that are also indicative of possible *future* channel form. The second part of the discussion will lend particular consideration to the hypothesis that sub-reach differences in macroinvertebrate community structure reflect the influence of sub-reach morphological processes of sediment storage and transfer.

4.5.1. Upstream variation in benthic velocity and POM, between sites 1 and 3

Between Luc-en-Diois and Recoubeau, the differentiation of an upstream sub-reach (sites 1, 2 and 3), on account of significantly faster benthic velocities and greater sample masses of POM, may reflect the unique mixed bed morphology of zone 1, and the supply and transfer of POM between the three upstream sites.

The faster benthic velocities and wider variance of benthic velocity at zone 1 sites 1 and 2 likely reflects the complex flow patterns within this upstream environment. Zone 1 is a

bedrock channel with gravel patches, and the contrasts in bed substrate, topography and texture, caused by juxtaposed patches of bedrock and gravel, causes relatively diverse hydraulic patterns compared to those at entirely alluvial sites.

Variation in sample masses of POM along the reach as a whole was indicated by PCA and CCA to be independent of longitudinal position (figures 4.9 and 4.17), but site 3 samples yielded almost twice as much POM (average 1.1 g) as the other nine sites (averages ≤ 0.66 g). Sites 1 and 2 also retained higher than average masses of POM (figure 4.6A). The retention of POM within riffles has been related to water depth, flow velocity, grain size and the distribution of clasts (Hoover *et al.* 2006, Gorecki *et al.* 2006), and it is possible that greater variation in these variables, caused by the morphological and hydraulic diversity of the mixed bedrock-alluvial channel bed is responsible for the prevalence of POM at sites 1 and 2. Coarse POM is readily supplied to sites 1 and 2 from the riparian forest that closely buffers the channel, and from upstream of the study reach. As part of the hypothesised model of sediment connectivity between channel zones, zone 1 acts as a conveyor feeding sediment into the zone 2 reservoir (section 3.5.2.1, figure 3.25). There appears to be little storage of sediment within zone 1 and in the same context it is considered there is also only little or part-time storage of POM within zone 1. The greatest average mass of POM collected at site 3 may thus reflect the collection of POM readily transferred from zone 1 (figure 4.20). Downstream of site 3, average site masses of POM are much smaller (figure 4.6D) as POM disperses when the channel becomes wider and multi-thread.

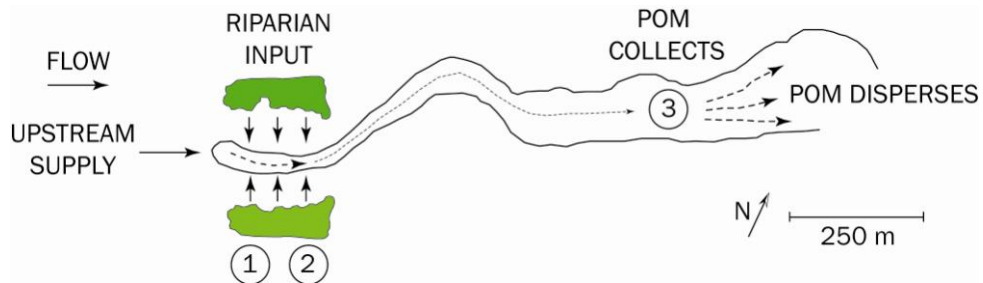


Figure 4.20. Schematic illustration of the hypothesised supply, transfer (dashed lines) and collection of POM along the upstream sub-reach between sites 1-3 (site number indicated within circle).

4.5.2. Spatial Structure in Macroinvertebrate Abundance

In order to exclude variation in physical 'habitat' as a possible explanation for spatial variation in macroinvertebrate organisation, macroinvertebrates were sampled from sites of similar substrate and flow. Limited variation in the physical variables measured at each Surber sample location (benthic velocity, mean velocity and conductivity) was therefore anticipated. PCA has confirmed that, with the exception of the upstream variance in benthic velocity and POM, all Surber sample locations were characterised by similar measurements in these variables (figures 4.13–4.16). CCA at the site scale suggests that the significantly faster

benthic flows and sample masses of POM, and greater variance in these two variables, may be a direct influence on the relatively high abundance counts of certain taxa, which are significantly greater at sites 1–3 (section 4.4.3.4, figure 4.18).

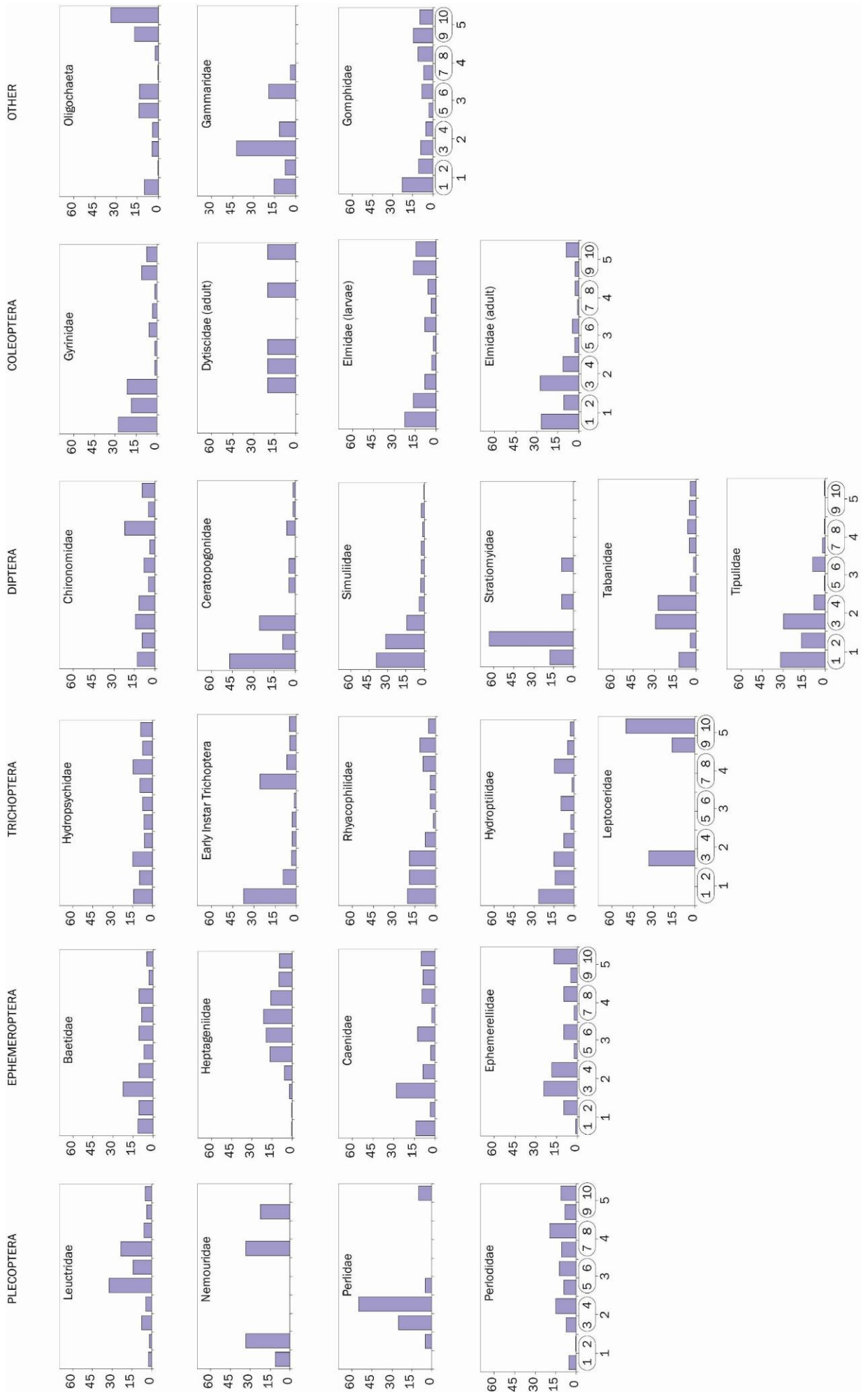
There is no clear relationship between macroinvertebrate abundance and benthic velocity when all 150 samples are considered ($r = 0.18$). There is, however, a significant relationship between sample abundance and POM ($r = 0.70$, $\alpha 0.01$), indicating the relative importance of this variable. The finding is consistent with the observation that greater sample masses of POM influence greater sample abundances, independently of water depth, Froude number and substrate composition (Gonzalez and Graca 2005). Almost half (42 %) of the total reach-scale macroinvertebrate abundance count was captured at sites 1–3. Moreover, the majority of taxa comprising the reach-scale community are more abundant at site 3 than they are at sites 1 and 2 (figure 4.21) further indicating that their distribution patterns are more strongly related to the greater sample masses of POM at site 3, than they are to the faster and more varied benthic flows at sites 1 and 2 (figure 4.6A and D). It is thus possible that greater sample masses of POM, and the patchiness of POM within sites 1, 2 and 3 explains the concentration of macroinvertebrate abundance along the upstream sub-reach as a whole.

The coincidence of greater variation in abundance and greater absolute abundance counts with faster benthic flows at sites 1 and 2 may nonetheless suggest that the complex hydraulic character of the channel bed in zone 1 produces patchy, high and low sample densities by mediating small-scale macroinvertebrate interactions. The matrix of bedrock and alluvial patches likely influences the dispersal and settlement of individuals throughout the zone. The ‘exchange’ of species [between patches] is a function of the distance between two substrate types (Beisel *et al.* 2000) and so the variation, or patchiness of abundance at sites 1 and 2 (figure 4.13A, error bars) could reflect adjacent and contrasting microhabitat suitability (Lancaster and Mole 1999). Samples with high abundance counts may indicate a patch of preferred hydraulic conditions, where more individuals have been able to settle out of the flow path, and samples with lower abundance counts may reveal patches where flow paths are not suitable for the movement and hydraulic requirements of a greater number of individuals. The variation in macroinvertebrate abundance through zone 1 may also reflect the patchy juxtaposition of a three-dimensional substrate ‘architecture’ (*sensu* Robson and Barmuta 1998) of gravel patches, and a flat, two-dimensional bedrock surface. Both flow and substrate variability between alluvial and bedrock patches likely also regulate the variation in POM through zone 1, and its patchy availability, may be a key influence on microhabitat suitability and thereby the variation in abundance (figure 4.6D, error bars). The considerations of patchiness in zone 1 are important, because the structural heterogeneity of the channel bed in this zone, and thereby the density of physical complexity, is unlike that of the other eight sites along the reach. Discussion of this observation is given in relation to the role of zone-scale morphological complexity in section 4.6.3.

The majority of macroinvertebrate taxa are omnipresent along the reach, and there are no 'indicator taxa' with systematic presences or absences between sites. The uneven pattern of reach-scale abundance may thus be better informed by spatial patterns in the relative abundances of individual taxa, which are instructive of macroinvertebrate community dynamics (Brown 2007) and may better indicate spatial variation in channel hydromorphology than gross-scale community indices (Dollar *et al.* 2007).

In this case, the reach-scale population distributions of Heptageniidae and Simuliidae in particular reflect the uneven reach-scale pattern of abundance (figure 4.21). They account for only 3 % and 8 % of the total reach-scale abundance count (figure 4.11), but occur within 78 % and 76 % of samples, respectively (figure 4.12). Heptageniidae are relatively scarce at sites 1, 2 and 3, but their abundances increase and, moreover, are even between sites 5–10. Heptageniidae are highly mobile mayfly larvae, and may not withstand the faster and varied benthic flows within the zone 1 environment. The morphology of mayflies renders them prone to dislodgment by the flow (e.g. Holomuzki and Biggs 2003). The majority (85 %) of all Simuliidae were collected at sites 1, 2 and 3, with very few occurring between sites 4–10. In contrast to Heptageniidae, these blackfly larvae are relatively passive, and may prefer the faster and varied benthic flows within zone 1 because they are suspension feeders. Simuliidae require a thin layer of smooth laminar flow for their attachment to rocky substrates, and to maintain a streamlined position for feeding, but also faster benthic flows atop this benign hydraulic layer for the supply of food (Wallace and Merritt 1980).

Figure 4.21 (following page) *Reach-scale distribution patterns of all twenty-six macroinvertebrate taxa. Upper X axis indicates site, and lower X axis indicates zone. Y axis indicates the percentage of the population of that taxon collected at each site.*



In addition to the upstream concentration of macroinvertebrate abundance at sites 1–3, macroinvertebrate abundance appears to be structured by zones (figure 4.15). Zonation is not obvious in the individual reach-scale distributions of all twenty six taxa, because there is clear between-site dissimilarity in their abundance counts, within each zone (figure 4.21). However, a pattern of zonation is evident in the collective proportion of Ephemeroptera, Plecoptera and Trichoptera (EPT) at a site (figure 4.22). There is clear between-site similarity in zones 1, 2, 3 and 5 and between-zone differences are evident. At the upstream site in zone 4, the proportion of EPT comprising total site abundance is similar to that in zone 3, and the proportion at the downstream zone 4 site is similar to that in zone 5.

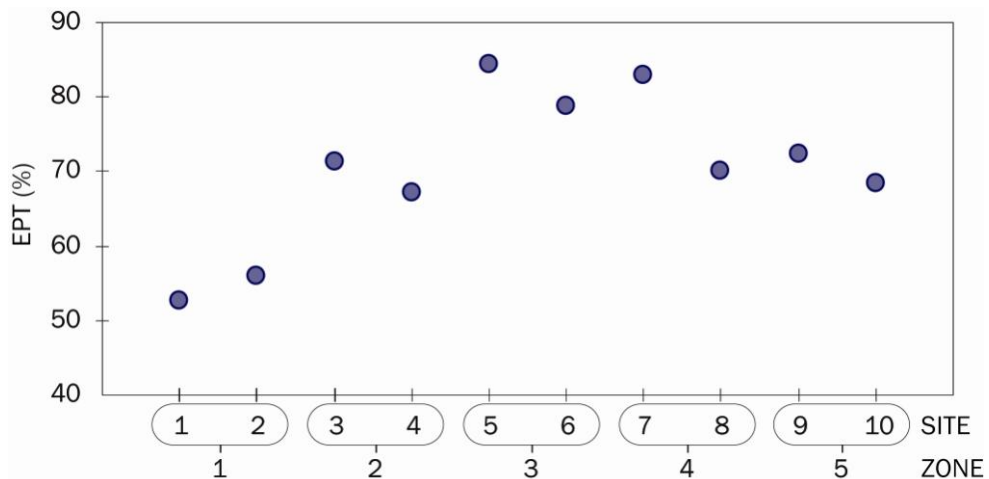


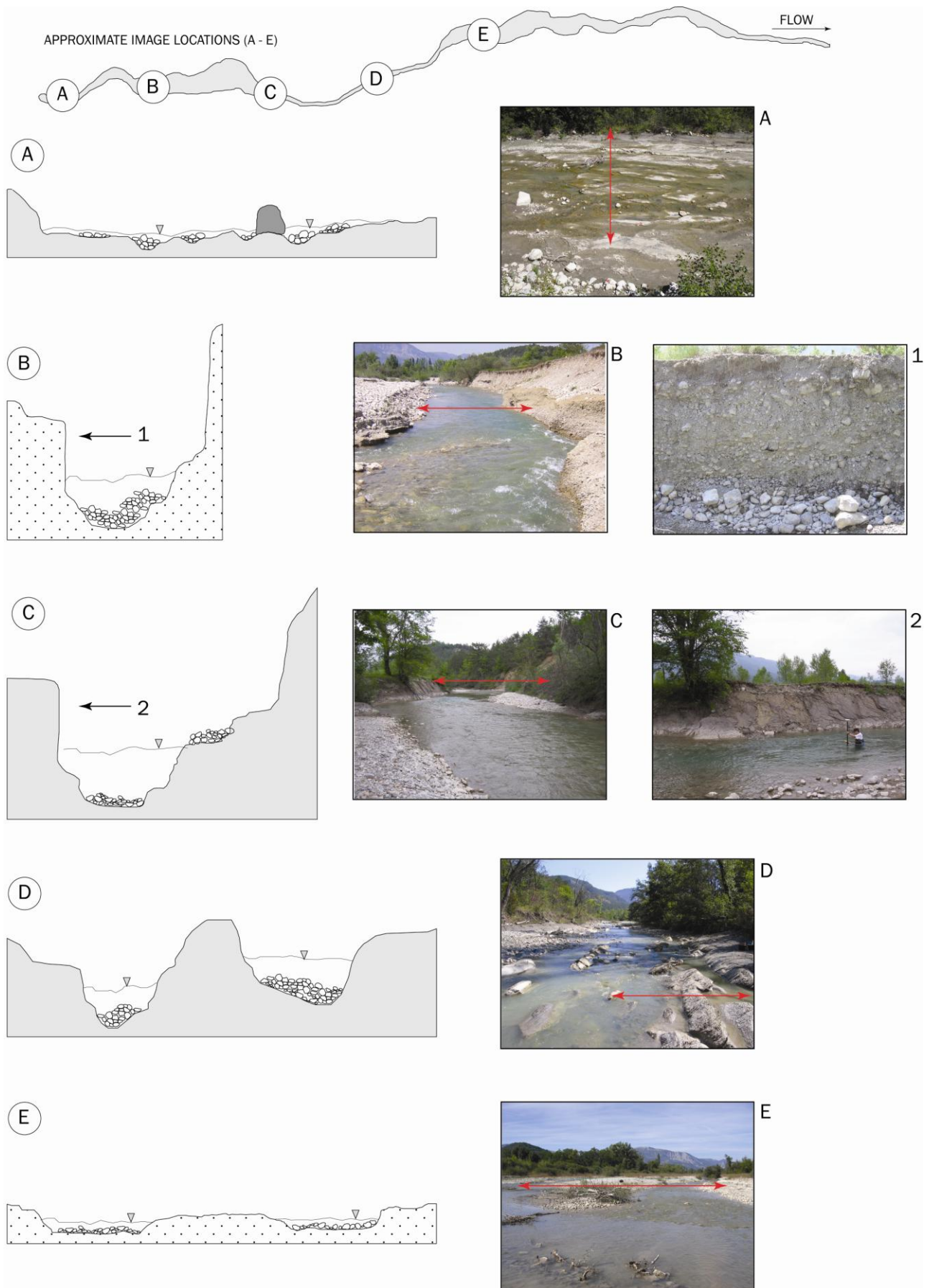
Figure 4.22 The proportion of EPT taxa comprising total site abundance, at all ten sites.

The proportion of EPT taxa present at a site has been traditionally used as a ‘biomonitoring’ metric, because these taxa are sensitive to stream water quality, and so pollution (Lenat and Penrose 1996). However, it is particularly noteworthy that Sullivan *et al.* (2004) identified a significant difference in the proportion of EPT taxa between stable and unstable reaches, in terms of both vertical and lateral channel planform adjustment. It is perhaps then possible that zone-scale variation in the intensity and frequency of both vertical and lateral processes of channel adjustment is reflected in the distribution of EPT taxa between Luc and Recoubeau (figure 4.22). In particular, the difference in EPT taxa between zone 4 sites is an important distinction. The similarity of sites 5, 6 and 7 may indicate the recent incision through the upstream part of zone 4, and the similarity of EPT at sites 8, 9 and 10 may reflect the redistribution of sediment into the downstream part of zone 4 and zone 5.

4.5.3. Sub-reach structure in grain-size characteristics, macroinvertebrate diversity, dominance and evenness

The preceding discussion has considered spatial structure in macroinvertebrate abundance, but this is only one of the five indices considered in the analysis of how macroinvertebrate communities are organised along the reach. Abundance is a gross count of the number of individuals, but does not account for the relative abundances of different taxa present at a site. The indices of diversity, dominance and evenness reflect these changes and thereby indicate important community dynamics of competition and exclusion, for example. The results showed that these different aspects of community structure (abundance, diversity, dominance and evenness) are manifest in different spatial ways. Zonation was identified in sample abundance counts using ordination analysis (figure 4.15) and can be seen in the proportional abundance of EPT (figure 4.22). In contrast, macroinvertebrate diversity, dominance and evenness are structured by sub-reaches (figure 4.13). Zones can be clearly differentiated on account of their planform style and channel bed structure, which have been identified to configure the reach-scale dynamics of sediment source, transfer and accumulation. More recently, however, it has been observed that reach-scale incision has altered these dynamics, such that processes of bedload transfer and storage may operate between sub-reaches, rather than zones. This has led to the hypothesis that sub-reach differences in macroinvertebrate community structure reflect the sub-reach variation in flow patterns and processes of channel bed scour associated with sub-reach regimes of sediment transfer and storage. This is a function of the variation in cross-sectional channel bed structure which is clearly discontinuous within and between the zones (chapter 2, figure 4.23). Zone 3 in particular is a unique morphological setting in which processes of sediment storage and transfer contrast to those effective in other zones. This mid-reach corridor is central to the hypothesis of how local differences in planform and channel bed structure influence the redistribution of bedload, and subsequently the organisation of macroinvertebrate taxa, by moderating intensities and frequencies of flow and channel bed disturbance. Outcropping bedrock structures interrupt the transfer of sediment between upstream and downstream zones (section 3.4.1.3), which is further suggested by patterns of grain size fining and sorting through the mid-reach (figure 4.13). These bedrock hummocks are exposed intermittently between alluvial patches and this provides a dynamic setting of channel bed patches exposed to frequent but moderate perturbation.

Figure 4.23 (following page) *Differences in cross-sectional channel bed structure between the zones. Letters indicate approximate location of sketches A-E, which illustrate the channel cross-section in photographs A-E, respectively. Red arrows on photographs indicate more precise sketch location. Grey inverted triangle indicates flow level. Grey shading denotes bedrock, white fill with dots denotes alluvium.*



Variation in the intensity and frequency of flow and substrate disturbances is known to affect the distribution of macroinvertebrate taxa (Poff and Allan 1995, Death and Winterbourn 1995), between patches that undergo scour, fill or otherwise remain stable (Matthaei *et al.* 1999, Effenberger *et al.* 2006, Olsen *et al.* 2007). These flow and substrate perturbations may not necessarily be 'disturbances' in geomorphic terms but associated with frequent flow events. The subtle and constant movement of small particles during baseflow has been shown to influence spatial patterns of macroinvertebrate diversity (Miyake and Nakano 2002), and Gibbins *et al.* (2007a) identified that very low rates of bedload transport can trigger the mass displacement of taxa, even during events that leave bed armour intact (Gibbins *et al.* 2007b).

Because these local disturbances can have long-term effects (Matthaei and Townsend 2000), the present-day snapshot of macroinvertebrate community organisation may thereby reflect the historical disturbance regimes founded by the morphological structure of the zones. This hypothesis is consistent with the view that macroinvertebrate communities are structured by their adaptation to the temporal and spatial heterogeneity of their 'habitat' (Huryn and Wallace 1987, Townsend and Hildrew 1994). In this instance, the consideration of 'habitat' appears to be relevant in at the zone scale: domains in which variation in different processes of sediment reorganisation, and associated flow patterns and bed scour, can be delineated.

Pattern does not necessarily indicate process, but it is possible to infer processes from interlinked patterns (Thorp *et al.* 2006). Combined with an understanding of how processes of sediment transfer and storage have been shaped through time, and how they operate along the reach at present (chapter 3), corresponding sub-reach structure in processes of bedload distribution and macroinvertebrate community structure is hypothesised to indicate that sub-reach settings of variable flow patterns and channel bed scour influences the organisation of macroinvertebrate taxa along the reach.

Depressions within the bedrock channel of zone 1 create areas of flow separation and the short-term settlement of relatively fine gravels (figure 2.6D), but there are few storage areas for coarser bedload. Indeed, bedrock runnels act to promote the downstream transfer of bedload (figure 2.6E). At the reach scale, mean flow velocity is highest within the zone, and the channel is highly competent because there is little resistance to the flow. Bedload may be conveyed downstream relatively rapidly, translating as relatively coherent waves (*sensu* Lisle *et al.* 2001). It is likely therefore that temporal variation in channel bed disturbance is different in this zone compared to the others along the reach. In particular, when a volume of bedload is supplied to zone 1 it is likely that it is conveyed relatively quickly through to zone 2, and so bed disturbance occurs intermittently, and is relatively short-lived, but is intense.

When bedload arrives in zone 2 alluvial bedforms of riffles and pools provide greater resistance than the bedrock in zone 1. With distance downstream, the active channel widens and multiple channels develop, suggesting that bed shear is reduced. Because the channel is then less competent and sediment disperses over a larger area, Bedload will perhaps then

take longer to disperse through zone 2. Bed disturbance probably occurs at a lower intensity to that within zone 1, but at a greater intensity to that within zone 3.

The dynamics of bedload transfer are scaled by supply (Nelson *et al.* 2009). Downstream fluxes of sediment supplied to the narrow mid-reach are moderated by structural constraint at the transition to zone 3 (section 3.5.2.1) and so smaller sediment pulses may enter the corridor. Temporal fluctuations in the intensity of bed scour through zone 3 may thus be small, but it is thought that the concentration of stream power and the relative decrease in resistance through the narrow, mixed bedrock channel will likely promote frequent bed scour. The fining and sorting of bed material through the mid-reach (figure 4.7), and the larger than average local differences in these grain-size characteristics (figure 3.10) indicates that sediment entering zone 3 is scattered and filtered. It is apparent that this fractionation is facilitated by bedrock structures (figures 2.7 and 3.10). The cross-sectional heterogeneity in channel bed topography, and the relative abundance of outcropping bedrock hummocks in zone 3 provides a complexity of bed morphology that contrasts with channel structure in the up- and downstream zones. The association between morphological complexity and the transfer of sediment is important, because the local flow and substrate disturbances associated with these interactions influence the dispersal and organisation of macroinvertebrate taxa, and the way in which habitat is created, modified and maintained. An abundance of less mobile structural elements, such as bedrock structures, has been significantly associated with high habitat heterogeneity by the localised forcing of scour and deposition (Yarnell *et al.* 2006). In this way, the bedrock structures mediate relatively frequent but intermediate intensities of flow and sediment disturbances.

Macroinvertebrate communities are significantly more diverse and significantly more even through the mid-reach, and these patterns may be influenced by the hypothesised frequent and intermediate intensity of disturbance. Other work has observed that macroinvertebrate diversity and evenness are higher in scour patches that undergo frequent (Miyake *et al.* 2005, Effenburger *et al.* 2008) and intermediate (Miyake and Nakano 2002) disturbance. In addition to this being a long-term effect (Matthaei and Townsend 2000), it has also been shown that community diversity is not reduced in the short-term by the flushing of flow and sediment (Mochizuki *et al.* 2008). Brown (2003, 2007) has considered that disturbances are buffered by morphological heterogeneity, and this mechanism may be effective in the mid-reach by the complexity of channel bed elements providing the most suitable mosaic of niches (*sensu* Beisel *et al.* 2000) for colonisation, and interstitial refugia during episodes of flow and substrate disturbance. This would also support the view that higher diversity is dependent on habitat being 'patchy' and dynamic (Wilson 1994), for competitive exclusion to be effective in conditions of intermediate disturbance (Connell 1978, Ward and Stanford 1983, Townsend *et al.* 1997).

The ability to compete for resources and interstitial refugia is dependent on the physiological traits of individual taxa, such as body size, flexibility and shape (Gayraud and

Philippe 2001, Lamouroux *et al.* 2004). The ability to resist dislodgment is also a function of physiological traits (Holomuzki and Biggs 2003, Mochizuki *et al.* 2008). Between Luc and Recoubeau the reach-scale association between macroinvertebrate diversity and *surface* grain-size diversity reflects these mechanisms of competitive exclusion. Well-sorted surface gravels support relatively diverse macroinvertebrate communities (figure 4.19), indicating that taxa unable to resist dislodgment from the substrate are removed by the scour-type disturbance associated with the process of sorting. In the same regard, the converse relationship between *subsurface* grain size and macroinvertebrate diversity ($r = 0.76$, $\alpha = 0.05$) may reflect the variable abilities of different taxa to take refuge in the subsurface. An increase in the diversity of grain sizes is associated with an increase in the diversity of interstitial niches, which has been shown to significantly influence spatial variation in community structure (Braccia and Voshell 2006). The amount of interstitial space in the subsurface thereby has a 'selective effect' (Gayraud and Philippe 2001) on the presence of taxa as a function of their physiological traits.

The consideration that a 'selective effect' may account for differences in macroinvertebrate community structure between zones of characteristic flow and sediment regimes, and associated channel bed disturbances, is consistent with Habitat Templet Theory (Southwood 1977), and subsequent work that has shown how different habitat conditions and associated patterns of disturbance 'filter' different taxa by their traits (e.g. Poff and Ward 1990, Resh *et al.* 1994, Death and Winterbourn 1995). While this study has not discriminated spatial patterns by way of physiological traits, there is evidence to suggest that taxonomic identification at family level can provide an accurate description of trait diversity (Dolédec *et al.* 2000, Gayraud *et al.* 2003). It is possible therefore that the spatial variation in macroinvertebrate community structure between Luc and Recoubeau reflects differences in taxon resistance and resilience to the variable intensity and frequency of channel bed disturbance in each zone.

The effect of competitive exclusion is also influenced by change in the availability of food resources (Lepori and Hjerdt 2006) and recovery of the food base following a disturbance (Death and Zimmerman 2005). It has also been shown that higher diversity under intermediate levels of disturbance can be influenced by the level of productivity (Haddad *et al.* 2008). Between Luc and Recoubeau, sub-reach variation in the supply of nutrients and productivity is reflected in the discontinuous riparian buffer (figure 3.7A) and this may further influence the patterns of macroinvertebrate community structure along the reach. Zones 1 and 3 are constrained by bedrock in the channel bed and the channel banks, which limits their lateral exchanges with the floodplain. In contrast, the alluvial zones 2, 4 and 5 are unconstrained and so their lateral exchanges are uninhibited. Lateral exchanges with the floodplain have been established as a primary source of nutrients and particulate matter in river channels (e.g. Junk *et al.* 1989, Tockner *et al.* 2000). Aguiar *et al.* (2002) showed that riparian features explained a higher percentage of variation in macroinvertebrate organisation

than the abiotic environment, and considered that this reflected the importance of food supply. It has also been observed that in confined reaches with little or no floodplain exchange, imported organic material is transported downstream relatively quickly with minimal processing by organisms (Sheldon and Thoms 2006). Through the narrow and constrained mid-reach this is likely facilitated by the relatively frequent dynamics of sediment transfer, and may be indicated by the reduced sample masses of POM between mid-reach sites (figure 4.6D). The mid-reach is also shadowed by an overhanging riparian canopy that would also provide a rich allochthonous [external] source of organic material. In constrained channels, carbon does not originate from upstream but is generated by autochthonous production [internally] and riparian inputs (Thorp and DeLong 1994). Reach-scale variation in carbon is not correlated with a longitudinal gradient (Hauer *et al.* 2000) but controlled by local channel morphology (Walters *et al.* 2007). Streambed sediments also typically function as carbon reservoirs (Shields *et al.* 2008). There is clear zone-scale variation in channel bed topography, and in the depth of the overlying alluvial fill of bedrock, and so relative amounts of streambed carbon are likely to vary within and between the zones.

The cross-sectional morphology and variable bedrock constraint of the channel further influence vertical exchanges between the channel bed and the sub-surface hyporheous, which are also important influences on the in-stream organisation of macroinvertebrate communities (e.g. Stanford and Ward 1988, 1993). In bedrock channels, differences in channel bed topography and depths of overlying alluvial fill cause variation in hyporheic exchanges (Packman and Bencala 2000, Wondzell 2006, Hester and Doyle 2008). There is a clear distinction between zones 1 and 3 in terms of their substrate proportion and structure and so there is likely to be a difference between them in terms of their vertical exchanges. The channel bed in zone 1 is dominantly bedrock, with relatively small, thin and transient patches of gravel in bedrock depressions. The channel bed in zone 3 is also composed of bedrock and gravel, approximately in equal proportion, but the topography and the cross-sectional structure of the channel is completely different to that in zone 3. Bedrock structures are 'hummocky' in zone 3 and in terms of their height and asymmetrical shape they are much larger. They cause the longer-term storage of gravel patches, which are much larger and deeper than those in zone 1. The alluvial zones 2, 4 and 5 have not scoured to bedrock, and so it is likely that their processes of vertical exchange contrast to those in the mixed bedrock-alluvial zones 1 and 3. So, in addition to the sub-reach variation in processes of sediment storage and transfer, there is likely to be clear discontinuity in lateral and vertical processes of connectivity between Luc and Recoubeau, which may further contribute to the sub-reach variation in macroinvertebrate community structure.

It is well established that discontinuities in flow and substrate are critical determinants of change in macroinvertebrate community structure, at different spatial scales (e.g. Statzner and Higler 1986, Brown and Brussock 1991, Grubaugh *et al.* 1996), but rather than identify 'settings' in which dominant controlling processes occur to generate corresponding

discontinuity in channel morphology and macroinvertebrate organisation (but see the channel 'links' of Rice *et al.* 2001), spatial variation in community structure has been predominantly related to spatial variation in local 'habitat' conditions of channel form: geomorphic units of riffles and pools, for example. This lacks an appreciation of how 'habitat' is dynamic, and constrained by geomorphic processes operating at larger spatial scales.

Between Luc and Recoubeau, the geomorphic zones delineate the scale at which dominant processes occur to produce the spatial structure of macroinvertebrate organisation. The zones have been interpreted as patches in which macroinvertebrate community structure respond to different disturbance regimes, which recognises them as 'process domains' (Montgomery 1999) or 'functional process zones' (Thorp *et al.* 2006). Describing 'habitat' at the scales of dominant controlling processes may be a more effective way of describing biological distributions (Strayer *et al.* 2006) because it identifies the 'setting' in which the 'mosaic' of different, smaller scale patches (for example, patches of bed scour and fill) for macroinvertebrate colonisation is regulated. Between Luc and Recoubeau, the dominant controls on macroinvertebrate community organisation are considered to be processes of bedload dispersal, which are controlled by zone-scale channel structure. In turn the maintenance of discontinuous and heterogeneous channel structure is influenced by the supply of sediment to the reach, and flood activity, processes that are ultimately constrained by the larger-scale and longer-term impact of forest cover within the Béoux sub-catchment (figure 4.24). The observation that macroinvertebrate community organisation is influenced by different processes operating at different scales enforces the key element of Hierarchical Patch Dynamics Theory (Lu and Woucks 1995, Poole 2002). Should there be any change in forest cover within the Béoux, then sediment supply to the reach will change. This will cause a change in the sub-reach dynamics of sediment transfer and storage; have implications for the zone-scale variation in the morphological structure of the channel, and thus the sub-reach domains of flow and substrate disturbance. This may result in a different configuration of zones and ultimately cause a change in the organisation of macroinvertebrate taxa along the reach. The findings of chapters 3 and 4 are, therefore, particularly significant in the context of management plans to reactivate the dominant supply of bedload to the reach. The implications of this action will now be considered in chapter 5.

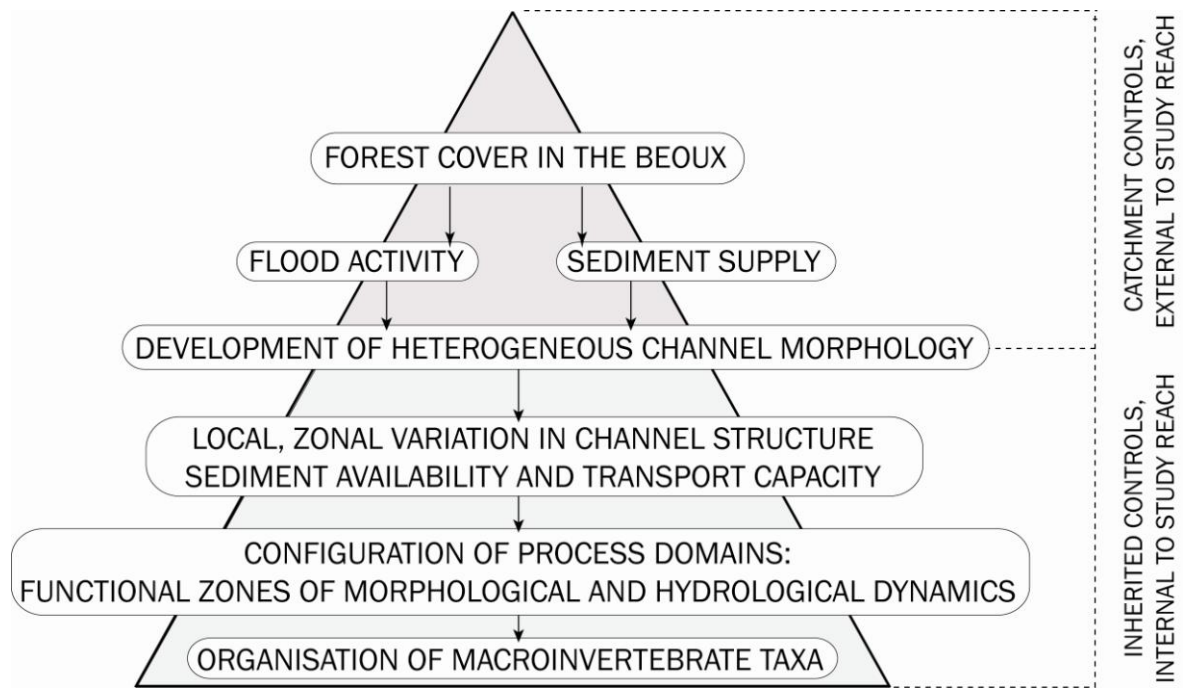


Figure 4.24. *Hierarchy of controls on macroinvertebrate community structure between Luc and Recoubeau.*

4.6. Chapter Conclusions

In response to the aims and objectives in section 4.2 this chapter has established that:

- The sub-reaches differentiated by regimes of sediment storage and transfer in chapter 3 are, to some degree, evident in the structure of grain size characteristics along the reach. Zonation is not clear in the physical variables examined.
- There is a greater amount of POM within upstream sites, owing to the supply from the riparian canopy within zone 1 and its conveyance and collection within the upstream part of zone 2.
- Macroinvertebrate abundance is significantly higher within upstream sites, and this is related to the upstream abundance of POM. POM is a significant influence on sample abundance, independently of longitudinal position along the reach.
- Macroinvertebrate diversity, dominance and evenness are structured between sub-reaches and this likely reflects zone-scale variation in flow patterns and channel bed disturbances, which is mediated by the zone-scale variation in channel bed structure and complexity.

5. Future Changes in Channel Morphology and Macroinvertebrate Community Structure between Luc-en-Diois and Recoubeau-Jansac

5.1. Introduction

This chapter aims to integrate the history of morphological change (chapter 3) with observations of channel behaviour, and present-day patterns of reach-scale macroinvertebrate community organisation (chapter 4) to predict possible future changes in the morphological and ecological character of the Drôme between Luc-en-Diois and Recoubeau-Jansac. These considerations are motivated by the planned remobilisation of sediment within the Béoux sub-catchment (chapter 1), because this intervention is intended to instigate long-term changes to the dominant supply of bedload to this reach, which will have possible implications for present-day morphological zonation and macroinvertebrate community organisation. The principal aim of remobilising sediment in the Béoux is to increase the supply of sediment to the Drôme so that degradation will be alleviated, both along the study reach and in downstream reaches. To evaluate the possible impacts of this strategy along the study reach, two circumstances of possible future change in channel morphology and macroinvertebrate community organisation will be considered:

- A *laissez-faire* approach, in which no management intervention would occur
- The successful remobilisation of sediment in the Béoux sub-catchment

Most of the following discussion on future changes in channel morphology and macroinvertebrate organisation is speculative. The evaluation of how sediment remobilisation in the Béoux may influence future morphological adjustments along the study reach is based on an understanding of present-day channel dynamics and propensity for change, and how this present-day condition has been shaped by historical channel behaviour. In the absence of any detailed measurement of how the present-day channel responds to changes in sediment load, and redistributes available bedload, this account is a rigorous basis for estimating likely future trajectories of morphological change (Brierley and Fryirs 2000, Fryirs *et al.* 2007). Finally, this chapter considers how the qualitative estimates of future change developed herein might be quantified using appropriate modelling tools.

5.2. Present-day Context of Sediment Supply, Flood Activity and Propensity for Morphological Change

At present, coarse sediment supply to the reach is very limited. Together with the capacity of the Upper Drôme as a natural sediment trap (section 2.2.2), the implementation of check-dams and extensive afforestation within the Béoux sub-catchment (section 2.3) has substantially reduced the supply of bedload to the reach. Should no management intervention be undertaken, these controls on sediment supply to the reach will be maintained and so sediment supply is likely to further decrease in the long term. Long-term records of flood activity at Luc-en-Diois show a clear ongoing trend of declining flood frequency (section 2.5) and so the intermittency of sediment supply to the channel is also expected to further decrease.

To date, the combined, long-term effects of a reduced sediment supply and less frequent flood activity have been reach-scale incision, straightening and narrowing. Overall amounts of degradation have been modest, but there is significant spatial variability in these trends and local amounts of incision, straightening and narrowing have been extensive. Between 1928 and 2003 more than 25 % of the channel had undergone incision in excess of 1.0 m, with a maximum amount of 2.1 m in the mid-reach zone 3 corridor (section 3.4.1.3).

There has also been a temporal change in channel adjustment. Between 1948 and 2001 the channel underwent localised expansion in zones 2 and 4, in response to flood events (section 3.4.2.4), but by 2006 it was clear that incision, narrowing and straightening were the dominant, ongoing morphological changes along the reach as a whole (sections 3.4.1.3 and 3.4.2.1). It was also evident that by 2006 reach-scale incision had caused a disconnection between the channel and the active floodplain (section 3.5.1.2) and exacerbated local differences in the storage, transfer and accumulation of available bedload. Between 1980 and 2001, these dynamics of bedload redistribution sustained the present-day zonation in channel planform and substrate (section 3.5.2, figure 3.25), but between 2001 and 2006 zone-scale changes in planform (the elongation of the zone 3 corridor, by the narrowing of zones 2 and 4, and the widening of zone 5) caused a reduction in the distinctiveness of channel zonation, which indicated a change in the dynamics of sediment redistribution (section 3.5.2.2). The source, transfer and accumulation of sediment no longer appeared to be operating at the zone scale, but between upstream, mid-reach and downstream sub-reaches.

Independent of sediment supply to the channel, the dominant control on the discontinuity in overall, long-term trends of degradation, present-day processes of channel adjustment, and future changes in channel morphology, is the discontinuity in channel constraint. Through the mid-reach, the channel is confined within a deep and narrow bedrock corridor, zone 3, which limits lateral channel adjustment. In contrast, the alluvial channel zones up- and downstream of the bedrock corridor are unconstrained and able to adjust

laterally into the floodplain. The importance of this discontinuity in lateral constraint is clear in the historical development of the two wide, alluvial zones 2 and 4 up- and downstream of zone 3. It is also apparent in the consistent patterns of change in channel width between zone boundaries, that have been stable through time (section 3.4.2.1), and between epochs that experienced variable degrees of flood activity (figure 3.18). A bottleneck is created as the channel narrows from zone 2 into the bedrock-confined corridor of zone 3 and this point of lateral constraint on the channel is an important long-term control on channel evolution, by forcing the course of the 1978 avulsion (section 3.5.1.1) and by controlling the connectivity of the zones, in terms of the downstream redistribution of bedload.

The significance of discontinuity in structural constraint also extends to reach-scale patterns of vertical channel adjustment. At least since 1928, variable changes in elevation have occurred between boundaries that match the transitions in channel width, and delineate the present-day zones. Moreover, there has been virtually no net change in channel elevation at the upstream and downstream boundaries of the mid-reach corridor (figure 3.9A, arrows X and Y) which indicates that bedrock has controlled channel adjustments at these locations, particularly upstream of the corridor (section 3.5.1.1, figure 3.19). It is also apparent that relative to the surface of the overlying alluvial fill, the topography of underlying base level bedrock is uneven, because there is differential exposure of bedrock in locations that have undergone similar amounts of incision (section 3.4.1.3). This is important, because where bedrock is exposed in the channel bed it is a significant influence on channel adjustment. The cross-sectional and three-dimensional structure of outcropping bedrock influences processes of sediment storage and transfer within the zones (sections 3.4.1.3 and 4.6.3) and relatively dynamic changes in channel profile in the short-term. Vertical channel adjustments within unconstrained alluvial zones, with relatively homogenous channel beds, are less variable, in space and in time (figure 3.9B). This context raises the following questions, which are addressed in sections 5.4.1 and 5.5.1.

- How might the discontinuity in structural constraint influence future channel adjustments, under a scenario in which there is a further reduction in sediment supply?
- Would zonation be reactivated in response to a renewed supply of sediment?

It was also apparent that by 2006, reach-scale incision and disconnection from the active floodplain has caused a change in the way the channel responds to flood events. Between 1980 and 2001, flood events locally widened unconstrained floodplain areas in zones 2 and 4 (figure 3.18), by reactivating former channel areas that were in the process of joining the floodplain, by the establishment of vegetation on lateral bar and bank surfaces. Between 2001 and 2006, however, lateral channel areas in zones 2 and 4 were not eroded, and the distinction of the zones was not reactivated, despite the occurrence of a large (1 in 44

year) flood in 2003. Instead, zones 2 and 4 underwent narrowing and straightening (figure 3.24), indicating that by 2006 the channel had incised to an extent at which it can contain and naturally 'channelise' flood flows, preventing the reactivation of sediment stores and lateral channel erosion.

The incision and narrowing of the channel into a 'chute' through zone 2 also caused a small and localised avulsion of the right bank, probably during the 2003 flood (figure 3.26) and this change in channel behaviour indicates that the channel may be primed for more substantive change.

At present, the channel is supply-limited, even availability limited (*sensu* Ferguson 2008) and, without a sufficient protective depth of alluvial cover, is prone to further flood-induced incision and a rapid adjustment of channel form, such as that seen in response to the 1978 flood. Between 1956 and 1978 the substantial reduction in sediment supply to the reach and the absence of flood activity primed the channel not for short-term localised expansion, but for substantial avulsion and channel straightening at the reach scale, and the creation of the narrow, mid-reach zone 3 corridor. Since this event, there has been a further decrease in flood activity, and sediment supply to the reach is quite feasibly the most limited it has been during its history. At the present day, therefore, the channel may be in a similar situation to that prior to the 1978 avulsion.

This was a pivotal change in the evolution of the channel and the catalyst of present-day zonation. Should the amount of channel straightening seen between 2001 and 2006 (a reduction in sinuosity of -2.2 % over 5 years) continue through the next five years, then the channel will undergo the same extent of reach-scale straightening seen between 1971 and 1980 (-5.5 % over 10 years), in response to the 1978 flood. It is clear that marked spatial variation in constraint on the channel will preclude the natural channelisation of the reach into a narrow, incised conduit linking up and downstream reaches of the Drôme. However this constraint may also cause channel avulsion during a large flood event, changing the morphological dynamics of the reach and the development of a different, reach-scale channel morphology. This raises an additional question, which is addressed in section 5.4.2.

- Has the fundamental behaviour of the channel changed to an extent whereby channel zonation can no longer be maintained?

5.3. Present-Day Context of Macroinvertebrate Community Organisation

The importance of structural constraint and within-zone variation in channel structure is further emphasised in chapter 4, in terms of how it influences the organisation of macroinvertebrate taxa along the reach. The zones are domains of variable structural complexity, which regulates both within-zone and zone-scale variability in processes of bedload dispersal, flow patterns, lateral exchanges with the floodplain, and vertical exchanges with the subsurface hyporheos. The dispersal of bedload within the zones is thought to be moderated by the three dimensional and cross-sectional channel structure of each zone, and is hypothesised to create variable intensities and frequencies of bed scour and fill. In turn, the dispersal of bedload is hypothesised to be the dominant control on the spatial patterns of macroinvertebrate community structure along the reach, which reflect the different abilities of individual taxa to tolerate or resist these different bed disturbance regimes.

Macroinvertebrate communities in the upstream sub-reach are significantly less diverse and more dominated than those in the mid-reach. Sediment is infrequently supplied to the reach, and when it arrives in zone 1, it is conveyed rapidly downstream into zone 2 in relatively coherent waves. Compared to the mid-reach, the reduced diversity and the relative dominance of macroinvertebrate communities sampled in the upstream sub-reach is considered to reflect the infrequent and intense bed disturbances caused by this dynamic of sediment transfer.

Macroinvertebrate communities in the downstream sub-reach are also significantly less diverse and more dominated than those in the mid-reach. In the downstream part of zone 4 and in zone 5, the accumulation of sediment is hypothesised to exert relatively more frequent and relatively more intense channel bed disturbances than those experienced in the upstream sub-reach, as the associated 'fill' of the channel bed reduces the availability and suitability of patches that could otherwise provide refugia for different taxa.

Macroinvertebrate community diversity and evenness is significantly higher through the mid-reach than in the upstream and downstream sub-reaches (tables 4.10 and 4.11), where bedrock structures create a diversity of flow patterns. The size-fractionation of bedload through the mid-reach (figure 3.10) is considered to further indicate that these protruding bedrock structures filter the dispersal of bedload across the channel bed, by acting as small topographic 'barriers' that moderate the intensities of bed scour. The relatively dynamic changes in channel profile in this morphological setting (section 3.4.1.3) further suggest that processes of bedload dispersal and thus bed scour are also relatively frequent. These processes are hypothesised to exert intermediate disturbances, more frequent but of relatively reduced intensity compared to those in both up and downstream sub-reaches.

The proportion of EPT taxa at a site is also greatest within the mixed bedrock-alluvial mid-reach (figure 4.22). This metric is well established as an indicator of 'stream health' (Lenat and Penrose 1996). Stream health has also been linked to physical diversity (Norris

and Thoms 1999) and these associations support the hypothesis that at present there is an apparent optimum of both physical and macroinvertebrate (biophysical) diversity through the mid-reach. Should there be an increase or a reduction in the diverse morphological structure of the mid reach, then an associated change in flow patterns and processes of bed scour are likely to cause a decrease in macroinvertebrate diversity, dominance, evenness, and the proportion of EPT taxa.

It is clear from these observations that compared to the upstream and downstream sub-reaches, which are dominantly bedrock and alluvial, respectively, the mixed bedrock-alluvial morphology of the mid-reach supports the most diverse and least dominated macroinvertebrate communities. It could thence be argued that if the reach was allowed to incise to bedrock, such that the channel was characterised by a homogeneous morphology characteristic of zone 1, then there would be a reduction in the diversity of in-stream macroinvertebrate taxa, and a decrease in the proportion of EPT taxa. In the same regard, it could also be seen that these same changes in the reach-scale macroinvertebrate population would occur if the reach developed an entirely alluvial morphology typical to that of zones 4 and 5. In the absence of within-reach, zone-scale controls on sediment distribution, these scenarios could be possible. However, it is clear that the channel cannot develop a homogeneous reach-scale morphology, because of fundamental differences in the propensity and the capacity of the channel to adjust (chapters 3, 4, and section 5.2). This precludes the possibility of the reach becoming a five-kilometre bedrock channel, or a braided alluvial system. Equally, it is clear that the channel cannot develop a mixed bedrock-alluvial morphology characteristic of zone 3. Under the two contrasting management scenarios, future increases or decreases in sediment supply to the channel will yield different amounts and patterns of channel degradation and aggradation within and between the zones, rather than have a reach-scale effect. As a result, the channel will not undergo uniform changes in macroinvertebrate community structure, but relative increases or reductions in diversity, dominance and the proportion of EPT taxa between the zones. This raises one final question that is addressed in section 5.5.2:

- Which of the two management scenarios would be 'ecologically meaningful' in the sense that the present-day macroinvertebrate community characteristics would not be reduced?

5.4. Possible Future Changes in Morphology and Macroinvertebrate Community Organisation under a *Laissez-Faire* Strategy

5.4.1. How might the discontinuity in structural constraint influence future channel adjustments, under a *laissez-faire* strategy?

If there is no change to the currently limited supply of sediment, it might be hypothesised that reach-scale trajectories of channel narrowing, straightening and incision will continue, and cause the reach to become a straight, narrow, and incised conduit, linking upstream and downstream reaches of the Drôme. However, this would not allow for the critical importance of local controls on channel form. Because of the spatial discontinuity in the propensity and the ability of the channel to adjust, both laterally and vertically (section 5.2), future channel changes will not be uniform along the reach as a whole. Despite the submission that the present-day zonation of the study reach may diminish, and that a tripartite structure may be the next phase of channel development, it is unlikely that these changes are stages along a trajectory of homogeneous reach-scale incision and degradation. The channel zones are variably sensitive to change, and this will not permit a total elimination of morphological heterogeneity.

Zone 1 is considered to act as a ‘conveyor’ feeding sediment that is delivered from upstream rapidly into zone 2 (figure 3.25). Depressions within the bedrock channel of zone 1 create areas for the short-term settlement of relatively fine gravels (figure 2.6D), but there are no storage areas for coarser bedload. The bedrock channel is highly competent and so as long as the current supply of sediment remains stable, it is likely that the downstream conveyance of bedload will continue, and that there will be little vertical channel adjustment in this zone. Given the long-term trend of declining flood frequency, any further reduction in sediment supply to the reach may accelerate erosion of the bedrock in zone 1, but the principal impact would be a reduction in the amount of bedload supplied downstream to zone 2.

5.4.2. Has the fundamental behaviour of the reach changed, to an extent whereby zonation can no longer be maintained?

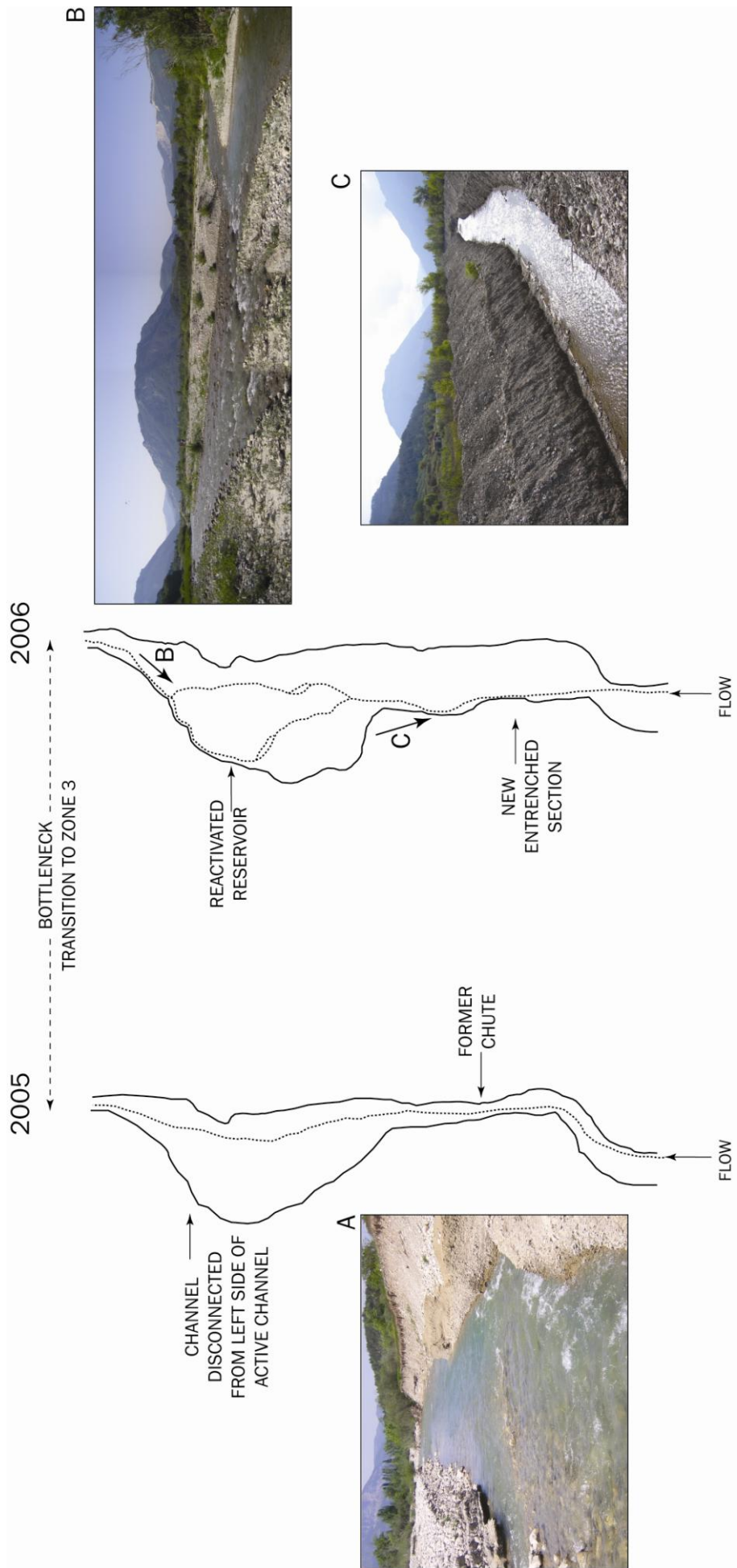
In September 2005, the unexpected construction of a small trench along the upstream part of zone 2 (section 3.3.1) did not change the total channel boundary, and so it was not considered in the analysis of natural historical change in channel planform (chapter 3). This management intervention has, however, caused a substantial change to the course of the active channel. Prior to the intervention, flow and sediment was funnelled downstream in a natural ‘chute’ along the right bank (figure 5.1, photo A). The active channel had incised deeply beneath the surface of and subsequently disconnected from the wide, formerly braided left bank bar (figure 5.1, photo B). The small entrenched section has routed the channel away from the right bank chute, realigning it along the left bank in the upstream part of zone 2 and

between former braid arms in the downstream part of the zone (figure 5.1, photo C). This has reconnected the active channel to the wide, left bank bar complex in the downstream part of the zone, reactivating large stores of sediment for redistribution downstream to zones 3–6.

Under the *laissez-faire* scenario, it is possible that the channel realignment will have a further influence on downstream sediment yield. It could be seen that the construction of the narrow, entrenched section through the upstream part of zone 2 has relocated the former chute from the right side of the channel boundary to the left side of the channel boundary (figure 5.2). With a declining upstream supply of bedload, the relative competence of the narrow entrenched section may promote future incision through the upstream part of zone 2, which would increase the downstream transfer of bedload to the lower part. At the downstream boundary of zone 2, the channel narrows to a bottleneck (figure 3.3). This restricts further downstream bedload dispersal and encourages sediment accumulation (section 3.5.2.1, figure 3.9, arrow X). An increase in sediment accumulation at the bottleneck might cause the channel to avulse laterally into the left bank, circumnavigating the bottleneck, and in doing so increase sediment supply into zone 3. The currently vegetated floodplain on the left bank in zone 3 was once part of an active braid plain (figure 5.3) and so avulsion into a former channel is feasible. There has also been previous avulsion at the bottleneck during the 1978 flood (section 3.5.1.1 and figure 3.19).

At present, the bottleneck at the transition between zones 2 and 3 appears to control the supply of small and frequent bedload fluxes to the zone 3 corridor. Within zone 3, the downstream transfer of bedload to zone 4 is then controlled by the cross-sectional and three-dimensional structure of the channel (sections 3.4.1.3 and 4.6.3, figure 4.23). So long as the rate and volume of sediment supplied to zone 3 continues to be moderate, therefore, it is likely that processes of sediment dispersal within the corridor, and the present-day rate and volume of sediment supplied to zone 4 will be maintained. However, should the supply of sediment to zone 3 increase, as a consequence of avulsion at the bottleneck, then any associated aggradation could smother outcropping bedrock structures, cause a loss of structural morphological diversity, and change the rate, volume and calibre of bedload transferred downstream through the corridor to zone 4. Maintenance of the current zone 3 morphological diversity, and the present-day downstream transfer of bedload to zone 4, therefore depends on maintenance of moderate sediment fluxes from zone 2.

Figure 5.1 (following page) *Planform view of the channel in zone 2 in 2005, prior to the construction of the trench, and in 2006, following the construction of the trench. Unbroken outer lines indicate total channel boundaries. Dashed centrelines indicate courses of the active channels. Arrows A, B and C indicate the direction of capture of the photographs. (A) the former natural chute along the right side of the channel boundary (downstream view), (B) the wide, alluvial left bar in zone 2 (upstream view), and (C) the entrenched section of the channel in the upper part of zone 2, along the left side of the channel boundary (upstream view).*



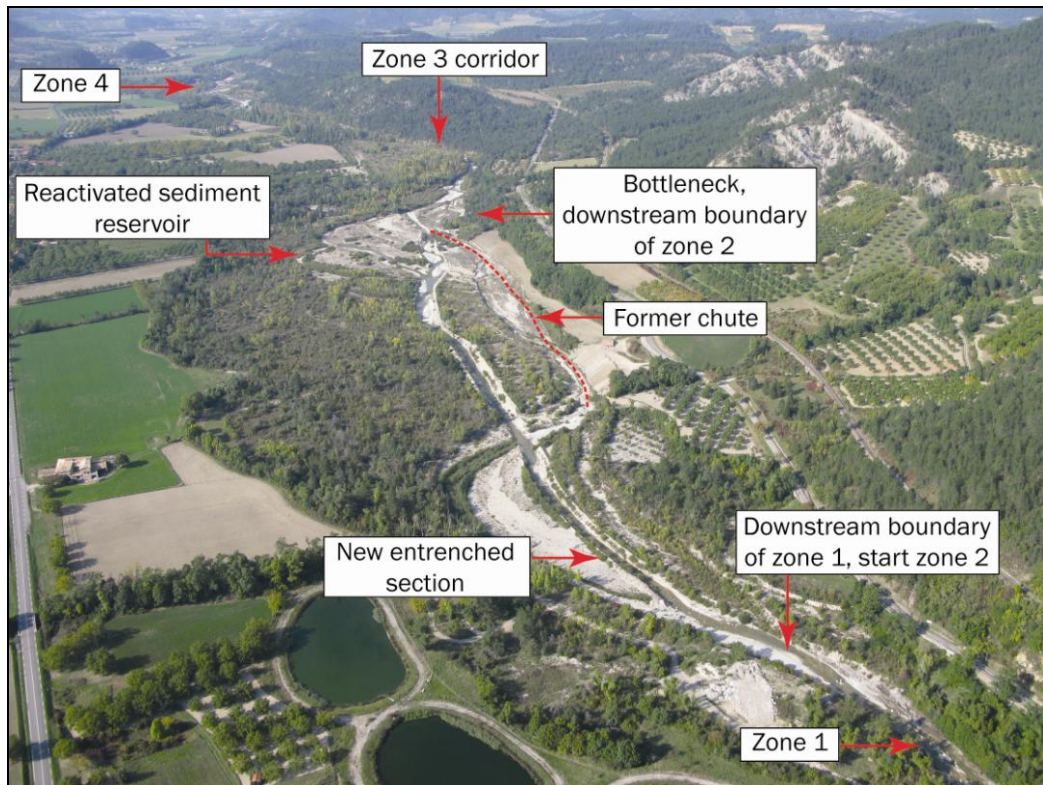


Figure 5.2. Oblique, aerial view of the channel in 2006. Note that the angle of capture has foreshortened the length of the downstream bedload reservoir, and that in reality it approximates the length of the upstream entrenched section (figure 5.1).

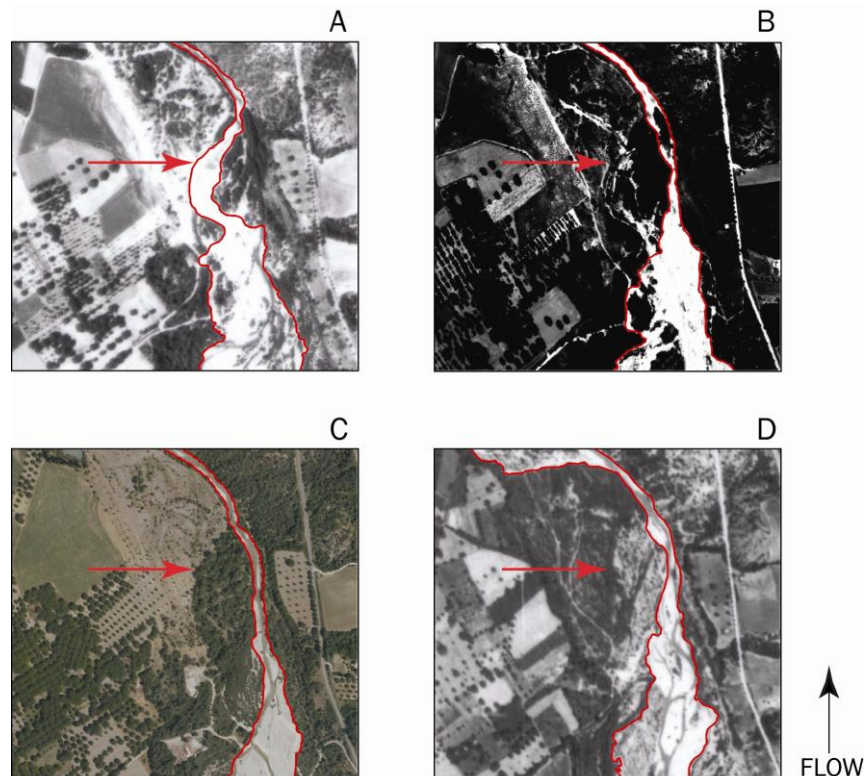


Figure 5.3. Previous channel avulsion at the bottleneck. The former active channel flowed through the left bank in (A) 1971, prior to the 1978 flood, which caused (B) channel avulsion into the right bank, seen in 1980. The ongoing accumulation of sediment at this bottleneck, seen in 2006 (C) is hypothesised to cause possible future avulsion and the reoccupation of a former channel. This area was active prior to 1948 (D). The red arrow indicates the formerly active channel area and its position is maintained in all images. Red lines delineate outer channel boundary in all images.

Historically, bedload has been transferred downstream from zone 2 through zone 3, and has accumulated in zone 4 (figure 3.25). Thus, the wide, alluvial and braided character of zone 4 is dependent on zone 2 providing a sufficient supply of bedload for downstream redistribution. However, between 2001 and 2006, incision and narrowing in zone 4, and aggradation and widening in zone 5, reflected the localised sourcing and redistribution of sediment, respectively, because the supply of sediment from zone 2 was no longer sufficient to maintain their previous morphological distinction (section 3.5.2.2). Under the *laissez-faire* scenario, the reduction in zonation between the downstream zones may be alleviated in the short term, by the renewed supply of sediment from the zone 2 reservoir. In the long term, however, a further decrease in sediment supply to the reach, and incision in zone 2 is likely to maintain the current situation of zone 4 degradation and zone 5 aggradation, because the upstream source would become deficient again.

Incision in zone 2 is hypothesised to cause excessive sediment loading at the bottleneck. Should there be an avulsion around this constraint, sediment may continue to be remobilised downstream in the newly avulsed channel and supplied to zone 3. The channel in zone 3 is a deep, narrow bedrock slot and once the flow enters this corridor, this constraint will stop any further lateral avulsion or migration of the channel. This constraint will persist through time, but there will be a change in the processes of downstream bedload transfer. Aggradation in zone 3, resulting from any increase in bedload supply, could slow the transfer and reduce volumes of bedload supplied downstream to zone 4. This could cause the local sourcing of bedload from the upper part of zone 4 for downstream redistribution, in the same way as a deficient supply of sediment from zone 2 has caused this effect at the present day, and so exacerbate degradation through the upper part of zone 4, and accumulation downstream in zone 4 and in zone 5. Any associated local increase in sediment supply to zone 6 would most likely result in aggradation, and would be promoted by the weir at the downstream end of zone 6. The impact of sediment accumulating within this lower 500 m of the channel may be overbank flooding onto the agricultural floodplain. To alleviate this consequence, sediment accumulating in zone 6 against the downstream weir could require periodic dredging.

The predictions of future channel change under a *laissez-faire* scenario can be summarised into two possible stages of channel adjustment:

(1) The reconnection of the channel with the alluvial reservoir in zone 2, caused by the 2005 realignment, will initially increase downstream sediment yields, in particular in zone 4, and maintain zonation in the short term.

(2) In the long term, a reduction in sediment supply to the reach will cease the restocking of the zone 2 reservoir and reduce the supply of sediment for downstream redistribution. A deficit of sediment will also likely cause incision through the upper part of zone 2, and in turn cause the narrow entrenched section to act as a chute. This would increase the accumulation of sediment downstream in zone 2. Excessive sediment loading at

the bottleneck will eventually cause the channel to avulse, increasing sediment supply to zone 3. This will change the dynamics of source, transfer and accumulation along the entire reach.

5.4.3. What are the potential impacts of morphological adjustments under a *laissez-faire* scenario on in-stream macroinvertebrate community organisation?

Following the reconnection of the channel with the alluvial reservoir in zone 2, the hypothesised short-term maintenance of channel zonation would also likely maintain the present-day, reach-scale pattern of macroinvertebrate community organisation in the short term, because the zone-scale domains of longitudinal (bedload conveyance), lateral (floodplain connection) and vertical (subsurface exchanges) processes would continue to operate and influence the present-day distribution of macroinvertebrate taxa in the same way.

In the long term, however, a further and ongoing decrease in sediment supply to the reach is hypothesised to change the structure and functioning of the zones between Luc and Recoubeau, and so this will create a different reach-scale pattern of macroinvertebrate community organisation. In particular, the greatest change could occur in zone 3. If sediment loading becomes excessive at the bottleneck, this may cause the channel to avulse into zone 3. Any aggradation associated with the increased supply of sediment to the corridor may eliminate the diverse morphological structure of the mid-reach, and this would change the variability in flow patterns and processes of bedload dispersal, which are hypothesised to be the dominant controls on the significantly more diverse and less dominated macroinvertebrate communities, and greater proportions of EPT taxa found through the mid-reach. Under a *laissez-faire* scenario, a long-term, ongoing reduction in bedload supply to the reach could therefore cause a reduction in macroinvertebrate diversity, evenness, and proportions of EPT taxa through the mid-reach.

Should there be avulsion at the bottleneck, aggradation in zone 3 may also slow the downstream transfer and reduce volumes of bedload supplied to zone 4. This would exacerbate degradation in zone 4 and aggradation in zone 5 that would be instigated by a deficient upstream supply from zone 2. Thus, under a *laissez-faire* scenario, it may be also possible that there is a reduction in macroinvertebrate diversity, evenness, and proportions of EPT taxa within the downstream part of the reach.

At present, bedload is infrequently received in zone 1, and the bedrock conveyor rapidly transfers sediment downstream to zone 2. Should there be a long-term, ongoing reduction in bedload supply to the reach then this situation is not likely to change, and so the infrequent, intense bed disturbance associated with this dynamic may maintain similar characteristics of macroinvertebrate community structure to the present-day along the upstream part of the reach.

5.5. Possible Future Changes in Morphology and Macroinvertebrate Community Organisation, in the Context of a Renewed Sediment Supply

5.5.1. Would zonation be reactivated in response to a renewed sediment supply?

Should the remobilisation of sediment within the Béoux catchment successfully increase the supply of sediment to the Drôme, it could be hypothesised that the increased sediment yield will blanket the morphological diversity of the reach, causing reach-scale aggradation and the loss of bedrock and mixed alluvial-bedrock zones. However, the view that increases in sediment load will reduce the morphological complexity of a stream, and in turn, the diversity of habitat for in-stream macroinvertebrate communities (Bartley and Rutherford 2005) does not account for fundamental spatial variation in the propensity and the capacity of the channel to adjust to changes in sediment load. There is substantial discontinuity in bedload transport capacity between the zones, as a function of the variable resistance of the channel boundary both within and between bedrock, alluvial and mixed bedrock-alluvial zones. It is most likely that in response to an increased sediment supply, bedload will not be redistributed evenly along the reach and so future changes in channel morphology and macroinvertebrate community structure will not be uniform.

Between 2001 and 2006, channel narrowing and straightening occurred downstream in zone 2 and upstream in zone 4, reducing the distinction of these wide alluvial zones from the mid-reach corridor. It appeared that if this degradation was to continue, then a tripartite structure of upstream, mid-reach and downstream sub-reaches would develop (section 3.5.3, figure 3.28), because this sub-reach structure was being generated by processes of sediment supply, transfer and deposition that were no longer operating at the zone scale, but within these sub-reach domains. However, the reactivation of the sediment reservoir in zone 2, and the resultant increase in sediment supplied downstream to zone 4, may avert this situation. By restoring the dynamics of sediment supply, transfer and accumulation (figure 3.25) it is possible that the distinction of the zones will be restored. Under a *laissez-faire* scenario, this is hypothesised to be a short-term effect. Should the remobilisation of sediment within the Béoux maintain a frequent and moderate supply of bedload to the reach, however, then it is possible that the zone-scale discontinuity in channel planform and substrate will be maintained in the long term, because the supply of sediment will sustain the processes of sediment storage, transfer and accumulation responsible for zonation.

Any sediment supplied to the reach will continue to quickly translate into zone 2 from the bedrock conveyor of zone 1. It is likely that sediment will reside longer when it arrives in zone 2 because it disperses over a wider channel area, there is greater resistance to its transit and, within the downstream part of the zone, it is spread across multiple channels. Sediment will continue to accumulate in and be sourced from this zone for downstream transfer, and the role of zone 2 as a reservoir will continue. The ongoing deposition and erosion of bedload in

the reservoir will preclude large volumes of sediment entering zone 3 and accumulating at the bottleneck. The bottleneck will also continue to moderate the downstream transit of bedload and thence enable the processes of sediment transfer in zone 3 to continue to operate as they do at present. The structure of the channel through the mid-reach corridor will maintain the filtering and grain size fractionation of bedload, and transfer sediment supplied from zone 2 into zone 4. In zone 4, bedload may accumulate and alleviate the more recent incision seen in the upper part. This will also limit the accumulation of sediment downstream in zone 4, within zones 5 and 6 and so prevent the likely consequences of overbank flooding.

It is most likely that the maintenance of present-day morphological zonation would also maintain the present-day pattern of macroinvertebrate community structure, because longitudinal (bedload conveyance), lateral (floodplain connection) and vertical (subsurface exchanges) processes that are regulated by the zonal channel structure will continue to operate in the same way as they do at present.

5.5.2. Which of the two management scenarios would be 'ecologically meaningful'?

In terms of maintaining present-day morphological zonation, and the reach-scale pattern of macroinvertebrate community structure, the long-term reintroduction of sediment appears to be an effective strategy. But, why would it be desirable to maintain present-day zonation? The present-day pattern of zonation, in terms of morphology and macroinvertebrate community organisation, is just one configuration of process domains that has developed through time. Since 1948 the channel has been characterised by different arrangements of different numbers of zones (section 3.4.2.3, figure 3.17). It is clear in figure 4.13 and in section 5.3 that the present-day mixed bedrock-alluvial morphology of the mid-reach supports more diverse and less dominated macroinvertebrate communities, and greater proportions of EPT taxa than the upstream bedrock part of the channel, and the downstream alluvial section of the reach. At both reach and sub-reach scales, therefore, the diversity of present-day channel morphology may be more 'ecologically desirable' than the relatively more homogeneous morphology of the historical alluvial channels, particularly those of 1948, 1956 and 1971, prior to the inheritance of mixed bedrock-alluvial channel conditions during the 1978 flood. The maintenance of present-day zonation would, therefore, be 'ecologically meaningful' in the sense that it could maintain and not reduce the present-day ecological attributes of the reach.

Given the desirable ecological characteristics of the mixed bedrock-alluvial morphology, one possible management objective could be to promote and extend this biophysical diversity to other parts of the reach. However, it is clear that the biophysical characteristics of zone 3 cannot be imposed on the alluvial zones 2 and 4, for example, because of their inherent differences in their boundary conditions and valley setting. The alluvial zones are wide and unconstrained and their underlying bedrock is apparently much

deeper relative to their alluvial cover. The cross-sectional and three-dimensional morphology of the alluvial zones will not produce the diversity of flow patterns, nor create the bed disturbances that generate the patterns of macroinvertebrate organisation characteristic of the mixed bedrock-alluvial mid-reach.

The relatively heightened biophysical characteristics of the mid-reach are a function of how sediment is routed within and between zones 1 and 2, and supplied to zone 3. This is enabled by the configuration of the zones and the connectivity of the zones. Thus, the optimal macroinvertebrate community characteristics of the mid-reach are not just a function of the mixed bedrock-alluvial morphology, but the arrangement of and the linkages between the zones. In the same regard, this also influences the biophysical characteristics of zones 4 and 5; their morphological and ecological patterns are created by the collective functioning of zones 1, 2, and 3. In zone 6, the accumulation of sediment along the lower 500 m of the reach is dependent on upstream processes within and between zones 1, 2, 3, 4 and 5. It can thus be seen that the present-day, reach-scale pattern of morphology and macroinvertebrate community organisation is a sum of its parts. Changing the arrangement and the connectivity of the zones would change the morphological dynamics and thence the ecological dynamics of the reach (e.g. Fisher *et al.* 1998).

It is clear that the function of zone 2 as a sediment source is fundamental to maintaining the present-day pattern of zonation. It is important to prevent incision in zone 2 to sustain its function as a sediment source, because the storage and reactivation of sediment in the alluvial reservoir is dependent on the channel being connected to its active floodplain. Preventing incision in zone 2 will also maintain a moderate supply of bedload to the zone 3 corridor and thereby secure the morphological complexity of the mid-reach. It will also preclude excessive sediment loading at the bottleneck and consequent avulsion, and maintain a sufficient supply of sediment for downstream redistribution. This will prevent degradation in zone 4, and the accumulation of sediment in zones 5 and 6. Thence, it is fundamental to ensure that the zone 2 reservoir continues to receive a sufficient supply of sediment. A *laissez-faire* scenario, in which there would be an ongoing reduction in sediment supply to the reach, does not appear to be a desirable, or 'ecologically meaningful' management strategy.

In the same way that a sediment deficit will alter the zone-scale regimes of bedload redistribution, excessive sediment loading in the channel will also imbalance the yield and transfer of sediment between the zones, and thereby change the dynamics that sustain zonation. It is then most likely that the present-day, reach-scale patterns of morphology and macroinvertebrate community organisation will only be maintained if the increased supply of sediment to the reach is moderate in volume and intermittent in delivery. While it is uncertain how much or how often bedload will be delivered to the reach following the remobilisation of sediment in the Béoux sub-catchment, it is considered that this long-term strategy will provide the reach with the 'drip feed' required to sustain present-day zonation, and as such, appears to be a desirable, management strategy.

5.5.3. Sediment remobilisation as a long-term strategy for alleviating reach-scale channel degradation

The principal aim of remobilising sediment in the Béoux is to alleviate degradation along the study reach, and increase the supply of sediment to degraded downstream reaches. It is likely that this intervention will indeed alleviate degradation along the study reach, but it is clear that this effect will not be spatially uniform, and dependent upon the frequency and volume of bedload supply. This exemplifies that management goals targeted towards the rehabilitation of an 'equilibrium' state (such that the channel does not tend to overall degradation or aggradation) can be inappropriate in river channels characterised by non-linear dynamics (Phillips 2003). Along the length of the five kilometre reach, the downstream transfer of sediment is not a simple, linear dynamic. It will take time for bedload to be received in degraded areas downstream of the reach. The volume of bedload that does reach downstream areas will have been reduced by the transit and storage of bedload in zones 2 and 4, in particular, but perhaps also by temporal accumulation in the downstream zones 5 and 6, as more sediment is reworked through the reach and stockpiled against the weir at the end of zone 6. The calibre of bedload that is transferred downstream of Recoubeau will also change. The storage of coarser material within the upstream zones may mean that downstream areas will perhaps not receive the coarser sediments intended for their rehabilitation.

Following the remobilisation of sediment, an increase in bed-level would be only one gross measure of channel recovery from incision (Madej and Ozaki 1996). Between Luc and Recoubeau the maintenance of zonation would further indicate that the channel has returned to its non-linear and self-regulating equilibrium of sediment supply, transfer and accumulation. The reinstatement of this balance, in which it is reconnected to its historical floodplain, would provide a better indication of channel recovery (Beechie *et al.* 2008, Madej *et al.* 2009).

5.5.4. Quantifying the sediment regime

As Gregory and Downs (2008) point out, river channel management and restoration initially requires identification of the spatial and temporal arrangement of causes of change within a conceptual framework. Stewardson and Rutherford (2008) further acknowledge that such a conceptual model is also the largest source of uncertainty in river restoration, not least because it is a complex assemblage of hypotheses (Beck *et al.* 1993). To evaluate the accuracy of the hypothesised processes of river channel structure, function, and macroinvertebrate community organisation established in this thesis, it is first necessary to test them.

The downstream routing of bedload described in chapters 3 and 4 is a useful conceptual tool, but to understand the mechanics of bedload redistribution along the reach, it is first necessary to quantify amounts of sediment storage and rates of bed material transfer

within and between the zones. This could be achieved by developing suitable modelling tools, which would then allow for the prediction of future changes in channel morphology, under different scenarios of sediment supply and flow regime. This could then inform the question of how the channel may respond to a renewed sediment supply; whether it would successfully reactivate zonation and reverse degradation. Quantifying the bedload regimes of the zones would also quantify the creation and disappearance of benthic habitat, and project spatial and temporal change in their availability.

Quantifying the source, transfer and accumulation of sediment along the reach was beyond the scope of this project, but might be achieved using a sediment routing model. Computational models such as SEDROUT (Hoey and Ferguson 1994), TRIB (Ferguson *et al.* 2006), and the model of Cui *et al.* (2003) use width-averaged values of flow, bedload transport and channel boundary conditions to predict local changes in channel elevation and grain size distribution, and thus channel behaviour in response to changes in bedload volume and calibre through time. These models do not account for lateral variation in flow, bedload transport and channel boundary conditions, yet it is clear that supply-limited channels do not transport bedload uniformly across their width (Nelson *et al.* 2009) and that a heterogeneous mixed bedrock-alluvial channel morphology creates significant cross-channel variation in flow strength and bedload flux. Reach-scale laws of bedload transport and erosion cannot therefore be used to describe local rates of bedload transport and erosion over the channel cross-section and between the channel zones (e.g. Turowski and Rickenmann 2009). There is a clear need for the development of a routing model that accounts for this lateral (Ferguson 2003) and longitudinal variability in sediment supply and transport capacity through time.

5.6. Chapter Conclusions

It can be seen that zonation is a type of self-regulating channel behaviour, in the sense that the channel has become adjusted to intrinsic spatial variation in sediment storage and transfer, and its ability to adjust both laterally and vertically. This is a function of differences in the cross-sectional and three-dimensional structure of the reach, and this constraint on the channel was most likely inherited from reach-scale incision, straightening and mid-reach avulsion during the 1978 flood. Prior to 1980, the channel is wide and braided with alluvial islands along its length. The system is now operating under altered boundary conditions, that will not permit the development of a homogeneous alluvial morphology, and so intentions to restore this former landscape will likely be unsuccessful. It is most likely that a management strategy that does not account for the fundamental spatial differences in channel constraint and behaviour will have limited success.

Any change to the morphological dynamics responsible for this pattern could induce a metamorphosis of channel form, because it would force the channel to exceed intrinsic thresholds of flow and sediment regime, and cause the channel to operate outside of its

natural range of variability. Should there be a sediment deficit relative to the present-day within-reach flow and sediment regimes (for example, under a *laissez-faire* scenario), then it is hypothesised that channel avulsion will occur at the bottleneck, and change the morphological dynamics of the reach. It is also hypothesised that this could also occur should there be excessive sediment loading in the channel. Present-day zonation will likely be sustained if the channel receives a 'drip feed' of bedload, in the sense that moderate volumes would be received in the channel at regular intervals.

Present-day zonation is only one of several patterns that have developed since 1948. In terms of in-stream biodiversity, the 2006 pattern of channel zonation may be more desirable than other historical configurations because at the reach scale, the diverse mixed bedrock-alluvial channel morphology probably supports more diverse and less dominant macroinvertebrate communities, and greater proportions of EPT taxa than entirely bedrock or entirely alluvial channel morphologies. The planned remobilisation of sediment is hypothesised to maintain the morphological diversity and dynamics that maintain these desirable characteristics and thus appears to be an effective, 'ecologically meaningful' management strategy.

6. Conclusions

6.1. Introduction

Chapter 3 investigated changes in the morphology of a mixed bedrock-alluvial reach of the Drôme River over a 58 year period, and examined the development of the striking present-day morphological zonation. In chapter 4, the current organisation of macroinvertebrate communities along the reach was characterised and related to patterns of channel behaviour. Based on these observations, chapter 5 considered possible future changes in channel morphology and macroinvertebrate community organisation under different management scenarios. This final chapter aims to summarise the main findings established within each of these parts and relate these observations to current perspectives of river channel change and macroinvertebrate community organisation.

6.2. Mixed Bedrock-Alluvial Channel Evolution: Past, Present and Future

While much attention has been given to small-scale, experimental modelling of rates and patterns of incision in bedrock-constrained channels (e.g. Sklar and Dietrich 2001, Finnegan *et al.* 2007, Chatanantavet and Parker 2008), few studies have provided a reach-scale perspective on how the evolution of a mixed bedrock-alluvial morphology constrains these processes of channel adjustment. Given relatively recent, widespread acceptance that sustainable river channel management is best achieved by a large-scale and long-term strategy that accounts for long-term channel behaviour (e.g. Brierley *et al.* 2008, Gregory and Downs 2008); and that once incised to bedrock, the subsequent evolution of a river channel and its surrounding landscape is controlled by this inherited constraint (e.g. Attal *et al.* 2008, Stark *et al.* 2009); spatial and temporal variations in rates and patterns of channel adjustment in mixed bedrock-alluvial channels is a particularly interesting research area.

The first main part of this thesis hereby aimed to examine the long-term evolution of a mixed bedrock-alluvial reach of the Drôme River. Between Luc and Recoubeau the channel is characterised by a striking pattern of wider, alluvial and narrower, bedrock sub-reaches. The reach is strongly coupled with the Béoux sub-catchment, a tributary that joins the Drôme 200 m upstream of the reach. In response to long-term changes in land use within the Béoux, and larger scale climatic effects (Liébault 2003) there have been substantial long-term changes in flow and sediment regimes along this reach of the Drôme. It therefore provided an interesting setting in which to examine the historical evolution of a mixed bedrock-alluvial river channel with particular reference to larger-scale and long-term controls on its development.

Between 1948 and 2006, there has been channel narrowing, straightening and incision along the reach as a whole. However, overall amounts of degradation have been

modest and there is significant spatial variability in these trends. Abrupt downstream transitions occur between channel zones that have experienced different overall directions and amounts of morphological change, as a function of differences in their propensity and capacity to adjust. This has emphasised a discontinuous reach-scale pattern of wider, alluvial and narrower, bedrock zones.

The 2006 pattern of channel zonation therefore describes a discontinuous morphological **form**, in terms of channel style, structure and substrate (chapter 2). It is also clear that zonation describes a reach-scale **dynamic** of bedload redistribution between zones of sediment source, transfer and accumulation (figure 3.25). This process is a sum of its parts. The individual functioning of a zone is dependent on the behaviour of upstream channel zones, and in turn controls downstream channel behaviour. The reach-scale pattern of zonation is thereby dependent on the mechanisms that facilitate sediment connectivity. The three-dimensional structure of channel bedrock is one such mechanism, controlling processes of bedload storage and transfer within and between the zones. In zone 1, for example, the relatively flat, smooth bedrock channel is devoid of storage areas, and acts to rapidly convey bedload downstream; while in zone 3, outcropping bedrock hummocks create areas of flow separation and sediment storage such that gravel bars are formed.

Between 1948 and 2006 the development of zonation has been shaped by general long-term reductions in sediment supply and flood activity, but dominated by a few key actions and events. During this period the reach experienced four large floods and the channel has responded differently to each of these events, demonstrating a clear temporal change in the propensity and the capacity of the channel to adjust, and reaffirming the importance of historical contingency that has been emphasised in other work (e.g. Newson 1980, Church 1996, Lane and Richards 1997, Rice and Church 1998, Mosley and Schumm 2001, Wallick *et al.* 2008). The response of the channel to each flood has been determined in part by channel condition at the time of impact, which has been determined by antecedent actions and events. A given flood may have had a different impact if it had occurred at a different point in time.

The 1 in 44 year flood of 1978 was a key event in the evolution of the reach by causing substantial channel straightening and incision, particularly along the right side of the channel boundary. Most importantly the flood also caused avulsion at the mid-reach bottleneck and sculpted a new, straight and incised channel through the right bank floodplain. This avulsion was likely primed by the long-term reductions in sediment supply and flood frequency, caused by climatic improvements at the end of the little Ice Age, circa 1850; and the considerable increase in forest cover within the Béoux sub-catchment, due in part to managed afforestation between 1886 and 1914 (Liébault and Zahnd 2001) but predominantly by the natural reforestation of abandoned agricultural land (Liébault 2003). The avulsion also appears to have been a lagged response to the sudden further decrease in flow and sediment supply caused by the 1965 construction of the Trescherènes dam in the Béoux sub-catchment; and there is a possibility that an episode of unauthorised gravel mining in the channel may have

further contributed to the cause and effect of the flood (section 3.5.1.1). In response to these events, the heightened sensitivity of the channel prior to the 1978 flood likely explains why morphological changes of such magnitude were accomplished by a flood sixty percent smaller than the 1 in 99 year flood of 1993, which did not cause any major change in channel morphology. Such 'anthropogenic conditioning' and 'natural triggering' has been acknowledged in other observations of channel change (Brewer and Lewin 1998, Warburton *et al.* 2002).

By locking the channel into a narrow, mid-reach corridor, 1978 flood set important structural constraints on the channel and thus imposed significant spatial discontinuity in the ability of the channel to adjust. Unconstrained zones 2, 4 and 5 have subsequently undergone consistent patterns of channel widening and narrowing, while constrained zones 1 and 3 exhibit little change in channel planform. It is apparent that interactive processes of flood activity and vegetation encroachment are responsible in part for the maintenance of this discontinuity in channel behaviour, leading to a third description of zonation as a **flood-induced phenomenon**. In the absence of flood activity, channel narrowing occurs in unconstrained zones by the encroachment of vegetation on lateral channel margins. During large flood events, vegetation is removed and former channel areas are reactivated, locally increasing channel width and sustaining the discontinuity in channel planform.

Between 2001 and 2006 it is clear that there had been a fundamental change in zonation, in all three of its expressions; as a form, as a dynamic and as a flood-induced phenomenon. Although in 2006 the pattern of zonation was evident on the ground, and on aerial photography, these snapshots did not reveal that the distinctiveness and functionality of the zones had diminished compared to the relatively recent past. The large flood event of 2004 did not cause unconstrained zones to expand, and in contrast, between 2001 and 2006 the channel narrowed in locations that previously underwent channel expansion in response to large flood events. Because the flood of 2004 did not reactivate the pattern of zonation, the distinctiveness of the zones was reduced, and further indicated that the functioning of the zones had changed. By 2006 it is apparent that the redistribution of bedload now operates between sub-reaches, rather than the discernible zone boundaries.

It is hypothesised that this change in channel behaviour was caused by an increase in the extent of incision along the reach as a whole, in response to the long-term general reductions in sediment supply and flood activity, but particularly in response to incision in zone 2, which had formerly acted as a source of sediment for downstream reaches. This function had been lost by progressive disconnection of the channel from the reservoir in preceding decades, and since the active channel was routed into an incised chute along the right side of the floodplain during the 1978 flood. Once incised beneath bar and bank height, the ability of the channel to access these stores of bedload for downstream redistribution is limited. The disconnection between the channel and these formerly active channel surfaces also precludes the inundation and removal of vegetation establishing on lateral bar and bank surfaces,

further increasing the resistance of these channel areas to reactivation during flood events. This causes the local sourcing of sediment from where it is available, changing the dynamics of bedload redistribution and thus the processes driving reach-scale morphology. It is clear that the functioning of zone 2 as a sediment source is fundamental to maintaining the present-day pattern of zonation.

The channel is set within a context of decreasing flood activity and sediment supply, which is, quite feasibly, the most limited it has been during its history. It is clear that the channel has incised beneath the floodplain along the length of the reach. Into the future, further incision and channel straightening should, therefore, be likely, because an ongoing reduction in flood activity will cause less frequent flood-induced reactivation of channel bars and margins, enabling undisturbed vegetation encroachment. The cohesive strength of vegetation will increase the resistance of lateral channel bars and banks to flood-induced erosion, and by also constricting the channel, force it to cut down into its bed, further increasing the disconnection between the active channel and formerly active channel areas. It can so be seen that the present-day disconnection between the channel and the active floodplain will enable incision to continue via a feedback loop.

However, in 2005 local river managers unexpectedly realigned the channel through zone 2, reconnecting it to large stores of sediment in the formerly active left bank bar complex. It is hypothesised that by reactivating zone 2 as a sediment source, this intervention could lift the reach out of the cycle of degradation described above. Under a *laissez-faire* management strategy, in which sediment supply to the reach is expected to further decrease, it is likely that this will be a short-term effect, because the source of sediment in the downstream part of zone 2 will eventually become deficient again. In the long-term, a sediment deficit is hypothesised to cause incision in zone 2 and promote excessive sediment loading at the channel bottleneck between zones 2 and 3. The accumulation of sediment at this point could cause a future avulsion of the bottleneck, and this scenario is also likely should the reintroduction of bedload be excessive to the present-day regimes of sediment storage and transfer.

Should the remobilisation of sediment in the Béoux catchment secure the reach with a moderate and intermittent supply of bedload, then it is hypothesised that the dynamics responsible for present-day zonation may be maintained. The ongoing deposition and erosion of bedload into and from the zone 2 reservoir will prevent incision and the consequent disconnection between the channel and the bedload stores, and preclude excessive sediment loading at the bottleneck.

It is suggested that if the channel is connected to its active floodplain, and receives a sufficient external supply of bedload, then the reach-scale dynamic of zonation is self-regulating behaviour, and to intervene without consideration of this inherent spatial and temporal variability may induce an unsustainable type of 'engineered' intervention. In the context of rehabilitating channel degradation in downstream reaches of the Drôme, it is

necessary that any management strategy understands this reach-scale dynamic. Management strategies are more likely to be successful if they work with these natural, present-day conditions than if they 'fight the site' (Brierley and Fryirs 2009).

It is clear that the degradation of a formerly braided channel is not a simple linear trajectory of evolution, a finding that echoes more recent observations at larger, catchment scales (Piégay *et al.* 2009). The effects of individual events in the evolution of the morphological zonation between Luc and Recoubeau were conditioned by historical changes in the Bédoux and its strong connection with the study reach. General 'laws' or models of river channel adjustment developed in other catchments do not explain the variation in channel form seen along the Drôme between Luc and Recoubeau because of this particular situation (Leopold and Langbein 1963, Beechie *et al.* 2008), confirming the suggestion of Hynes (1975) that 'every stream is likely to be individual' and reflecting the 'primacy of place' (Phillips 2001). This work hereby demonstrates that the evolution of a river channel cannot be understood in isolation from its geography or its history. The present-day channel is operating under an altered set of boundary conditions to those that produced it, yet this change in channel behaviour is not apparent from present-day channel form. Thus, a long-term perspective of channel evolution is required in order to predict likely future changes in channel morphology, a finding that accords with more recent calls for a long-term and large-scale perspective of channel behaviour, in order to understand how a river channel is likely to adjust into the future (e.g. Brierley *et al.* 2008, Gregory and Downs 2008).

This work echoes the finding that in mixed bedrock-alluvial channels the long-term evolution of discontinuous channel geometry is an important control on short-term and smaller-scale patterns of bedload transport and erosion (Snyder and Kammer 2008), but also shows that small-scale, internal mechanisms feed back to create spatial and temporal variability in overall trends of adjustment. The interpretation of present-day channel behaviour and the prediction of likely future channel changes thus also rely on an understanding of how channel adjustment is constrained by form and process at and between different spatial and temporal scales.

6.3. Macroinvertebrate Community Organisation in a Mixed Bedrock-Alluvial Channel

Patterns of macroinvertebrate community organisation are well-documented in alluvial channels, and in response to widespread acceptance that discrete changes in habitat conditions parallel discrete changes in macroinvertebrate community structure (e.g. Southwood 1977, Townsend and Hildrew 1994), a majority of published research has compared macroinvertebrate community structure between relatively small-scale 'habitat' or 'flow' types, delineated by differences in substrate and flow characteristics (e.g. Scarsbrook and Townsend 1993, Newson *et al.* 1998, Brussock and Brown 2001, Reid and Thoms 2008).

It is apparent in this work that 'habitat' is considered as a relatively static entity and thus these perspectives significantly lack an appreciation of how 'habitat' is dynamic, in the sense that it is created and maintained by short term and small scale morphological processes, which are further constrained by long term processes operating at larger spatial scales.

Chapter 4 suggested that the **dynamics** of reach-scale channel behaviour are the most important controls on the organisation of in-stream macroinvertebrate communities. With the exception of three parameters (mass of particulate organic matter (POM) and the heterogeneity of surface and sub-surface grain size), analysis showed that relatively static, physical habitat characteristics are not related to significant spatial differences in macroinvertebrate community structure along the reach. However, spatial differences in longitudinal, lateral and vertical processes within and between the zones do provide a reasonable explanation for the corresponding spatial differences in macroinvertebrate community diversity and dominance.

Abrupt transitions in cross-sectional channel geometry and bed morphology delineate the present-day channel zones and their obvious differences in flow and sediment regimes, and, as a function of how they are variably constrained, the zones also appear to have characteristic differences in their lateral and vertical connections with the active floodplain and the sub-surface hyporheos. In particular, it is hypothesised that between Luc and Recoubeau, the redistribution of bedload is the dominant control on the present-day pattern of macroinvertebrate community organisation. Sub-reach differences in macroinvertebrate community structure reflect the different resistance and resilience of different taxa to variable intensities and frequencies of channel bed scour and fill, which are caused by spatial differences in processes of bedload transfer.

The conclusion that macroinvertebrate community structure is controlled by processes of bedload redistribution was not empirically tested, but the physical characteristics to which macroinvertebrate abundance, diversity and dominance were statistically related (the mass of POM and grain size diversity at a site) are fundamentally controlled by these same dynamics. While the relatively greater upstream site masses of POM are caused in part by external supply to the reach, the masses of POM and bedload grain size distributions sampled at all sites along the reach are controlled by processes of storage and transfer. The conclusion that spatial differences in macroinvertebrate community structure reflect processes of bedload redistribution is further supported by the type of analysis undertaken, which considered only macroinvertebrate sample abundance counts. Detrended Correspondence Analysis does not integrate any physical data, and so any emergent spatial structure (discernible by the arrangement of samples with similar characteristics) can be considered to indicate levels of macroinvertebrate organisation that are autonomous and uninfluenced by an objective morphological structure. One fundamental limitation of using a 'top down' morphological approach to understanding patterns of in-stream macroinvertebrate organisation is that spatial and temporal holons, or levels of ecological organisation may not parallel the spatial

and temporal scales of morphological processes (Levin 1992, O'Neill 2001). It is particularly significant, therefore, that spatial structure apparent in the DCA also reflected locations characterised by their different channel behaviour.

Between Luc and Recoubeau, spatial differences in processes of bedload storage and transfer are controlled by spatial differences in cross-sectional channel morphology and three-dimensional bed structure, which result from zone-scale differences in channel constraint. This has been shaped by the long-term evolution of the channel, which in turn, was controlled by changes in land use within the B  oux sub-catchment. Thus, interpretation of present-day macroinvertebrate community organisation relies on an understanding how the dominant controlling processes are constrained by a hierarchy of spatial and temporal controls (figure 4.24). Hierarchical frameworks of channel structure and function developed in alluvial channels do not account for the particular historical and morphological context of the study reach and so this work is concurrent with the more recent suggestion that such a conceptual framework should be catchment-specific (Frothingham *et al.* 2002).

While this study has focussed on the relative importance of longitudinal bedload redistribution, patterns of in-stream macroinvertebrate community organisation are also controlled by lateral and vertical processes (e.g. Junk *et al.* 1989, Stanford and Ward 1993). The structure and landscape setting of a channel will determine which spatial vector will be the dominant influence on macroinvertebrate community structure within any given channel (Poole 2002), and is controlled by spatial and temporal changes in channel patterns and connectivities (Wu and Loucks 1995). Between Luc and Recoubeau, relative differences in lateral and vertical processes also contribute to spatial differences in macroinvertebrate community structure but it is considered that there may be relatively greater variation in rates of bedload supply and transfer than in other controlling processes. This could be true of bedrock-constrained channels in a more general context. Compared to alluvial systems, the variable resistance of a mixed bedrock-alluvial channel boundary creates substantial heterogeneity in, and highly dynamic processes of, bedload transport. The significance of this transience has been recognised in terms of its importance for long-term channel adjustment (e.g. Stark *et al.* 2009), but has further fundamental importance for the dynamics of in-stream macroinvertebrate communities, because it creates heterogeneous and dynamic habitat conditions. The association between channel bed structure and the transfer of sediment is important, because the local flow and substrate disturbances associated with these interactions influence the dispersal of macroinvertebrate taxa and thence macroinvertebrate community organisation, and how habitat conditions are created, modified and maintained.

Compared to the upstream and downstream sub-reaches, which are dominantly bedrock and alluvial, respectively, the mixed bedrock-alluvial morphology of the mid-reach supports the most diverse and least dominated macroinvertebrate communities, and greater proportions of EPT taxa. The diverse mixed bedrock-alluvial morphology of the present-day

channel may therefore be more 'ecologically desirable' than historical, alluvial and braided channels, because it likely supports more diverse and less dominated macroinvertebrate communities, and greater proportions of EPT taxa. This questions the utility of a 'reference condition' (a state of natural morphological and ecological functioning similar to that which is expected to have existed prior to anthropogenic impact) and the assumption that present-day disturbed landscapes are less desirable than pristine, undisturbed environments (e.g. Hilderbrand *et al.* 2005, Nagel 2007, Dufour and Piégay 2009). These findings also offer a new perspective on the relative ecological importance of braided river patterns, and multiple channel sections as 'enhanced islands of good habitat' (Jähnig *et al.* 2009) that has been considered in other work (e.g. Rempel *et al.* 2000, Robinson *et al.* 2002, Tockner *et al.* 2006, Gray and Harding 2009). This work has shown that the macroinvertebrate fauna of a braided system may not necessarily be more 'ecologically desirable' than communities present in single-thread or bedrock channels, questioning the suggestion that the restoration of multiple channels may increase habitat heterogeneity and macroinvertebrate biodiversity (Jähnig and Lorenz 2008).

The optimal biophysical characteristics of the mid-reach are a function of the configuration and the connectivity of the zones. As noted in section 5.2, zonation operates as a sum of its parts and so the characteristics of the mid-reach cannot be replicated without the particular arrangement of channel morphology, processes and linkages that produce them. These characteristics are a function of spatial differences in landscape setting, that exerts variable constraint on the channel and thus the propensity and the capacity of the channel to adjust. In other words, the present-day pattern of macroinvertebrate community structure is a product of the geography and history of the study reach. It is likely that if future bedload supply to the channel is not deficient or excessive to present-day flow and sediment regimes then the present-day morphological diversity of the reach will be maintained. This will also maintain present-day patterns of macroinvertebrate community structure, and so if the reintroduction of bedload from the Béoux secures the reach with a moderate volume and frequent supply of sediment, then this 'drip feed' would be an 'ecologically meaningful' management strategy.

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Appendices

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