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Biological processes in running waters and their implications for the assessment of ecological integrity

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Abstract

Although biomonitoring approaches are being increasingly used in the measurement of stream and river health, critical assumptions about the nature of biological populations and communities that underpin them are often ignored. Many approaches based on pattern detection in plant and animal communities assume high temporal persistence in the absence of anthropogenic disturbances. However, this has been rarely tested with long-term data sets and there is evidence that this assumption is not true in some river systems. Biological processes, such as predation and recruitment, can account for considerable spatial and temporal variation in the structure of some stream communities. These processes may prevent the development of robust predictive models or indices based on pattern detection. Measurements of population or community attributes also are often used to infer ecosystem processes, yet the link between pattern and process has rarely been demonstrated. Many goals of river management relate to the maintenance of natural ecological processes and ecosystem function; direct measurement of these processes is, however, often neglected in assessment programs. Such measures are often sensitive to causal factors that are known to affect river health and it is possible to develop simple but powerful predictive models. Perhaps more importantly, should an impact to be detected, strategies for remediation are more obvious as the causal processes are generally better known. The ultimate success of biomonitoring approaches depends on how well we understand the biophysical processes that influence the structure and dynamics of stream and river systems, and the way they function.

Introduction

Assessing the ecological “health” of rivers and streams is a fundamental and increasingly important water management issue worldwide and, as a consequence, a vast array of biological monitoring approaches has been developed. These range from measurements of subtle changes at the sub-organism level to those directly measuring changes at the population, community and ecosystem level (see Norris & Norris, 1995 and references therein). Although selection of appropriate assessment methods is often the subject of considerable debate (Bunn, 1995; Wicklum & Davies, 1995; Wallace *et al.*, 1996), there is no doubt that such biological monitoring approaches are essential to achieving the goals of ecological sustainability, which espouse protection of biodiversity and the maintenance of essential ecological processes and life support systems (Karr, 1991; Council of Australian Governments, 1992).

Biomonitoring approaches, especially those based on pattern detection, make several critical assumptions about the nature of biological populations and communities. In particular, they assume that, in the absence of anthropogenic disturbance, spatial and seasonal patterns in stream animal (and plant) communities will be consistent from year to year. This assumption of high temporal persistence (*sensu* Grossman *et al.*, 1982) has rarely been demonstrated with long-term data sets. Furthermore, they assume that the structure of stream communities is primarily determined by the nature of the physical habitat (Huryn & Wallace, 1987; Pringle *et al.*, 1988; Townsend, 1989; Schofield & Davies, 1996) and often ignore the possibility that marked variation in natural community patterns can occur as a direct result of biological processes (e.g. competition, recruitment, predation). The ultimate success of

biomonitoring approaches depends on how well we understand the biophysical processes that influence the structure and dynamics of stream and river communities, and the way in which they function.

The aim of this paper is to explore some of the assumptions that underpin predictive models that are widely used to assess the ecological integrity of streams and rivers. Rather than attempt to provide a broad overview, we wish to draw on recent experiences in developing strategies for monitoring river health in Australia. We begin by looking at whether high temporal persistence is a feature of stream macroinvertebrate communities and, if not, what are the implications for the development of predictive biomonitoring models based on pattern detection? We then consider some of the biological processes that may be responsible for marked changes in the dynamics of stream populations and ultimately patterns in community structure, both in space and in time. We briefly examine whether measures of patterns (at the community or population level) can tell us much about essential ecosystem processes (an important component of river health), and conclude with an example of how direct measurements of these processes can be used to indicate river health.

Definitions of terms such as ecological “health” and “integrity” are often the subject of much contention (e.g. Schaeffer *et al.*, 1988; Karr, 1991; Suter, 1993; Wallace *et al.*, 1996). Ecosystem health has been recently defined in terms of system organisation, vigour and resilience, as well as the absence of ecosystem stress (Rapport *et al.*, 1998). The latter emphasises essential ecosystem functions and life support systems, which are key elements of ecological sustainability (Council of Australian Governments, 1992). Throughout this paper, we have used the term

“integrity” to refer to minimal deviation from a natural reference condition, and “healthy” as shorthand for good condition as per Karr (1991) and Karr (this volume). In agreement with Rapport *et al.* (1998), we also consider that ecosystem processes are key indicators of river health and integrity (Bunn *et al.*, 1999).

Materials and Methods

Much of the original data presented in this paper is derived from ongoing comparative studies in three different forested biomes within Australia: the Mary River catchment (sub-tropical rainforest) in southeast Queensland (152°40'E, 26°45'S), the Johnstone River catchment (tropical rainforest) in far north Queensland (145°39'E, 17°30'S) and from the northern jarrah forest (Mediterranean, dry sclerophyll) in southwestern Western Australia (116°05'E, 32°50'S). A full description of the study streams can be found in Bunn *et al.* (1986), Davies (1994), Hughes *et al.* (1996), Hancock & Bunn (1997), Mosisch & Bunn (1997) and Bunn *et al.* (1999).

Persistence in benthic community structure

Temporal persistence of stream benthic fauna was determined from a long-term monitoring programme of macroinvertebrates collected in southwestern Australia. Quantitative samples were collected with a modified Surber sampler (250µm mesh, area of base 0.0625m²) (Surber, 1970) from two sites in the North Dandalup catchment (ND1: Foster Brook and ND3: North Dandalup River) and two in the Canning catchment (CD2: Death Adder Creek and CD3: Poison Gully). Sites were situated in first and second order upland streams in relatively undisturbed forest and

were sampled seasonally from 1984 to 1988 (inclusive). During this time, sites in the North Dandalup catchment were permanently flowing and sampled four times a year and the Canning catchment sites were seasonally intermittent and sampled twice a year (winter and autumn). For details on collection and laboratory processing of samples see Storey *et al.* (1990).

At each site during each time, six random Surber samples were collected from riffles. This number of samples was sufficient to collect all but the rarest taxa (i.e. those comprising less than 0.5% of the total abundance of fauna) (Storey *et al.*, 1990). Macroinvertebrates were identified to the lowest taxon possible (in most cases genus or species) and community data were ordinated by detrended correspondence analysis (DECORANA: Hill, 1979) using the mean abundance of the total fauna collected from each site during each year. Data were transformed using $\ln(x+1)$ and an option to downweight rare species in proportion to their abundance was utilised (i.e. Hill, 1979).

Community patterns versus ecosystem processes

Community metabolism is a fundamental ecological process describing the movement of carbon (e.g. Bott *et al.*, 1985; Bunn *et al.*, in press). At seven sites in southwestern Australia, benthic metabolism was measured by monitoring dissolved oxygen by dataloggers within Perspex chambers over 24 h (see Bunn *et al.*, 1999). The amount of carbon produced (benthic gross primary production; GPP) and consumed (respiration; R_{24}) at the stream reach scale was estimated by patch-weighting the habitat-level metabolism values (e.g. Naiman, 1983).

At the same sites and during the same seasons, the “health” of these streams was determined by the AUstralian RIVer Assessment Scheme (AusRivAS; Schofield & Davies, 1994), which is a national protocol based on the RIVPACS approach used in the United Kingdom (Wright *et al.*, 1984; Wright, 1995). AusRivAS uses family-level identifications of benthic macroinvertebrates and associated measurements of environmental variables to derive predictive models of river health for different biomes. The model then uses the observed (O) families of taxa in the collected sample to determine if the faunal composition is what would be expected (E) from an undisturbed site in the same region. The ecological condition of a site is tested by calculating the O/E ratio number of families. The resulting O/E values are banded to provide a classification of the health of a study site (for further details of methodology see Kay *et al.*, 1999; Smith *et al.*, 1999).

Relationships between benthic community patterns (O/E scores) and ecosystem processes (GPP, R_{24}) were then examined using simple correlations. The relationships between these biological variables and water quality parameters, including turbidity and nutrients, were also examined.

Spatial and temporal patterns in community structure

Many strategies for assessing ecological integrity of streams and rivers are based on direct measures of populations and communities (Bunn, 1995). Examples are the National Monitoring River Health Initiative in Australia (AusRivAS, Schofield &

Davies, 1996) and the RIVPACS approach in the United Kingdom (Wright, 1995).

The general approach is:

- selection of control or reference sites which are deemed to be largely free from human disturbance, taking care to distinguish between broad ecoregions (e.g. climate, vegetation, biogeographical differences);
- development of predictive models that describe spatial patterns and relate these to abiotic variables (e.g. classification and ordination techniques that underpin AusRivAS and RIVPACS); and
- use of the models to predict patterns at other sites. Deviations from expected reference condition are assumed to reflect changes in ecological integrity and provide an assessment of river “health”.

Biogeographical considerations

Recognizing the existence of natural geographic variation in species distribution and abundance is an important consideration in the development of biomonitoring programmes, particularly at large spatial scales (Karr, 1991; Resh *et al.*, 1995). At regional or continental scales, biogeographical differences are likely to give rise to inherent differences in biota despite similar local attributes (such as climate and geology). Developing a national framework to biomonitor streams and rivers in a country the size of Australia is clearly no small undertaking (Schofield & Davies, 1996). There are considerable variations in climate and hydrology (Keast, 1981), ranging from cool temperate systems with winter rain (i.e. the southern regions) to arid regions of highly episodic and unpredictable rainfall events (i.e. much of northern and central Australia).

Comparison of streams in southwestern and southeastern Australia provides a striking example of the difficulties in developing national guidelines. Both regions share a similar climate and common Gondwanan history but there are major differences in the composition and biodiversity of the fauna (Bunn & Davies, 1990). Some groups (e.g. Plecoptera and many families of algal-grazing insects) are naturally absent or poorly represented in the southwest compared with similar streams in southeastern Australia. This has been attributed, in part, to the unique geological history of southwestern Australia (Bunn & Davies, 1990). As a consequence, indices based on species richness of particular groups would give a poor ranking of southwestern Australian streams if based on seemingly similar reference sites (based on climate, vegetation, physical habitat) from the southeast. For example, mean EPT taxa (Ephemeroptera, Plecoptera, Trichoptera; see Resh *et al.*, 1995) for forest streams in southwestern Australia was only 33 ± 1 compared with 122 ± 8 in southeastern Australia (mean \pm 1S.E.; see Bunn & Davies, 1990 for details). Using the SIGNAL rapid assessment procedure proposed by Chessman (1995), which incorporates pollution grades for each family, the mean score (out of a maximum of 10) for benthic invertebrate families in southwestern Australia forest streams (6.5 ± 0.1) was significantly lower than that observed in similar streams in the southeast (7.4 ± 0.03). Perhaps more disturbing is that the SIGNAL value for streams in southwestern Australia is close to the “doubtful water quality” status (SIGNAL = 5-6; see Chessman, 1995), even though the sites are in undisturbed forest. These biogeographical distinctions emphasise the need for careful selection of reference sites and the futility of developing nationwide indices of stream health (see Resh *et al.*, 1995).

Temporal patterns and community persistence

Biological monitoring studies typically emphasise the importance of spatial differences and tend to neglect temporal scales. However, an underlying assumption is that the communities monitored show high persistence. High persistence indicates a community is deterministic or regulated and therefore has an underlying structure (Grossman *et al.*, 1982; Zaret, 1982; however, see Ebeling *et al.*, 1990) and low persistence describes communities that are more likely produced by stochastic processes (Sousa, 1979; Moyle & Vondracek, 1985).

High persistence indicates that the community structure changes little between years. If we return to the same sites, year after year, we would expect the biota to be essentially the same unless some disturbance (either natural or anthropogenic) has occurred. For example, if the benthic fauna of two reference streams is sampled each summer and winter over several years, we can represent the spatial and temporal variation in community structure in ordination space (Fig. 1). If the community showed high temporal persistence with either little seasonality (Fig. 1a) or a strong seasonal pattern (Fig. 1b), we can easily develop a robust predictive model for biomonitoring. However, the spatial pattern could also change from year to year due to low persistence. Both sites could show a similar temporal trend in community structure, perhaps in response to inter-annual variation in environmental conditions (Fig. 1c), or vary completely independently of each other with no obvious causal explanation (Fig. 1d). In the former case (1c), observed in some streams in northern Australia (Faith *et al.*, 1995), dissimilarity between the two sites would be constant over time because the communities were changing in parallel rather than not changing at all. We would need to continually sample reference sites to account for natural

temporal shifts in assemblage structure. In the latter example (1d), we would have little confidence in the predictive capacity of our model based on reference sites. Unfortunately, there are few published long-term data sets available to provide convincing evidence that stream benthic community patterns are persistent over time.

Ordinations of benthic community data, collected over a 5-year period from perennial and intermittently flowing streams in southwestern Australia, provide a good example of the range of temporal patterns we might find (Fig. 2). These reference streams flow through relatively undisturbed sclerophyll forest in one of the most predictable climatic regions of the country (Bunn *et al.*, 1986). The two perennial streams in the North Dandalup catchment (ND1 and ND3) show little inter-annual variation in benthic community structure over the 5-year period (Fig. 2). In contrast, the two intermittently flowing streams in the adjacent Canning River catchment (CD2 and CD3) show marked variation over time with no obvious pattern, similar to that suggested in Figure 1d.

As longer-term data sets are gathered, it is becoming increasingly apparent that not all assemblages show high persistence. In some instances, this may be a function of inter-annual variation in environmental conditions (e.g. stream benthic communities in the wet-dry tropics of Australia, Faith *et al.*, 1995). However, temporal changes in community composition may be more stochastic and seemingly unrelated to inter-annual variation in environmental parameters. For example, species turnover between years in some arctic and subarctic streams (Miller & Stout, 1989) and cold desert spring-streams (Cushing & Gaines, 1989) is very high and the process of species extinctions and immigrations is thought to be largely stochastic. Similar stochastic

patterns in space and time have been observed in subtropical streams in southeast Queensland (Bunn & Hughes, 1997) and are also expected throughout drought-prone regions of warm-temperate eastern Australia.

High temporal variability in community structure has the potential to limit the sensitivity of biomonitoring approaches such as AusRivAS and RIVPACS. Low persistence in benthic community structure makes it extremely difficult to construct robust predictive models and will increase the likelihood of failure of the models (i.e. falsely conclude that observed changes in patterns are a consequence of changes in ecological health).

Influence of biological processes on community structure

There are many possible explanations for high levels of spatial and temporal variation in benthic community structure in some streams. One obvious conclusion is that such variation simply reflects a direct response of the fauna to changes in abiotic conditions (e.g. associated with floods and droughts), and therefore it may be possible to factor this into predictive models. The seemingly overriding importance of abiotic processes and habitat has been discussed by Petts (this volume). However, we must also acknowledge that marked spatial and temporal variation can also be the result of several important biological processes, including competition, predation and recruitment. Of these, we will focus attention on the latter two. There is little evidence to suggest that interspecific competition can result in major changes in the structure of stream benthic assemblages (Hildrew & Townsend, 1987). At most,

competition may result in shifts in abundance of interacting pairs of species (e.g. Allan, 1983), but cascading effects are unlikely.

Predation

Predators are common in streams, although their role in structuring aquatic communities is the subject of considerable debate (Hildrew, 1992; Cooper *et al.*, 1990). Spectacular evidence of strong predation effects comes from work on Californian streams (Power *et al.*, 1985; Power, 1990). These studies have demonstrated that predatory fish can have a “cascading” effect on the stream biota, through direct effects on small fish and predatory invertebrates, to primary consumers and ultimately both the composition and biomass of benthic algae. In the presence of predatory fish, smaller predators were reduced, tube-weaving chironomid larvae proliferated, and the benthic substrate was reduced to a midge-infested residue (Power, 1990). Predation effects of this kind clearly can be a major cause of spatial and temporal variation in stream community structure. Biomonitoring models based entirely on abiotic variables would be unable to predict such marked changes in the nature of the stream. Predator-mediated shifts in benthic community structure would be classified as a change in ecological integrity and mistakenly attributed to some form of anthropogenic disturbance.

As an aside, the notion that “all species are not equal” is an important consideration in selecting taxa for bioassay studies or as indicators (see Bunn, 1995). Selection of species on the basis of their high functional importance (i.e. those that provide important links in food webs or are important in organizing the community – see Hurlbert, 1997) should be a primary criterion.

Recruitment and dispersal

The important role of population-level processes such as dispersal and recruitment is not new to ecology. The “supply” of recruits is a well-known process in marine systems and can be of over-riding importance in determining community structure and dynamics (Underwood & Fairweather, 1989; Sale, 1990). However, the influence of recruitment and dispersal on the structure and dynamics of stream communities has been downplayed in the past (Bunn & Hughes, 1997). Stream and river animals are generally considered to have high dispersal capabilities and, given the extensive geographic distributions of some species, it is apparent that viable mechanisms for dispersal either do exist or at least must have existed in the past (e.g. Wallace, 1990; Mackay, 1992).

Recent work on the genetic structure of stream and river invertebrates, however, suggests that this is not always the case (Bunn & Hughes, 1997). For fully aquatic animals, such as atyid shrimps, there appeared to be limited movement even on a small spatial scale (e.g. streams within the same subcatchment) (see Hughes *et al.*, 1995; Hughes *et al.*, 1996). Although widespread adult dispersal of stream insects was apparent, movement of larvae between reaches was also limited. The realisation that larval insects sampled at the reach scale were the offspring of only a few matings implies that populations can be accounted for by the chance oviposition of only a few females (Bunn & Hughes, 1997). Such genetic studies provide strong evidence that dispersal capability and the stochastic effects of recruitment can easily explain the observed marked spatial and temporal variability in community structure.

The role of biological processes

In light of the above, underlying biological processes cannot be ignored when developing predictive multivariate models or even simple metrics for biomonitoring that are based on measures of populations or communities. Selecting reference sites for predictive models requires considerable care to ensure there are no inherent biogeographical constraints to the distribution of biota. Although stream benthic organisms generally respond in a predictable fashion to variations in the physical habitat, this may be over-ridden by marked variation resulting from biological processes such as predation and recruitment. Observed deviations from reference condition could result from stochastic processes such as larval recruitment and be misinterpreted as changes in ecological integrity.

Pattern and process

These limitations aside, what else can we infer about the health of rivers from measurements of patterns alone (i.e. populations, communities)? Many goals relating to river management and protection refer to ecosystem-level processes, with the notion that streams and rivers should function in the same way as they do in undisturbed catchments. This is an important element of the principles of ecological sustainable development (ESD), which consider not only the protection of biodiversity, but also the maintenance of essential ecological processes and life support systems (Council of Australian Governments, 1992; Commonwealth of Australia, 1996).

Often, we use patterns of species richness and composition as surrogate measures of these fundamental processes. However, pattern and process are not necessarily linked (see Bunn, 1995): changes in patterns can occur without any detectable change in processes (e.g. functional redundancy). Even if pattern and process are linked, there may be a lag before a modification in an ecological process is manifest as a change in pattern. Alternatively, changes in processes may occur without any detectable change in population or community attributes. There is little doubt that simple structural indices of stream health (e.g. EPTs) can be used to track ecosystem processes (e.g. secondary production, leaf processing rates) in the case of extreme disturbance (e.g. Wallace *et al.*, 1996). However, this may not be the case at lower levels of disturbance.

Comparisons of measures of benthic metabolism (GPP, R_{24}) and AusRivAS scores from small forest streams in southwestern Australia provide an example of the latter (Fig. 3). AusRivAS scores (O/E) reflect the deviation from reference condition and it is worth noting that all of these sites score in the “undisturbed” category. Although there was a marked (10-fold) spatial variation in GPP and R_{24} , this was clearly not correlated with O/E scores (i.e. pattern and process were not related – Fig. 3). The observed variation in GPP and R_{24} , however, was clearly related to spatial differences in water quality (Fig. 4a). Specifically, these measures of benthic metabolism were correlated with nitrogen concentration and turbidity – two variables likely to affect river health. Importantly, there was no correlation between any of the water quality parameters tested and O/E scores based on benthic macroinvertebrate communities (Fig. 4b). In this case, predictive models based on patterns were not sensitive enough to detect changes in ecological integrity.

Ecosystem processes and river health

Because of the above issues (lack of persistence and unpredictability of fauna, and the lack of obvious links between patterns and process), we have argued that direct measures of ecosystem attributes should form an integral component of river health assessment in Australia (Bunn, 1995; Bunn *et al.*, 1999). In our recent work, we have used replicated and patch-weighted measures of benthic metabolism, and stable isotope analysis to track the sources and fate of organic carbon and nitrogen. These are direct measures of “vigor” and “organization”, considered to be key indicators of ecosystem health (*sensu* Rapport *et al.*, 1998).

A particular focus of our work has been to determine whether such indicators of ecosystem health are influenced more by changes in riparian condition than by land-use activities elsewhere in the catchment. Using data from 20 streams in the Mary River catchment in southeast Queensland, it has been possible to develop simple but powerful predictive models to describe the response of these indicators to changes in aspects of riparian and catchment condition (Bunn *et al.*, 1999). We have shown that riparian canopy cover is by far the best predictor of benthic metabolism. Values of GPP and R_{24} from undisturbed forest catchments provided reference values to assess changes in ecological integrity. Stimulation of GPP was shown to occur when the canopy cover was reduced to below approximately 75% (= average cover for forest streams), however, major changes in health occurred when the canopy was lower than 40-50% and GPP exceeded R_{24} . At this point, much of the aquatic plant production shifted from palatable microalgae to filamentous algae and macrophytes, which do not

appear to enter the food web (Bunn *et al.*, 1999). The proliferation of these aquatic plants is also associated with a major decline in water quality (Bunn *et al.*, 1998).

Conclusions

If we are to rely solely on measures of ecological patterns to assess the ecological integrity of streams and rivers, then we must use caution developing and applying predictive models and simple biotic indices. Changes in patterns (abundance, richness, species composition) do not always equate to changes in ecological integrity. Marked changes can and do occur as a result of natural biological processes and may falsely lead to conclusions that impacts have occurred when they have not (i.e. Type I statistical error). Conversely, patterns may not change even when important ecosystem processes do. Biomonitoring approaches reliant solely on pattern detection may be unable to detect changes in ecological integrity (i.e. Type II statistical error). Measurement of patterns alone often tells us very little about the essential life support systems that are an integral component of ESD. Direct measurements of ecosystem processes are often neglected in river health assessment programs (Bunn, 1995). However, they are sensitive to factors that are known to directly influence river health and it is possible to develop simple but powerful predictive models. Importantly, should changes in ecological integrity be detected, it is possible to recommend strategies for remediation because the causal processes are generally well known.

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Figure captions

- Fig. 1.* Temporal variation in benthic community structure from two hypothetical streams (plotted in ordination space), where sites show: (a) high temporal persistence and no seasonal pattern; (b) high temporal persistence and strong seasonal pattern; (c) low temporal persistence with similar trends among sites; and (d) low temporal persistence and no consistent trends among sites (from Bunn, 1995).
- Fig. 2.* Ordination of annual benthic macroinvertebrate samples from two seasonally intermittent (CD2 and CD3) and two perennial (ND1 and ND3) forest streams in southwestern Australia, collected over five years.
- Fig. 3.* Relationships between benthic community metabolism (GPP = diamond symbols; R_{24} = square symbols) and AusRivAS scores (O/E) for small forest streams in southwestern Australia.
- Fig. 4.* Relationships between water quality (total nitrogen concentration and turbidity) in small forest streams in southwestern Australia and (a) benthic community metabolism (GPP = diamond symbols; R_{24} = square symbols) and (b) AusRivAS scores.







