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# Mechanisms of maintenance of tropical freshwater fish communities in the face of disturbance

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Community resistance to, and resilience from, perturbation will determine the trajectory of recovery from disturbance. Although selective timber extraction is considered a severe disturbance, fish communities from headwater streams around Danum Valley Field Centre, Sabah, Malaysia, showed few long-term changes in species composition or abundance. However, some species showed short-term ($< 18$ months) absence or decrease in abundance. These observations suggested that both resistance and resilience were important in maintaining long-term fish community structure. Resistance to perturbation was tested by monitoring fish communities before and after the creation of log-debris dams, while resilience was investigated by following the time-course of recolonization following complete removal of all fish. High community resistance was generally shown although the response was site-specific, dependent on the composition of the starting community, the size of the stream and physical habitat changes. High resilience was demonstrated in all recolonization experiments with strong correlations between pre- and post-defaunation communities, although there was a significant difference between pool and riffle habitats in the time-course of recovery. These differences can be explained by the movement characteristics of the species found in the different habitats. Resilience appeared to be a more predictable characteristic of the community than resistance and the implications of this for ensuring the long-term persistence of fish in the area are discussed.

**Keywords:** resilience; recolonization; freshwater fishes; resistance; Malaysia

## 1. INTRODUCTION

Perturbations (or disturbance) are an integral and ubiquitous part of ecological systems (Holling 1973; Neubert & Caswell 1997). For a system at equilibrium the response to disturbance depends on the resistance, the magnitude of change in population density following an instantaneous disturbance (Pimm 1984); and the adjustment stability, the ability to return to pre-disturbance conditions (Connell & Sousa 1983). 'Resilience' is often used synonymously for adjustment stability and will be used in this capacity for the rest of the paper. Resilience, in turn, depends on the amplitude of disturbance from which recovery can take place and elasticity, the rate of recovery (Connell & Sousa 1983). The sum of resistance and resilience has been used as one measure of the stability of the ecosystem (Connell & Sousa 1983; Ives 1995).

Much ecological theory has been based on the effects of disturbance on ecosystems including maintenance of levels of species diversity (Sousa 1979), the relative importance of biotic versus abiotic control (Schoener 1987), or the selection of particular life-history strategies or trophic dynamics (DeAngelis *et al.* 1989). It is generally accepted that disturbance plays a highly important role in natural systems and that investigation of responses to disturbance can provide insight into ecosystem processes (Mittelbach *et al.* 1995).

It has been demonstrated that the response of an ecosystem to disturbance is highly dependent on the duration of the stressing force (Detenbeck *et al.* 1992). Press disturbances have a duration greater than the life span of the longest-lived species, while pulse disturbances are relatively discrete events with a duration less than the life span of the longest-lived species (Bender *et al.* 1984). Resistance may be a more important attribute of a community subject to a press disturbance unless undisturbed refugia are present. Both types of disturbance can involve changes in biotic or abiotic factors and be natural or anthropogenic. Many anthropogenic activities such as mining, agriculture or timber extraction are severe press disturbances that can have profound effects on ecosystems (e.g. Detenbeck *et al.* 1992).

This paper summarizes the results of investigations into the effects of one type of press disturbance, selective timber extraction, on a tropical freshwater fish community. Predictions about the resistance and resilience of this system were then tested experimentally, together with investigation of one proposed mechanism.

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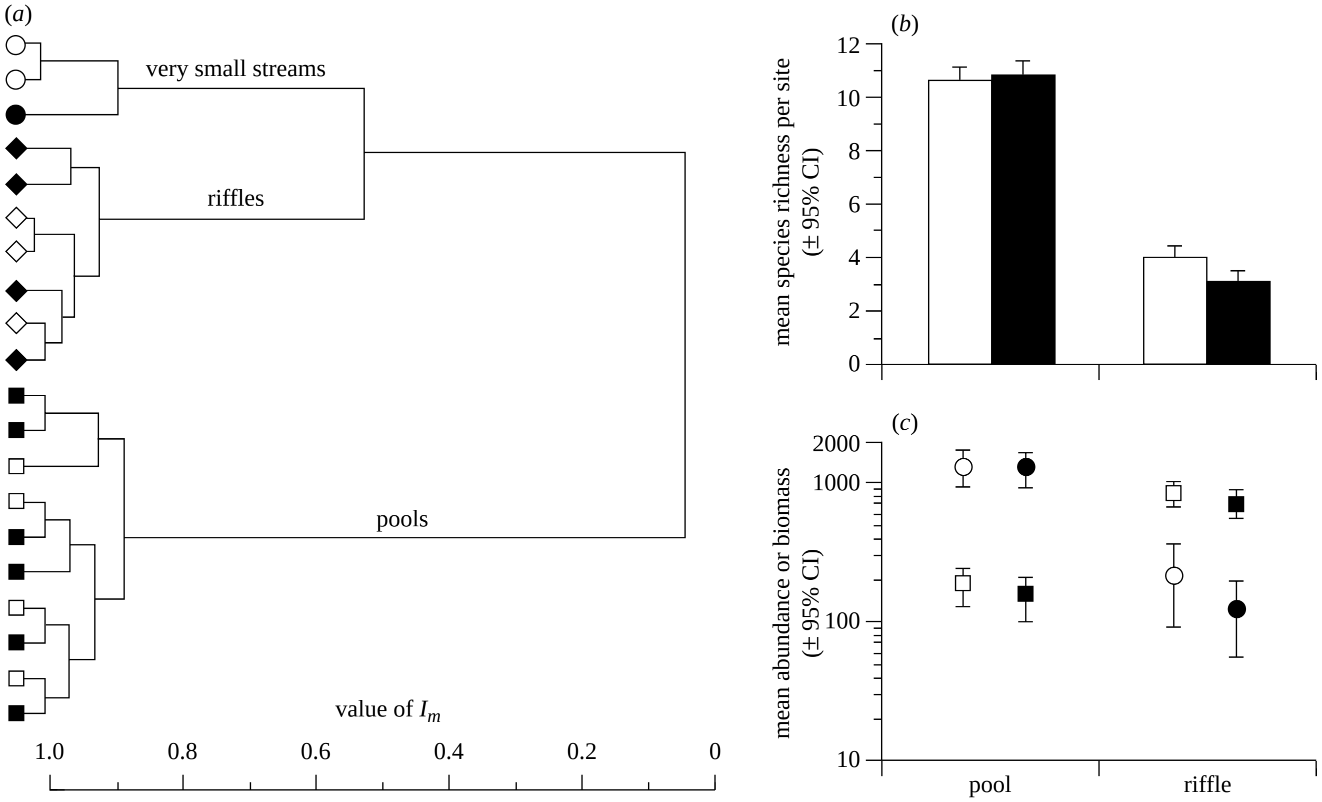

Figure 1. Spatial survey of fish communities with respect to logging and mesohabitat. Unlogged sites represented by open symbols, logged sites by filled symbols in all cases. (*a*) Cluster analysis of sites using Morisita's index of similarity. (*b*) Mean species richness. (*c*) Mean abundance (squares) and biomass (circles). Modified from Martin-Smith (1998*a*,*b*).

## 2. EFFECTS OF SELECTIVE TIMBER EXTRACTION ON FRESHWATER FISHES IN SABAH

Disturbance to freshwater ecosystems caused by timber extraction (logging) is often considered to be severe (Blackie *et al*. 1980; Campbell & Doeg 1989; Detenbeck *et al*. 1992). In a review of studies on temperate-stream fish communities, Detenbeck *et al*. (1992) concluded that stream and river fish communities were not resilient to logging in the absence of mitigation efforts. Detailed investigations of the effects of selective timber extraction around Danum Valley Field Centre (DVFC), Sabah (4°57′40″ N 117°48′00″ E) were conducted by a series of quantitative spatial and temporal surveys (Martin-Smith 1998*b*,*c*). Fish communities were compared between streams running through undisturbed forest and those running through forest logged 3–18 years previously (Martin-Smith 1998*b*) and for a period of 24 months during and following logging (Martin-Smith 1998*c*).

There were few gross changes in community structure of fish communities following logging. Analysis of patterns of abundance, biomass or species composition showed mesohabitat (pool or riffle) and stream size to be more important determinants of community structure than logging history (figure 1). Distinct pool and riffle faunas were found with few species in common between them and those species which were found in both mesohabitats showed size-specific habitat use, with juveniles preferring fast, shallow water and adults slower, deeper water (Martin-Smith 1998*a*). Similarly, there were few significant differences in abundance, biomass or species richness for two streams during and immediately following logging (figure 2*a*,*b*). However, a third stream showed increased species richness and a significant increase in biomass in the 12 months immediately post-logging (figure 2*c*).

The group of species which showed significantly reduced abundance or biomass in the spatial survey (a guild of microherbivores including *Garra borneensis*, *Lobocheilos bo* and *Osteochilus chini*) were among the species which were absent during this initial post-logging period (Martin-Smith 1998*b*,*c*). Biodiversity plots of rank-abundance showed small shifts in community structure to less even distributions in both recently logged and old-logged areas, suggesting long-term persistence of the new state. Similar patterns of higher dominance of some species was found during road construction and logging although recovery of the system was evident after 12 months (Martin-Smith 1998*c*).

These findings suggested that both resistance and resilience were important in maintaining fish communities in Sabah following logging. Although the life spans of fish species in the community are not known they would appear to be relatively short (< three years) compared to the duration of the physical effects of logging (Greer *et al*. 1995; K. M. Martin-Smith, unpublished data). On a theoretical basis, it might be expected that resistance was more important than resilience in maintaining fish communities in the face of such a press disturbance. Thus, experimental manipulations were performed to investigate separately the resistance and resilience of the fish community.

Community resistance was tested by altering the physical habitat occupied by the fish community by construction of large woody debris dams (LWDDs).

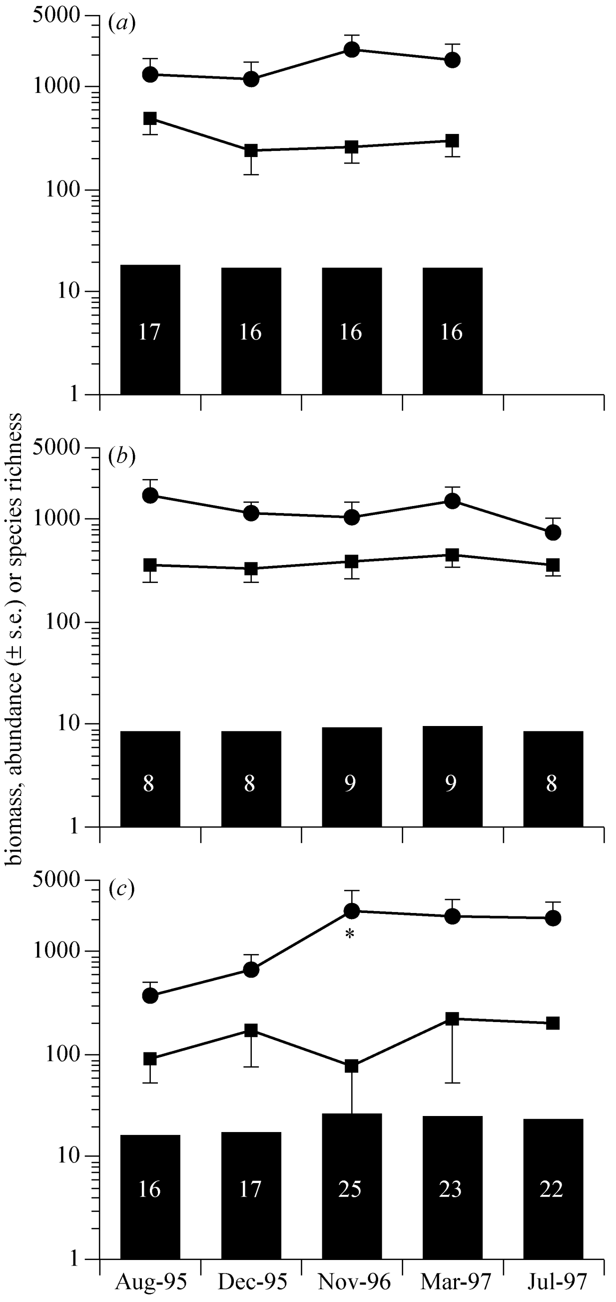

Figure 2. Temporal survey of fish communities in three streams during and after logging. Mean abundance (squares), biomass (circles) and species richness (filled bars with number of species indicated). (*a*) Stream SAN (sample in July 1997 not taken due to landslide). (*b*) Stream SCA. (*c*) Stream TOR (asterisk indicates significant difference between adjacent samples). Modified from Martin-Smith (1999).

Major changes in input of LWD occur during and after logging (Campbell & Doeg 1989) and it has been shown around DVFC that LWD increases substantially after logging which can alter the physical stream habitat considerably (I. Douglas, personal communication). In addition, there is a substantial body of literature from temperate regions showing the importance of LWD in structuring fish communities (e.g. Angermeier & Karr 1984; McMahon & Hartman 1989). Although there is no comparable research from tropical regions, it might be expected that LWD would have a similarly important role in aquatic ecosystems. Experimental LWDDs allowed the fish communities to be quantified both before and after perturbation.

Community resilience was tested with a series of experiments wherein localized catastrophic disturbances were simulated by removing all of the fish from an area, followed by observation of recolonization in time and space (Sheldon & Meffe 1995; Lonzarich *et al.* 1998). This type of experiment simulates, on a small scale, the effects of natural or anthropogenic pulse disturbances such as the release of a toxic agent, stream diversion or severe drought. Without alteration to the physical habitat, resilient fish communities would be expected to reform quickly, although species composition and relative abundance would depend on whether the system was largely deterministic or stochastic (Meffe & Sheldon 1990).

## 3. EXPERIMENTAL METHODS

### (a) *Community resistance*

Six sites (three experimental and three control) were selected on each of three streams. The fish communities at all sites were quantitatively sampled by multiple-pass electrofishing (Martin-Smith 1998*a*). At experimental sites, LWDDs were created by the felling of selected live or dead trees, which were then positioned, perpendicular to the stream flow. Smaller woody debris and/or rocky material were added to simulate the natural accretion process. Sites were resampled by multiple-pass electrofishing 70 and 110 days after the creation of the LWDDs. All fish were identified, standard length (SL) measured and returned. Quantitative habitat measurements were taken as in Martin-Smith (1998*a*). Biomass for each individual was calculated from standard length–weight regressions (Martin-Smith 1996). Abundance (number of individuals) and biomass were then standardized to unit area, calculated from habitat measurements, and log-transformed to normalize their variance. A quantitative similarity measure, Morisita's index ($I_m$), was calculated for both abundance and biomass data to compare the initial communities with those after the perturbation. This index was used since it is relatively robust and insensitive to sample size (Wolda 1981; Magurran 1988). Data for all response variables (log abundance, log biomass, $I_m$ (abundance), $I_m$ (biomass) and species richness) were analysed using a mixed-model analysis of variance (ANOVA) with streams as blocks and treatment (LWD or control) and sampling day (70 or 110 days) as fixed factors.

### (b) *Community resilience*

Recolonization experiments were stratified by mesohabitat (Martin-Smith 1998*a*) with four experiments conducted in pools and two in riffles; all experiments were conducted using the same protocol. Experimental sections were isolated with upstream and downstream stop-nets (5 mm stretched mesh) and were then electrofished in a downstream direction. Multiple passes were undertaken until fewer than five fish were caught on the final pass (often this figure was zero). Typically, three to seven passes were required to achieve this. All fish caught were identified to species and SL measured; these individuals were either transported to a different stream or > 750 m downstream and released. At specified times sites were revisited and one or two electrofishing passes were undertaken. All fish were identified and returned to their point of capture. In two pool and both riffle experiments SL was measured for all fish. Details of number of sites, location and times of sampling are given in

Table 1. *Experimental details for recolonization experiments* (*stream locations and details are given in Martin-Smith* (*1998a*))

| experiment | dates | stream | mesohabitat | no. of sites | sampling times (days) |
|---|---|---|---|---|---|
| P1 | 26/10/96–4/11/96 | SKA | pool | 5 | 0.15, 0.90, 7 |
| P2 | 14/08/96–14/09/96 | PTA | pool | 4 | 8, 13, 22, 31 |
| P3 | 29/01/96–28/03/96 | CSR | pool | 4 | 15, 36, 49, 58 |
| P4 | 12/08/96–13/09/96 | BKT | pool | 4 | 7, 14, 21, 31 |
| R1 | 07/02/97–07/07/97 | CSR | riffle | 8 | 1, 2, 3, 4, 7, 8, 16, 21, 28, 42, 80, 150 |
| R2 | 02/05/97–08/07/97 | DSS | riffle | 5 | 66 |

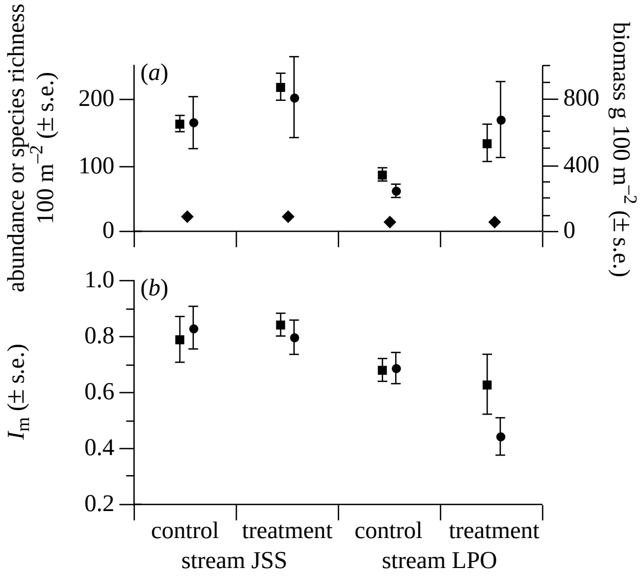

Figure 3. Changes in fish communities for control and experimental sites after construction of LWDDs. (*a*) Mean abundance (squares), biomass (circles), species richness (diamonds). (*b*) Mean similarity using $I_\mathrm{m}$ calculated from abundance (squares) or biomass (circles).

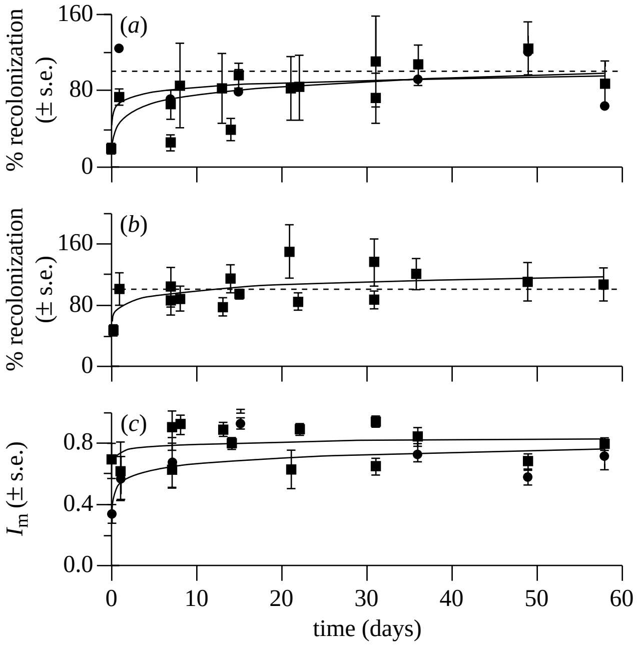

Figure 4. Recolonization of pool habitats with fitted logarithmic regressions. Dotted lines indicate initial levels. (*a*) Mean abundance (squares) or biomass (circles) (error bars omitted from biomass for clarity). (*b*) Mean species richness. (*c*) Mean similarity using $I_\mathrm{m}$ calculated from abundance (squares) or biomass (circles).

table 1. Abundance and biomass were calculated and standardized as above to habitat dimensions. Data from all experiments were converted to percentages and data for each mesohabitat were combined. $I_\mathrm{m}$ was calculated to compare each site with initial (pre-defaunation) conditions. Recovery rates were assessed using a logarithmic model of the form $\ln(\%\text{recovery} + 1) = \ln(a) + b\ \ln(\text{day} + 1)$ which has been shown to provide the best fit to temperate recolonization data (Sheldon & Meffe 1995; Lonzarich *et al*. 1998).

## 4. EXPERIMENTAL RESULTS

### (a) *Community resistance*

There were no significant differences in species richness, abundance and biomass between experimental and control sites before the LWDDs were constructed (two-way analysis of variance, $F_{1,16} < 0.58$, $p > 0.10$ in all cases). The data set from one stream (site SKA) had to be excluded from post-perturbation analyses because of a drought that isolated the dammed sections of the stream. Fish communities were resistant to the experimental perturbations in some community variables with species richness, biomass and $I_\mathrm{m}$ (abundance) not significantly affected by the construction of LWDDs ($F_{1,19} < 1.27$, $p > 0.10$). However, other community variables showed significant treatment effects: abundance ($F_{1,19} = 6.08$, $p < 0.03$), which was significantly higher in experimental treatments compared with controls, and $I_\mathrm{m}$ (biomass) ($F_{1,19} = 4.57$, $p < 0.05$), which was significantly lower (figure 3).

### (b) *Community resilience*

Fishes recolonized pool habitats quickly with some individuals being found at all sampling time points (figure 4). Logarithmic regressions fitted the data well for most community attributes, the exception being biomass, which had fewer sample points (table 2). Species richness was the most resilient community attribute with full recolonization occurring in less than ten days. Abundance and biomass took longer to recover although both were not significantly different from initial values after 25 days.

Recolonization of riffle habitats took much longer than for pools (figure 5). Logarithmic regressions did not fit the data as well as for pools with significant regressions only found for abundance and $I_\mathrm{m}$ (biomass) (table 2). Again, species richness recovered more quickly than other

Table 2. *Parameters of logarithmic regressions for recolonization experiments*

($n = 15$ for pool experiments, $n = 13$ for riffle experiments.)

| variable | recovery rate, $b$ (±s.e.) | intercept, ln ($a$) (±s.e.) | $R^2$ | $F$-value |
|---|---|---|---|---|
| pool | | | | |
| abundance | 0.665 (±0.171) | 2.325 (±0.477) | 0.519 | 15.11 |
| biomass | 0.193 (±0.153) | 3.804 (±0.437) | 0.242 | 1.60 |
| species richness | 0.576 (±0.193) | 2.868 (±0.538) | 0.388 | 8.89 |
| $I_m$ (abundance) | 0.070 (±0.028) | 0.367 (±0.079) | 0.305 | 6.13 |
| $I_m$ (biomass) | 0.084 (±0.034) | 0.249 (±0.091) | 0.501 | 6.75 |
| riffle | | | | |
| abundance | 0.500 (±0.188) | 2.319 (±0.534) | 0.415 | 7.09 |
| biomass | 0.432 (±0.228) | 2.704 (±0.563) | 0.264 | 3.58 |
| species richness | 0.463 (±0.211) | 2.724 (±0.603) | 0.325 | 4.82 |
| $I_m$ (abundance) | 0.050 (±0.026) | 0.343 (±0.076) | 0.261 | 3.53 |
| $I_m$ (biomass) | 0.049 (±0.019) | 0.222 (±0.055) | 0.392 | 6.44 |

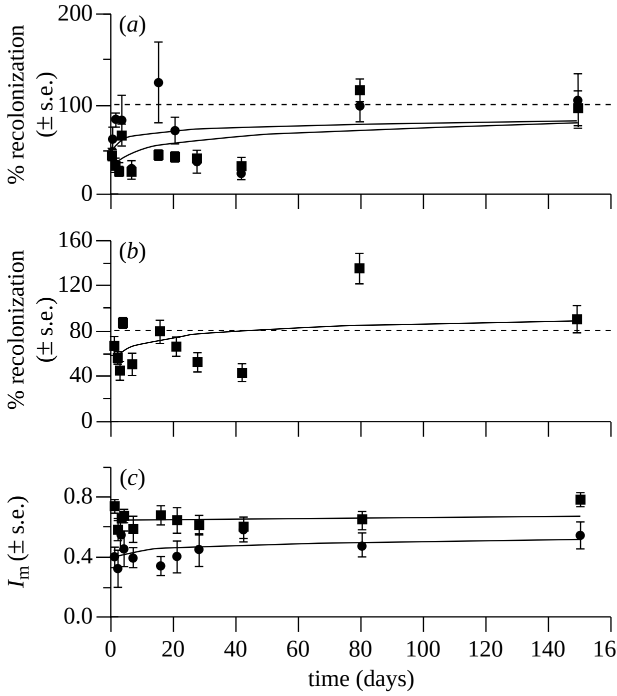

Figure 5. Recolonization of riffle habitats with fitted logarithmic regressions. Symbols as in figure 4.

variables but it took *ca.* 100 days to attain pre-defaunation levels. Abundance and biomass were still significantly lower than pre-defaunation levels at the termination of the experiment at 150 days. Recovery rates were significantly lower (ANCOVA, $F_{1,25} > 10.25$, $p < 0.01$) for riffles than pools for all community parameters except biomass, for which the rates were not compared because of poor regression coefficients (table 2).

## 5. MOBILITY OF FISHES

One possible mechanism that has been suggested to explain high resilience in fish communities is high rates of movement of individuals (Pearsons *et al.* 1992; Sheldon & Meffe 1995). This was investigated for fishes around DVFC in a series of mark–recapture experiments (Bullough 1996; Lewis 1997; Martin-Smith *et al.* 1999). Individuals of common species from each

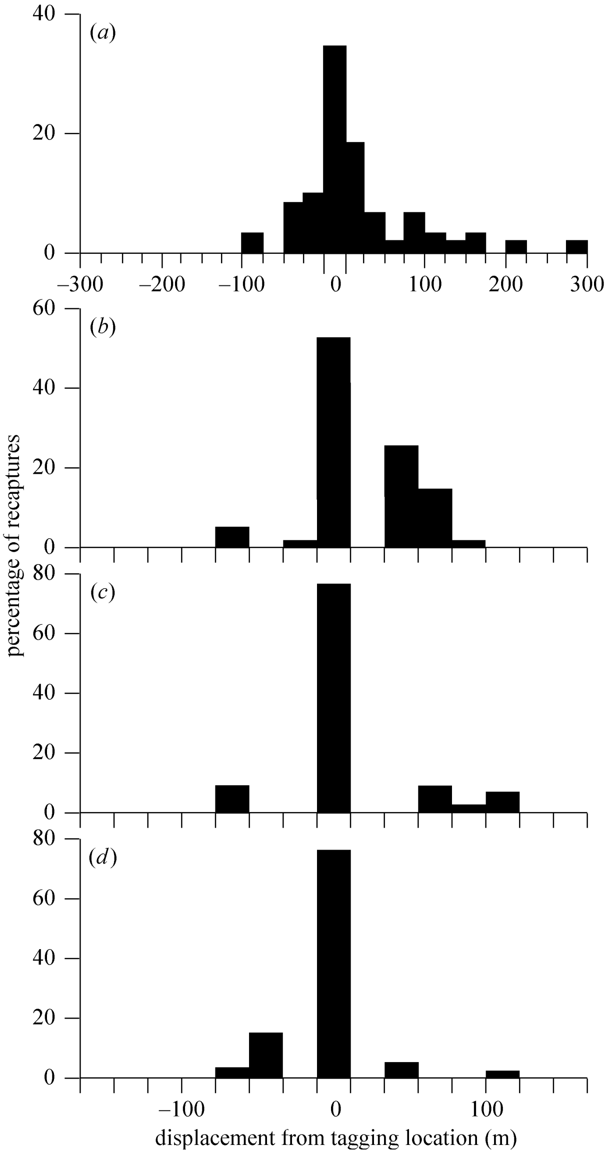

Figure 6. Movements of eight cyprinid species in four mark–recapture experiments. (*a*) River SEG (days 1–60), $n = 61$; (*b*) stream CSR (days 1–17), $n = 63$; (*c*) stream LPD (days 4–24), $n = 101$; (*d*) stream BKT (days 5–25), $n = 61$. Positive values indicate upstream movement, negative values downstream movement. Modified from Bullough (1996), Lewis (1997) and Martin-Smith *et al.* (1999).

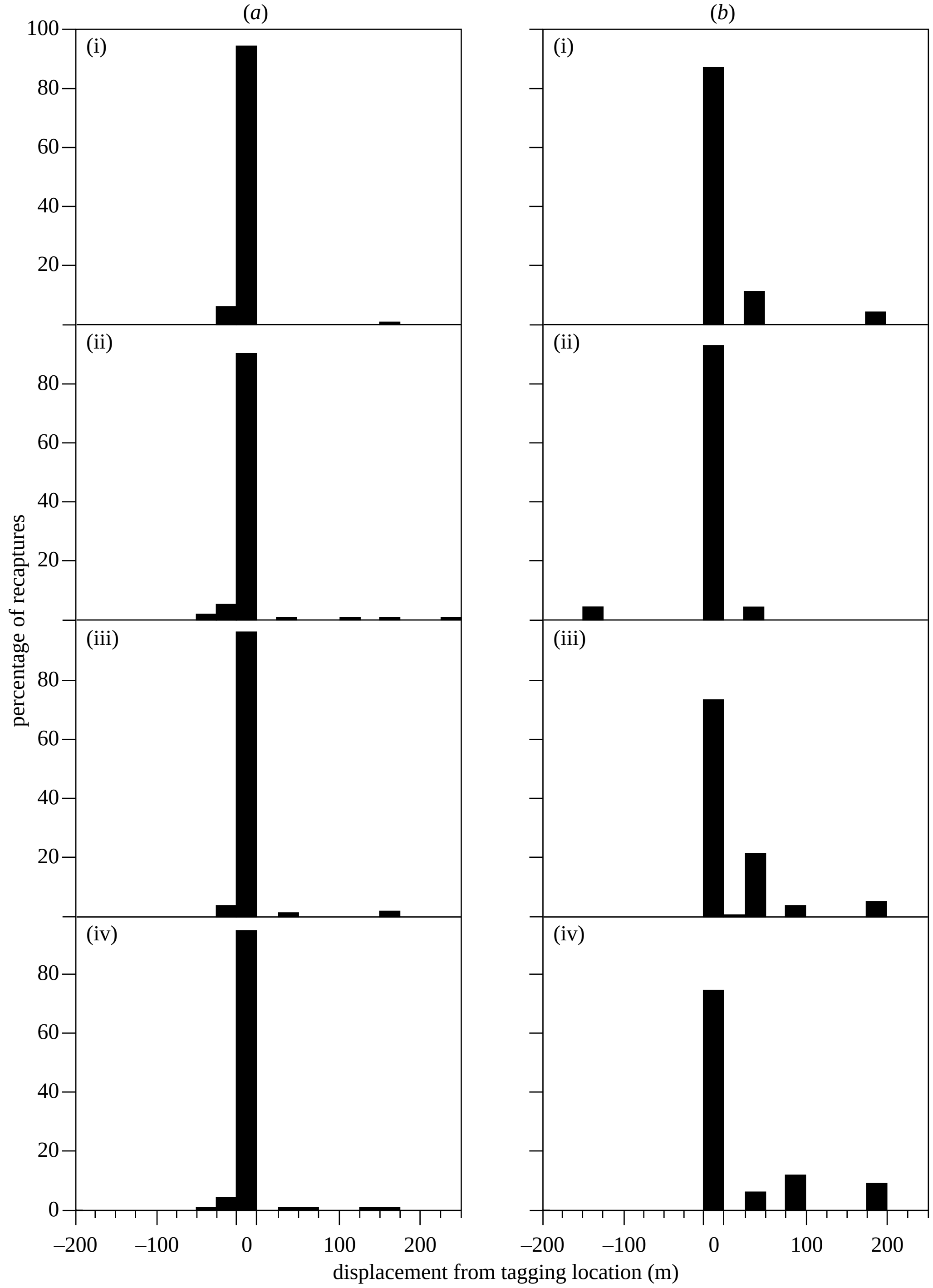

Figure 7. Movements of *Gastromyzon* species in two mark–recapture experiments. (*a*) Stream SBE: (i) day 10, $n = 62$; (ii) day 22, $n = 87$; (iii) day 38, $n = 140$; (iv) day 58, $n = 126$. (*b*) Stream PTA: (i) day 17, $n = 26$; (ii) day 35, $n = 20$; (iii) day 49, $n = 27$; (iv) day 205, $n = 24$. Positive values indicate upstream movement, negative values indicate downstream movement. Note that four individuals were caught on day 292 in stream PTA but are not shown because of the small sample number. Modified from Lewis (1997) and Martin-Smith *et al.* (1999).

mesohabitat were either batch marked with a visible implant elastomer or individually marked with alphanumeric or Carlin tags. Sampling was undertaken at various periods up to 292 days post-tagging at original tagging locations and similar mesohabitats upstream and downstream.

The results of these experiments showed a clear difference in mobility between pool and riffle species. Species of cyprinid (e.g. *Garra borneensis*, *Lobocheilos bo*, or *Osteochilus chini*) that inhabited pools showed high rates of movement and turnover (figure 6). Fishes were recaptured up to 300 m from their original tagging locations in less than 60 days and up to 50% of recaptures were at different locations from their tagging location. Cyprinids were also observed to move both upstream and downstream, although it was generally not possible to test statistically whether there was a significant difference in the direction of movement.

Conversely, balitorids (e.g. *Gastromyzon danumensis*, *Gastromyzon lepidogaster*) adapted to living in riffle habitats, were extremely site-associated and persistent over long periods of time (figure 7). Up to 95% of recaptures were made at the original tagging location and some individuals were found within 3 m of their original location after 292 days. Although movements both downstream and upstream were recorded, significantly more individuals moved upstream (Martin-Smith *et al.* 1999).

## 6. DISCUSSION

Although there is considerable evidence that selective logging causes significant changes in hydrological parameters such as stream flow, sediment load or large woody debris (Abdul Rahim & Harding 1992; Greer *et al.* 1995), fish communities around DVFC showed high similarity between areas logged more than three years previously and unlogged areas (Martin-Smith 1998*b*). In addition, there were only limited effects in the two-year period during and immediately following logging (Martin-Smith 1998*c*). These indirect measures of community stability were confirmed by small-scale press and pulse disturbances addressing community resistance and resilience respectively.

Community resistance to disturbance is difficult to demonstrate purely by correlation, if the magnitude of the disturbing force is not known (Connell & Sousa 1983). Experimental confirmation is usually required where the size of the perturbing force is known and/or controlled. The construction of LWDDs was a significant perturbation, but was accompanied by few significant changes in the fish community. A highly significant site effect was found in the data analysis, implying that resistance was not necessarily a predictable attribute of a particular community. One of the sites (stream LPO) showed increased biomass and lower similarity at dammed sites; this appeared to be due to the movement of larger individuals of some locally common cyprinids into the experimental sites. These species were not present in the local species pool at the other site and so the response was not observed.

Community resilience was demonstrated to be high for pool fishes around DVFC. The time taken for complete recovery of abundance and biomass was approximately 30 days, which is similar to findings from temperate recolonization experiments (estimated time to complete numerical recovery for pools close to colonization sources: ten days, Peterson & Bayley 1993; 32 days, Sheldon & Meffe 1995; 30 days, Lonzarich *et al.* 1998). The similarity of recovery times may indicate that the same recolonization processes were occurring in all of these studies. Using linear regressions for colonization data, Peterson & Bayley (1993) estimated that it would take 1.5–4.1 years for a temperate fish community to be re-established in an 8 km stream reach. This work implies that, in the streams around DVFC, it would not have been possible to detect even the complete removal of the fish community at the time of logging, since the minimum time since logging was three years and most streams were less than 5 km from an undisturbed source of potential colonists.

Peterson & Bayley (1993) concluded that the mechanism of recolonization over short time-scales was haphazard movement of individuals, which is supported in the present study by the results of the mark–recapture experiments. Cyprinids showed high measured rates of movement between mesohabitats over short time periods. It is likely that actual rates of movement were even higher, since detection probabilities were lower for moving than stationary individuals (Goforth & Foltz 1998). Although there are few data on the movements of tropical cyprinids (Yap & Furtado 1980), the present data are consistent with those measured in temperate stream cyprinids (e.g. Hill & Grossman 1987; Goforth & Foltz 1998).

Similarity coefficients between pre- and post-defaunation pool communities were also high, indicating that fish colonized in approximately the same proportions as were initially present. This supports the hypothesis of Meffe & Sheldon (1990) that the communities were largely deterministic and highly predictable from local habitat structure. Pool communities can thus be represented, conceptually, as a dynamic equilibrium between the short-term movements of component species superimposed on a deterministic community structure defined by the physical habitat template.

Although the dynamics of recolonization of riffle communities were similar in form to those for pools, the time taken was much longer. Numerical abundance and biomass had not recovered to pre-defaunation levels at the end of the experiments after 150 days. It is hypothesized that this was a direct consequence of the site-associated nature of the species that make up the riffle communities. Tagged *Gastromyzon* individuals inhabited small areas of riffle for long periods (up to 292 days). Furthermore, *Gastromyzon* individuals have been observed in apparent territorial behaviour (K. M. Martin-Smith and L. M. Laird, unpublished data) which suggests they have small and predictable home ranges. The low rates of movement observed may indicate that recolonization of riffles was accomplished not by movements of adult fish, but by dispersal of juveniles.

The conservation and management implications of the current work are that the streams around DVFC need to be considered on a mesohabitat basis, rather than as whole streams. Although the riffle communities have lower species richness, they contain a high proportion of endemic species, some with very restricted known distributions (Inger & Chin 1990). Given that riffle communities demonstrated lower resilience to pulse disturbances, minimum criteria for recovery should be based on their dynamics.

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