Responses of stream macroinvertebrate communities to progressive forest harvesting: Influences of harvest intensity, stream size and riparian buffers

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ABSTRACT

Harvesting of forests causes a range of disturbances, including changes to hydrology, nutrient inputs, water quality, food sources, habitat structure and channel morphology, which can impact streams over several years and are reflected in changes in community structure. We aimed to determine the relative magnitudes of impact and rates of recovery of benthic macroinvertebrate communities, and associated changes in biotic indices (Quantitative Macroinvertebrate Community Index and an Index of Biotic Integrity), in reaches of different sized streams within progressively logged catchments. We conducted annual summer surveys over seventeen years in fifteen New Zealand streams that differed in size (upstream catchment area between 40 and 2360 ha, mean channel widths between 2.5 and 16 m) and harvest intensity in the surrounding catchment. The largest post-harvest changes in biotic indices and community structures occurred in streams draining relatively small to medium catchments (<500 ha) where >40% of the upstream catchment had been harvested, and particularly after harvesting of overstorey riparian vegetation adjacent to study reaches. The impacts of harvest on invertebrate communities were less evident in wider streams draining catchments over 500 ha, but the largest changes from pre-harvest biotic indices and community structure still generally occurred after harvesting of riparian vegetation along these streams. The changes in community structure after harvesting of riparian vegetation typically included increases in the densities of Diptera, Mollusca and Oligochaetes, and decreases in the densities of Ephemeroptera. These results demonstrate that impacts on benthic macroinvertebrate communities increased as the proportion of upstream catchment harvested increased and/or after riparian vegetation was harvested. Some of the communities in headwater streams had largely recovered towards pre-harvest structures, whereas post-harvest recovery was less evident in relatively large streams, over the duration of the study.

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1. Introduction

Harvesting of forests causes a range of disturbances to adjacent streams, including changes to hydrology, nutrient inputs, water quality, food sources, habitat structure and channel morphology, with concomitant changes in the structures of benthic macroinvertebrate communities and overall ecosystem function (Campbell and Doeg, 1989; Harding et al., 2000; Fahey et al., 2004). One of the major short-term impacts of clearcut harvesting results from increased terrigenous sediment input from recently exposed hillslopes, which typically alters community structure via negative effects on sensitive taxa, such as most Ephemeroptera, Plecoptera and Trichoptera, whilst favouring disturbance tolerant taxa, such as Diptera (e.g. Death et al., 2003; Collier and Smith, 2005; Martel et al., 2007). The amount of soil that is exposed and compacted during harvesting depends on the intensity of forestry operations, with erosion potential also influenced by physical properties of the catchment, including soil type and slope, and local climate (Marden et al., 2006). Large amounts of sediments, and associated nutrients, may be transported into streams via erosion and landslips of unconsolidated hillslopes during storms that occur soon after harvesting (Campbell and Doeg, 1989; Marden et al., 2006). Harvesting of overstorey riparian vegetation along stream banks results in alteration of thermal regimes, reduced allochthonous inputs, and increased autochthonous production (Campbell and Doeg, 1989; Fahey et al., 2004). Whilst the soil in the catchment may be stabilised relatively soon after harvesting, with the establishment of early succession vegetation (Olsson and Staaf, 1995; Langer et al., 2008), it may take several years before excess sediment is flushed from streams, and shading and allochthonous inputs return to pre-harvest amounts (Fahey et al., 2004; Davies et al., 2005; Quinn and Wright-Stow, 2008). Longer-term effects of harvest may also include changes to the physical structure of streams, as unvegetated banks are susceptible to channel widening and regrowth forests have no large...
logs to contribute to streams to potentially function as habitat and retentive structures (Bilby and Ward, 1991; Magilligan et al., 2008).

Numerous studies have demonstrated the impacts of forest harvesting on benthic macroinvertebrate communities, typically in low-order reaches with harvest occurring immediately adjacent to the reach or the entire upstream catchment cleared (see reviews by Campbell and Doeg, 1989; Harding et al., 2000; Fahey et al., 2004). Headwater reaches may recover from post-harvest changes in community structure within three years (Collier and Bowman, 2003; Haggerty et al., 2004), whilst impacts are still evident decades after harvest in reaches of some other larger catchments (e.g. Stone and Wallace, 1998; Davies et al., 2005; Zhang et al., 2009). However, previous studies have usually involved either one-off comparisons of post-harvest and nearby reference sites, or comparisons between one pre- and one post-harvest survey at logged sites, and we have minimal information about trajectories of ecosystem recovery from harvest impacts (but see Collier and Bowman, 2003; Collier and Smith, 2005; Quinn and Wright-Stow, 2008). There is also minimal information about how the magnitudes of impact and rates of recovery of stream communities vary depending on the intensity of logging operations and size of streams. Progressive logging is likely to result in smaller and more localised impacts, in comparison to whole catchment clearfelling operations (Davies et al., 2005; Kreutzweiser et al., 2005). Depending on the amount of upstream disturbance, there is the potential that these localised impacts can be, at least partly, ameliorated with the provision of buffers with intact riparian vegetation adjacent to reaches (Newbold et al., 1980; Davies and Nelson, 1994; Quinn et al., 2004). These buffers can stabilise stream banks, filter sediment and nutrients in runoff, maintain a high level of shading, and contribute allochthonous detritus (Climnick, 1985; Davies and Nelson, 1994). Those communities in narrower streams, which are naturally more dependent on overstorey riparian vegetation for shading and allochthonous inputs, may benefit more from provision of buffers than communities in wider streams (Quinn and Wright-Stow, 2008).

We conducted annual surveys over seventeen years to evaluate the effects of logging pine (Pinus radiata) plantations on benthic macroinvertebrate communities in forests of the Coromandel Peninsula, New Zealand. We aimed to determine: (i) the relative magnitudes of impact of progressive harvesting on benthic macroinvertebrate communities, by comparing pre- and post-harvest biotic indices (the Quantitative Macroinvertebrate Community Index, QMCI and an Index of Biotic Integrity, IBI) and community structure, for streams of different sizes which were impacted by varying amounts of upstream harvest; (ii) the association between harvesting of riparian vegetation adjacent to these study reaches and the relative magnitudes of impact; and (iii) the rates of recovery towards pre-harvest structure for benthic macroinvertebrate communities in small streams, which are naturally more dependent on riparian vegetation, would be more severely impacted by forest harvesting than those in larger streams, particularly after harvesting of riparian vegetation. We also predicted that the communities in smaller streams would recover from riparian harvesting more rapidly than those in larger streams (see Quinn and Wright-Stow, 2008), reflecting more rapid recovery of shading and allochthonous inputs to pre-harvest amounts.

2. Methods

2.1. Site descriptions

The study was conducted in twelve stream reaches that differed both in size (upstream catchment area between 40 and 2360 ha, mean channel widths between 2.5 and 16.0 m) and amounts of progressive harvesting that had occurred in the surrounding commercial exotic pine plantations, in the Whangapoua and Tairoa Forests, Coromandel Peninsula, New Zealand (36.9°S, 175.7°E, see Quinn and Wright-Stow, 2008 for location and photographs of Whangapoua Forest sites). These forests are on strongly rolling to very steep landscape (dropping from ~450 to 500 m to sea level in ~6 km). Soils are predominantly clay and yellow-brown earths overlaying weathered greywacke and andesite rocks. Mean monthly air temperatures in the region range from 10.5 °C in July to 19 °C in January (Meleason and Quinn, 2004). Mean annual rainfall is high (~2400 mm at ridge tops to 1700 mm at lower edges of the forests), with frequent cyclonic storms and highly variable stream flows. The study streams have predominantly gravel-cobble-boulder beds, with summer baseflows of ~0.081 L ha⁻¹ s⁻¹ (Quinn et al., 2004).

The native forest in the region was first logged selectively for kauri (Agathis australis) from the early 1800s to 1930s. Lower slopes were used for grazing at low stocking rates until the 1940s, prior to the plantation of pines in the 1960s. The harvest of first rotation tree crops from Whangapoua Forest (harvest sites WH1, WH2, WH3, WH4, WH5, WH6, WH7 and WH8) commenced in 1992, whilst harvesting of Tairoa Forest (harvest sites TH1, TH2, TH3 and TH4) commenced in 1993. Harvesting involves progressive clearcutting of varying portions of each catchment on an approximately 25–28 year cycle, with logs typically removed using skyline cable haulers, with heel-boom loaders or ground basedtractors in flat terrain. This system has generally kept machinery and earthworks associated with landing and road construction clear of major watercourses.

Pines are typically replanted at 850 stems per hectare in the winter following harvest.

In addition to those sites within plantation forest, surveys were conducted at a nearby native forest reference site (NR1) over the duration of the study, which allowed the effects of harvesting disturbances on macroinvertebrate communities to be differentiated from natural interannual variation. Site NR2 was surveyed from 2004 to 2009, as an additional native forest reference site. Site PR was downstream of a catchment of the same area as that above site NR1, but was surrounded by unharvested pine forest, and was surveyed from 2005 to 2007 to determine the similarity in biotic indices and community structures between streams surrounded by native or pine forest in the absence of harvest.

2.2. Field surveys

Surveys were conducted in representative reaches from 40 to 120 m long (reach length was in proportion to the bankfull channel width at each site during initial surveys, measured across ten equidistant transects) under summer baseflow conditions over seventeen years, from 1993 to 2009. During each survey water temperature (YSI model 58 meter), streambed surficial sediment particle size distribution and biomass of epilithon were measured at each reach. Streambed particle sizes were determined following Wolman (1954), by classifying Wentworth scale sizes of >100 particles across ten equally spaced cross-sections along each reach. Fine sediments were defined as all silt, clay and sand particles <2 mm. Epilithon was removed from seven stones collected haphazardly from ‘run’ habitats (representing average hydraulic conditions between ‘rifles’ and ‘pools’) across each reach, using a nylon-bristled brush. Biomass was calculated as ash free dry mass (AFDM) per unit area of exposed stone surface area (assumed to be half of the area of the collected stones) calculated from measurements of the length, width and breadth of stones (Dall, 1979).

Benthic invertebrates were sampled by collecting five Surber samples (0.1 m², 250 μm mesh) from run habitats, evenly spaced along the length of each reach. These samples were combined and
Invertebrate densities for the entire combined sample were identified. From 2003 invertebrate processing year study period. Prior to 2003 all invertebrates within each combined sample were identified. From 2003 invertebrate processing involved subsampling and a count of at least 200 animals, plus a scan for uncommon taxa in the whole sample (which follows the national protocol for processing invertebrates in wadeable streams, see Stark et al., 2001). Invertebrate densities for the entire combined sample were estimated by multiplying subsample counts by the inverse of the proportion of sample that was sorted. This subsampling was adopted after it was found that it produced very similar values for biotic indices to full counts at the Whangapoua Forest sites (Wright-Stow and Quinn, 2003).

2.3. Biotic indices

The QMCI (see Stark, 1985), and multimetric IBI (expressed as a percentage of a ‘regional reference’ site, % IBI) modified from the version of the USEPA Rapid Bioassessment Protocol (Plafkin et al., 1989), were calculated for each sampling occasion. For calculation of % IBI site NR1 was used as the regional reference for most sites, which were on the eastern side of the Coromandel Peninsula, whilst NR2 was used as the regional reference site for WH8, as both of these sites were on the western side of the peninsula. Modifications from the USEPA version of IBI are detailed in Quinn et al. (2004). Changes in the proportions of different macroinvertebrate Orders (i.e., Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Diptera, Mollusca, and ‘Other’) present at each site over time were also calculated to facilitate exploration of the broad patterns for post-harvest changes in macroinvertebrate communities at each site.

2.4. Data analyses

To assess the general influences of increased harvest intensity on biotic indices across sites, mean values for the QMCI and % IBI were calculated for varying amounts of forest harvest within each site: prior to harvest; after 1–40% of upstream catchment was harvested; after 41–80% of upstream catchment was harvested; and, after riparian vegetation adjacent to the study reach was harvested (calculated from 1 to 3 yrs after riparian harvest in each site, as this was likely to be the period of maximum disturbance, see Quinn and Wright-Stow, 2008). Similarly, mean Bray-Curtis similarities to pre-harvest community structure (based on log-transformed community abundance data) were calculated for the three post-harvest categories listed above. Sites were arbitrarily separated into the two harvesting categories below and above 40% so that there was adequate replication within categories to allow analyses between them, and 40% harvest should not be interpreted as a threshold value. Three separate ANCOVAs (with upstream catchment area used as a covariate to account for possible differences in impact due to stream size) were conducted using these mean values to determine whether impacts differed amongst each harvest category, with post hoc Tukey tests used to identify which harvesting categories contributed to main effects significant differences. Across all sites, the linear regression relationship between upstream catchment area and mean channel width was highly significant (\( R^2 = 0.54, F_{1,13} = 15.2, P = 0.002 \)), and the patterns for relative amounts of impact were similar regardless of which of these values was used as the index of stream size. Catchment area was used as the index of stream size in the analyses, because it is at a more useful scale to guide management and is constant, unlike channel width which may vary over the harvesting cycle.

Multivariate Analyses of Similarity (ANOSIM) were used to determine whether the macroinvertebrate community structures at sites NR2 (native forest reference) and PR (plantation forest reference) were similar to those at site NR1 (native forest reference used as the regional reference for most sites in calculation of % IBI). Non-metric multidimensional scaling (MDS, see Clarke and Warwick, 2001) of macroinvertebrate community structure was used to determine patterns for the relative magnitudes of harvesting impacts, and evidence of recovery from these impacts amongst harvest sites. For each site, post-harvest divergence from the pre-harvest community structure, above that interannual divergence in community structure occurring naturally at the unharvested reference site NR1, was interpreted as being associated with har- vesting activities, whilst post-harvest convergence towards the pre-harvest community structure was interpreted as evidence of recovery. ANOSIMs and the ordination were based on Bray-Curtis similarities of log-transformed community abundance data from all sites. All taxa (genus-level or higher) were included in multivariate analyses, with log transformation applied to reduce the influence of a few highly abundant taxa on the results (Clarke and Warwick, 2001). Rather than analysing each site separately for the MDS ordination, it was necessary to include all sites and sampling times in the same analysis to allow assessments of relative magnitudes of impact and rates of recovery for macroinvertebrate communities with differences in stream size and proportions of upstream catchment harvest, although this resulted in increased ordination stress.

Multiple linear regression analyses were conducted to determine whether the relative positions of datapoints along either axis of the two-dimensional ordination were associated with the proportions of catchment harvest, and/or any of those measured variables that were likely to be influenced by harvest (i.e., epilithon biomass, temperature, and proportion of fine sediment on the streambed) (sensu Quinn et al., 2004), with stepwise simplification of the full model until only those predictors with significant explanatory power were retained (Crawley, 2007). Multivariate analyses were conducted using Primer v.6., whilst all univariate analyses were conducted using R (R Development Core Team, 2006).

3. Results

3.1. Physical parameters and storms

This study was focused on the impacts of progressive forest harvesting on macroinvertebrate communities, but there were also notable changes in other measured variables after harvest. Briefly, post-harvest increases in fine sediment on the streambeds of study reaches occurred in association with either upstream harvest exceeding 40% of total catchment area or after riparian vegetation adjacent to the reach was harvested (Table 1). However, there were no obvious post-harvest increases in fine sediment in the study reaches of the largest streams (>500 ha), where the proportions of upstream catchment harvest were usually relatively low. The highest temperatures recorded in the study reaches occurred after riparian harvest (Table 1), but these spot temperature measurements were only indicative of general trends. Prior to riparian harvest the densities of epilithon in streams were always relatively low (usually <10 g m\(^{-2}\)), but across all sites the mean biomass increased after removal of riparian vegetation (Table 1). Three-fold increases in epilithion biomass were common after riparian harvest, and generally occurred within two years of this harvest at sites draining catchments larger than 200 ha, but took four to five years after this harvest in smaller headwater streams (<200 ha).
Several large storms caused disturbances to streams over the duration of the study. The most notable impacts on macroinvertebrate communities from such an event occurred after a severe storm struck parts of the Whangapoua Forest (including sites NR1, WH2, WH4 and WH6) in early 1995. The extreme peak flows which occurred during that storm had an approximate return period of 20–50 yrs, and resulted in hillslope slips, severe gully erosion and downstream flood damage. The storm caused substantial changes to stream habitat, via widening of stream channels, turning over substrate on streambeds and the redistribution of large wood.

3.2. Overview of harvest impacts on macroinvertebrate communities

A total of 130 benthic macroinvertebrate taxa were collected during the seventeen year study, with similar pre-harvest community structures in sites from Whangapoua and Tairua Forests. The most diverse orders were Diptera (41 taxa), Trichoptera (29 taxa), Ephemeroptera (17 taxa), Mollusca (9 taxa) and Coleoptera (8 taxa). Across all sites, there were significant declines in the QMCI as the proportion of upstream catchment that was harvested reached above 40% and/or after logging of riparian vegetation (i.e., for the QMCI pre-harvest = 1–40% harvest > 41–80% harvest = riparian harvest, Fig. 1a, Table 2). Declines in % IBI were only significant after harvesting of riparian vegetation, with values in this harvesting category lower than those occurring both pre-harvest and after 1–40% of the upstream catchment had been harvested (Fig. 1b). The greatest divergences from pre-harvest community structures also occurred after harvesting of riparian vegetation, i.e. Bray–Curtis similarity to pre-harvest structure was lower for sites after riparian harvest than after 1–40% harvest, but not 41–80% harvest (Fig. 1c).

Although the lowest post-harvest QMCIs, % IBIs and similarities to pre-harvest community structures generally occurred at the smallest sites (Fig. 1), including upstream catchment area as a covariate did not significantly reduce the unexplained variation between harvest categories for any of these measures (Table 2).

Prior to harvest the values for biotic indices in plantation sites were generally relative high, but there were post-harvest decreases in these values with increasing harvest intensity in most sites (Fig. 2). These decreases in biotic indices were generally associated with decreases in the proportions of Ephemeroptera, and increases in the proportions of Diptera, Mollusca and/or Oligochaetes (Fig. 2). The stress for the two-dimensional MDS ordination was explained by including epilithon biomass, temperature, and proportion of fine sediment on the streambed in the linear regression model (full model: Axis 1 = cumulative % harvest + epilithon biomass + temperature + % fine sediment, Adjusted $R^2 = 0.57, F_{4,137} = 47.93, P < 0.001$). There was also a significant positive association between the position of datapoints along axis 2 of the MDS ordination and epilithon biomass (Axis 2 ~ epilithon biomass, Adjusted $R^2 = 0.02, F_{1,140} = 4.20, P = 0.042$), but none of the other variables listed above. Therefore, the communities subject to the largest amounts of disturbance from forest harvesting, and associated changes in epilithon, temperature, and fine sediment cover, appear farthest to the right of the two-dimensional MDS (Figs. 3 and A.1).

The pre-harvest community structures at most plantation sites were similar to those at the native forest reference site NR1 (i.e.,

![Fig. 1. Mean (+s.e.) values for (a) QMCI, (b) IBI and (c) Bray-Curtis similarities to pre-harvest community structure.](image)

### Table 1

<table>
<thead>
<tr>
<th>Harvest category</th>
<th>Fine sediment (%)</th>
<th>Temperature (°C)</th>
<th>Epilithon biomass (g AFDM m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-harvest</td>
<td>16.8 ± 1.8</td>
<td>18.6 ± 0.5</td>
<td>4.3 ± 0.8</td>
</tr>
<tr>
<td>1–40% upstream harvest</td>
<td>13.6 ± 1.3</td>
<td>18.3 ± 0.3</td>
<td>4.2 ± 0.5</td>
</tr>
<tr>
<td>41–80% upstream harvest</td>
<td>21.3 ± 4.2</td>
<td>18.9 ± 1.1</td>
<td>3.5 ± 1.2</td>
</tr>
<tr>
<td>Post-riparian harvest*</td>
<td>18.7 ± 2.7</td>
<td>19.8 ± 0.5</td>
<td>9.5 ± 2.2</td>
</tr>
</tbody>
</table>

* For each site, only those data recorded within the three years after riparian harvesting were included in the post-riparian harvest category.
regardless of the size of the upstream catchment and channel width, pre-harvest datapoints for most sites were within the range of those for site NR1 along axis 1 of the MDS (Fig. 3). A large proportion of each of the smallest catchments was logged over a relatively short duration (i.e., >80% cumulative harvest occurred within 5 yrs in those catchments <200 ha, Fig. 2). That was generally associated with marked post-harvest changes in biotic indices (Fig. 2d, e, g, and h) and community structure (Fig. 3d, e, g, and h), particularly after harvest of riparian vegetation adjacent to the study reaches. In the smallest streams (<100 ha, sites WH1 and WH2) there was substantial recovery towards pre-harvest biotic indices and community structures 6–8 yrs after riparian harvest, but recovery was less evident in sites draining catchments between 100 and 200 ha. Generally less than 50% of the medium catchments (300 to 500 ha, sites TH3, TH4 and WH5) were harvested, and that harvest intensity was associated with lower post-harvest divergences in biotic indices (Fig. 2i, k, and l) and community structures (Fig. 3i, k, and l) than those that occurred at smaller sites. However, 70% of the catchment was harvested above site WH4 (328 ha), which was associated with a relatively large post-harvest divergence in biotic indices (Fig. 2j) and community structure (Fig. 3j), but also relatively fast recovery towards pre-harvest community structure. Post-harvest divergences from pre-harvest community structures were least evident at: site WH3, where logging debris shaded the channel after harvest (Fig. 3f); site TH3, where only a small portion of the catchment was harvested and the riparian vegetation adjacent to the reach was left intact (Fig. 3i); and those sites draining catchments over 1000 ha (sites WH7 and WH8), where only small portions of the catchments were harvested (Fig. 3n and o).

In addition to harvesting impacts, there were also marked changes in macroinvertebrate community structure at some Whangapoua Forest sites after the storm in 1995, with movement to the upper left of the MDS ordination space for the reference site in 1996 (NR1, Fig. 3a), but to the lower right of the ordination for harvested sites in that year (WH2, WH4 and WH6, Fig. 3e, j, and m).

### 3.4. Small harvested sites (<200 ha)

Prior to harvest the relatively small sites (<200 ha, sites WH1, WH2, WH3, TH1 and TH2) generally had lower proportions of Trichoptera than the larger reference sites, with Ephemeroptera consistently being the most dominant order at these small sites (Fig. 2). After clearing of the entire catchment, including riparian vegetation, at site WH1 (46 ha) there was a large increase in the proportion of Diptera (chironomids) (Fig. 2d). From 1 to 4 yrs after harvest there were high proportions of Mollusca (mainly *Potamopyrgus antipodarum* and *Trichoptera* (*Oxyethira albiceps* and *Pycnocentrodes* sp.), as well as low proportions of Ephemeroptera at that site. The loss of sensitive taxa was reflected in post-harvest declines in QMCI and IBI (pre-harvest: QMCI = 5.8, ‘good’, IBI = 61%, ‘slightly impaired’; post-harvest lows: QMCI = 3.3, ‘poor’, IBI = 33%, ‘moderately impaired’). However, six years after harvest biotic indices had largely recovered back towards those occurring pre-harvest (during the last survey QMCI = 4.7, ‘fair’, IBI = 78%, ‘slightly impaired’). At that site, there were large differences between the pre-harvest community structure and those occurring in the years after harvest (Fig. 3d). However, the community had largely recovered towards pre-harvest structure after six years, albeit still with a relatively high proportion of Diptera (Fig. 2d).

There were large fluctuations in biotic indices and community structure at site WH2 (66 ha) in 1996/7, after harvesting of 78% of the catchment over 1994/5 and a severe storm in early 1995 (Figs. 2e and 3e). In the years after harvesting of riparian vegetation at that site in 1997 there was an increase in the proportions of Diptera (mainly chironomids) and Mollusca (mainly *P. antipodarum* (Fig. 2e). QMCI and IBI values declined from pre-harvest (QMCI = 6.5, ‘excellent’, IBI = 82%, ‘non-impaired’) and were relatively low and stable in the four years after riparian harvesting (mean QMCI = 3.7 ± 0.1, ‘poor’, mean IBI = 35 ± 4%, ‘moderately impaired’). Eight years after riparian harvest, the biotic indices had partially recovered towards those values occurring pre-harvest (QMCI = 4.9, ‘fair’, IBI = 66%, ‘slightly impaired’), associated with recovery of the community towards the structure occurring pre-harvest (Fig. 3e), although a relatively high proportion of Diptera persisted at the site (Fig. 2e).

There was logging debris left over the channel upstream of site WH3 (101 ha), which appeared to partially ameliorate the impacts of harvest on the macroinvertebrate community. Despite a cumulative harvest catchment of 80%, the shading from debris minimised post-harvest temperature increases, and the values for biotic indices (Fig. 2f) and community structure (Fig. 3f) diverged less from pre- to post-harvest at that site than at other similar sized streams. However, there were post-harvest declines in Ephemeroptera, as well as increases in the proportions of Dipterae after upstream harvest, and increases in molluscs (P.

### Table 2

Summary of results for ANCOVAs testing for differences in mean QMCI, % IBI, or community similarity between harvesting categories: prior to harvest; after 1–40% of upstream catchment was harvested; after 41–80% of upstream catchment was harvested; and, after riparian vegetation adjacent to the study reach was harvested, with stream size (indexed as upstream catchment area) as a covariate. Community similarity was calculated as Bray-Curtis similarities of log-transformed multivariate abundance data. Significant values (<0.05) are highlighted in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>QMCI</th>
<th>% IBI</th>
<th>Community similarity</th>
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<tr>
<td>Harvest category</td>
<td>df</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>3</td>
<td>10.531</td>
<td>18.354</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1</td>
<td>0.242</td>
<td>0.422</td>
<td>0.522</td>
</tr>
<tr>
<td>Residual</td>
<td>26</td>
<td>0.574</td>
<td></td>
</tr>
</tbody>
</table>
antipodarum and Latia neritoides) and Trichoptera (particularly Pycnocentrodes sp.) after riparian harvest (Fig. 2f). These changes in the macroinvertebrate community resulted in declines in both QMCI and IBI (pre-harvest: QMCI = 7.3, 'excellent', IBI = 72%, 'slightly impaired'; post-harvest lows: QMCI = 4.0, 'poor', IBI = 32%, 'moderately impaired').

Even with relatively low amounts of upstream catchment harvest there were high proportions of molluscs and Diptera at site TH1 (116 ha, Fig. 2g). There were declines in QMCI and IBI over the three years prior to riparian harvest, but lowest values for these biotic indices occurred after riparian harvest, in association with very high proportions of Diptera. Over the eight years since
harvesting of riparian vegetation the biotic indices (Fig. 2g) and community structure (Fig. 3g) at that site continued to diverge from pre-harvest, with a QMCI of 2.1 ('poor') and IBI of 6% ('severely impaired') during the last survey. After riparian harvest at site TH2 (131 ha) there were declines in biotic indices (pre-harvest: QMCI = 6.2, 'excellent', IBI = 75%, 'slightly impaired'; post-harvest lows: QMCI = 2.3, 'poor', IBI = 26%, 'moderately impaired'), associated with a large increase in the proportion of Diptera (mainly chironomids) and Trichoptera (mainly O. albiceps) (Fig. 2h). There were interannual fluctuations in biotic indices and the overall community structure at that site after harvest, and although there was a general trend of recovery the community had not returned to pre-harvest structure 11 yrs after harvesting of riparian vegetation at that site (Fig. 3h).
3.5 Medium harvested sites (300–500 ha)

At site TH3 (320 ha) less than 30% of the upstream catchment was harvested and riparian buffers of mature redwoods (*Sequoia sempervirens*) were left intact on both sides of the reach (buffer widths of ~20 m and ~50 m on true left and right sides of the stream, respectively). Whilst a post-harvest increase in the proportion of Diptera at a site resulted in declining QMCI and IBI values, these declines were less severe than at sites where there was riparian harvest (Fig. 2i). In most years QMCI has remained above 5 (‘good’ to ‘excellent’) and IBI above 60% (‘slightly impaired’ to ‘non-impaired’) at that site, whilst the post-harvest divergence in community structure was comparatively low (Fig. 3i).

Site WH4 (328 ha) drained a similar sized catchment to site TH3, and those sites had the same high ratings for QMCI (>6, ‘excellent’) and IBI (>80%, ‘non-impaired’) soon after harvesting began (Fig. 3j). However, in contrast to site TH3, a high proportion (70%) of the catchment surrounding site WH4 was harvested and there were large post-harvest impacts on the macroinvertebrate community at that site. Also, in contrast with most other sites, the largest divergence in community structure at site WH4 occurred prior to riparian harvest (in 1996), after 65% of the catchment had been harvested and a severe storm struck the site (Fig. 3j). In subsequent years oligochaetes, Diptera and molluscs (mainly *P. antipodarum*) were the dominant taxa, with post-harvest lows of 1.3% (‘poor’) and 5% (‘severely impaired’) for QMCI and IBI respectively (Fig. 2j). Although the community at that site appeared to have partially recovered towards pre-harvest structure 5 yrs after riparian harvest (Fig. 3j) there were very high proportions of molluscs during the last survey (Fig. 2j).

At site TH4 (412 ha) there was a post-harvest increase in the proportion of Diptera and Trichoptera (mainly Pycnocentrodes sp. and *O. albiceps*), and a decrease in the proportion of Ephemeroptera, particularly after riparian harvest (Fig. 2k). These changes resulted in declines in QMCI, from ‘excellent’ pre-harvest to ‘fair’ post-harvest, and fluctuations in IBI. However, the post-harvest change in community structure at that site was not as large as occurred in most of the smaller harvested sites (Fig. 3k). Site WH5 (495 ha) was impacted by a storm in 1996, and there were fluctuations in community structure even prior to the beginning of harvesting in the catchment in 2004 (Fig. 3l). Similar to site TH4, impacts of harvest on the macroinvertebrate community at site WH5 (37% of catchment harvested, including riparian vegetation) were not as severe as those at smaller sites or those associated with the disturbance from the pre-harvest storm (in terms of changes in QMCI and community structure, although the IBI indicated ‘moderate impairment’ in the two years after riparian harvest, Figs. 2i and 3l).

3.6 Large harvested sites (>500 ha)

Prior to riparian harvest the impact on the macroinvertebrate community at site WH6 (857 ha) was relatively low. Despite 67% of the relatively large catchment area being harvested above that site, the mean QMCI was 5.1 ± 0.3 (‘fair’ to ‘excellent’ in most years) and mean IBI was 75 ± 6% (‘slightly impaired’ to ‘non-impaired’ in most years, Fig. 2m), and the community structure was similar to that in the reference site, albeit with greater interannual fluctuations in the plantation site than in the reference site for several years after the storm affected both of these sites in 1995 (Fig. 3m). However, after harvesting of riparian vegetation at site WH6 in 2003 there was a notable change in the macroinvertebrate community, with consistently high proportions of Diptera (mainly chironomids) and low proportions of Ephemeroptera. These changes caused a decrease in both the QMCI and IBI values at that site, with lowest values during the last survey which was conducted 5 yrs after riparian harvesting (QMCI = 2.8, ‘poor’, IBI = 29%, ‘moderately impaired’).

Only relatively small proportions (<33%) of the large catchments above sites WH7 (1671 ha) and WH8 (2354 ha) were harvested. After riparian harvest at site WH7 there was a decline in QMCI and IBI values, associated with increases in the proportions of Diptera (mainly chironomids) and molluscs (*P. antipodarum*) in the first and second year after harvest, respectively (Fig. 2n). The community at that site appeared to have recovered towards pre-harvest structure in the third year after riparian harvest (Fig. 3n). However, the lowest QMCI (2.8, ‘poor’) and IBI (24, ‘moderately impaired’) occurred seven years after riparian harvest (Fig. 2n), and in association with increased epilithon biomass in the reach. This increased autotrophic growth was possibly due to the stable flows that occurred in the relatively open canopied site for several months prior to the survey. Only 10% of the relatively large catchment above site WH8 was harvested, and the QMCI (4.7 ± 0.2, ‘fair’ in most years), IBI (56 ± 3, ‘slightly impaired’ in most years, Fig. 2o) and community structure (Fig. 3o) were all relatively stable at that site over the six years of surveys. The effects of livestock and runoff from an unsealed public road above the site probably contributed more to the relatively low ratings for the biotic indices than the small amount of logging disturbance.

4. Discussion

The relative magnitudes of post-harvest changes in benthic macroinvertebrate communities in progressively logged catchments were associated with the proportion of the catchment that was harvested and whether riparian vegetation was removed. Relatively large divergences from pre-harvest biotic indices and community structure occurred in small to medium streams (<500 ha) where a large proportion (i.e., >40%) of the catchment was harvested over a relatively short duration. Large post-harvest changes in the communities in smaller streams may be largely attributable to these streams’ dependence on shading and allochthonous inputs from riparian vegetation, as the greatest divergence from pre-harvest community structures usually occurred after harvesting of riparian vegetation. Further, there was some amelioration of harvest impacts on macroinvertebrate communities in streams where riparian vegetation was left intact or harvest debris was left to shade the channel. However, there were still post-harvest increases in the proportions of Diptera in those streams with intact riparian vegetation, possibly due to increased amounts of fine sediment input from exposed land higher in the catchment. The post-harvest changes in macroinvertebrate communities were relatively small in streams where a lower proportion of larger catchments (>500 ha) were logged, but were still most apparent in these streams after removal of riparian vegetation. The communities in the smallest streams (<100 ha) had substantially recovered towards pre-harvest structures within 8 yrs of riparian vegetation being harvested. However, evidence of recovery was slower in larger streams and in some streams the values for biotic indices continued to increasingly diverge from those occurring pre-harvest up to 8 yrs after the harvest of riparian vegetation.

4.1. Magnitudes of harvesting impacts on macroinvertebrate communities

Prior to harvest the reaches surrounded by mature pine plantation forest generally had similar overall community structures to the unharvested native forest reaches, with relatively high proportions of Ephemeroptera and Trichoptera, which is consistent with previous studies in New Zealand (e.g., *Harding and Winterbourn*, 1995; *Friberg et al.*, 1997; *Quinn et al.*, 1997). The physicochemical changes which occurred after forest harvesting during the present study were also typical of those observed in previous studies, with
increases in temperatures, fine sediments and algal biomass (e.g., Graynoth, 1979; Campbell and Doeg, 1989; Death et al., 2003; Boothroyd et al., 2004; Quinn and Wright-Stow, 2008), which are the key drivers of post-harvest changes in macroinvertebrate community structure (Harding et al., 2000; Fahey et al., 2004). Across all reaches harvesting was associated with decreases in the proportions of Ephemeroptera (mainly chironomids) as well as molluscs and worms. The differential subsidy-stress responses (Oдум et al., 1979) to forest harvest disturbance for these Orders are consistent with previous studies conducted in small streams in both New Zealand (e.g., Graynoth, 1979; Death et al., 2003; Ballie et al., 2005; Collier and Smith, 2005), and Australia (Davies and Nelson, 1994; Grows and Davis, 1994). However, certain Ephemeroptera taxa of the U.S.A., such as Baetis, are tolerant of logging disturbance and increases in their densities have been observed in some harvested streams (e.g. Noel et al., 1986; Webster et al., 1992; Brown et al., 1997; Stone and Wallace, 1998). The increased densities of certain disturbance tolerant taxa may have been due to elevated water temperatures, increased fine sediment habitat, and/or increased autotrophic production after removal of shade (Quinn et al., 2004). Grazers, such as molluscs, certain chironomids and the algal-piercing caddisfly O. albiceps benefit most from increased algal biomass (Death et al., 2003), whilst increased fine sediment cover likely favoured chironomids and worms. Conversely, post-harvest increases in fine sediment cover and maximum summer temperatures cause stress for many taxa, particularly for most Ephemeroptera and Trichoptera (Quinn et al., 1994; Harding et al., 2000; Death et al., 2003).

The overall post-harvest trajectories of change in community structures were in the same direction in ordination space regardless of differences in the size of streams. However, the magnitudes of impact and rates of recovery of macroinvertebrate communities varied with differences in the intensity of forest harvesting, including both the proportion of upstream catchment that was harvested and the duration over which harvesting occurred (which were both related to upstream catchment size). Similar to the present study, most previous studies conducted in small streams where high proportions of the catchment, including riparian vegetation, were harvested over a relatively short duration have shown marked post-harvest changes in macroinvertebrate community structures (e.g., Newbold et al., 1980; Grows and Davis, 1991, 1994; Davies and Nelson, 1994; Death et al., 2003; Smith et al., 2009; Thompson et al., 2009). During the present study, harvesting impacts were less evident in larger streams (>500 ha), where lower proportions of the upstream catchments were harvested. The communities in these relatively wide streams (i.e., 6–16 m) were generally less impacted by removal of riparian vegetation than in smaller streams, as they are naturally less dependent on shading and allochthonous inputs from riparian vegetation prior to harvest (Vannote et al., 1980; Davies-Colley and Quinn, 1998). However, the largest divergences from pre-harvest community structures still occurred after harvesting of riparian vegetation in these larger streams. There have been few comparable studies of harvesting impacts on benthic macroinvertebrate communities in streams draining catchments >500 ha. In Oregon, Murphy and Hall (1981) found the largest and most consistent impacts of clearcut harvesting on invertebrate communities in small, high gradient streams, whereas the impacts in large (up to 1790 ha), low gradient streams were variable. In New Zealand, Collier and Smith (2005) found few clear changes in macroinvertebrate community metrics (i.e., total richness, EPT richness, evenness and diversity) related to progressive catchment or onsite harvesting across streams in catchments of a range of sizes (from 24 to 1973 ha) and no consistent post-harvest divergences from pre-harvest community structures, above those occurring prior to harvest, in the three streams with upstream catchments >500 ha. More research is required to determine the thresholds in proportion of upstream catchment harvest beyond which different sized streams are most likely to be impacted, and whether there are consistent declines in the impacts of harvesting on macroinvertebrate communities from headwaters to downstream reaches.

4.2. Rates of community recovery from harvesting impacts

The relative stabilities of communities are determined by both their resistances, and their rates of recovery, after disturbance (Resh et al., 1988). As predicted, the communities in smaller streams were more severely impacted, but also recovered from harvesting more rapidly than those in larger streams. The communities in those sites under 100 ha had substantially recovered towards pre-harvest structures within 8 yrs of riparian harvesting, albeit still with relatively high proportions of Diptera, but over the duration of the study community recovery was less evident in most of the larger sites with obvious signs of post-harvest impact. The values for biotic indices in some of these larger sites continued to increasingly diverge from those occurring prior to harvest. This may partly reflect the shorter duration of harvesting disturbance in small streams. Initial post-harvest changes in macroinvertebrate communities are likely to be directly influenced by the amount of physical disturbance that occurs during harvesting operations (Fahey and Coker, 1992; Collier and Bowman, 2003), with a severe but short pulse (i.e., 1–4 yrs) of this type of disturbance for streams closer to headwaters, compared to more sustained impacts with harvesting over 5 yr in larger catchments. Recovery towards pre-harvest physical structure, amount of allochthonous inputs, shade, temperature regimes and fine sediment cover can begin after the direct disturbance from harvesting operations ceases. The recovery of macroinvertebrate communities is likely to follow, although there may be some lag before populations are able to recolonise previously impacted reaches.

Recovery is also related to stream width, with previous studies showing that recovery of thermal regimes (e.g., Gomi et al., 2006; Gravelle and Link, 2007) and macroinvertebrate communities (e.g., Collier and Bowman, 2003; Haggerty et al., 2004) may occur within 3 yrs in narrow headwater streams, but take considerably longer in wider streams. In Whangapoua forest sites, Quinn and Wright-Stow (2008) found that restoration of thermal regimes to those occurring pre-harvest took ~5–8 yrs after harvesting riparian vegetation in streams with 2–4 m wide channels, which was similar to the time taken for recovery of macroinvertebrate community structure in the smallest streams (<100 ha, channel width 3 m) during the present study. Recovery of thermal regimes was predicted to take 12–16 yrs after riparian harvest in medium sized streams in Whangapoua forest sites (6–12 m wide channels, Quinn and Wright-Stow, 2008), which was beyond the duration of this and most previous studies, but similar to the predicted time for recovery of macroinvertebrate communities in other pine plantations in New Zealand (Death et al., 2003). Longer-term studies are required to confirm that recovery towards pre-harvest community structure is primarily controlled by canopy regrowth in larger streams. There may be ongoing impacts on benthic macroinvertebrate communities decades after logging disturbance in some streams, even after regrowth of overstorey trees, due to the lingering impacts of sedimentation and/or lowered inputs of large wood until later stages of forest succession (e.g., Murphy and Hall, 1981; Bilby and Ward, 1991; Zhang et al., 2009). Thus, it is possible that the communities in some sites may be unable to fully recover within the 25–28 yr regrowth period between harvesting rotations in pine plantations.

High loads of fine sediment may have been the reason for the persistence of relatively high proportions of Diptera in those small streams where community structures had otherwise largely recov-
ered to those occurring pre-harvest. Depending on peak discharge, slope, underlying substrate composition, retentive structures and erosion potential in the surrounding catchment, storms may act to either flush fine sediments downstream and accelerate post-harvest recovery from sedimentation (Death et al., 2003; Davies et al., 2005), or transport large amounts of sediment into streams (Miller et al., 2003; Marden et al., 2006). Movement of sediment into streams is most likely when recent harvesting coincides with large storms, as occurred across sites WH2, WH4 and WH6 in early 1995. In addition to altering reach-scale habitat structure, such high flows also displace animals downstream (Bond and Downes, 2003), and after this storm there were relatively large changes in community structure at those harvested sites, as well as the native reference site. In the reference site the community structure returned towards that occurring prior to the storm relatively quickly, but in harvested sites the communities were not as resilient to the natural disturbances. Recovery of macroinvertebrate communities from natural disturbances are typically more rapid than from anthropogenic disturbances (Yount and Niemi, 1990; Death et al., 2003), but resilience to natural disturbances may be reduced for stream communities already impacted by anthropogenic disturbance (Collier and Quinn, 2003).

Although the QMCI was originally developed to assess impacts of pollution from runoff, point sources and/or organic discharges (Stark, 1985), it has also been shown to be sensitive to a range of other disturbances, including forest harvesting (Harding et al., 2000; Death et al., 2003). Both the QMCI and IBI had similar sensitivities to impacts from forest harvesting during the present study. At most plantation sites pre-harvest values for both biotic indices were relatively high, and similar to values in unharvested reference reaches. Values declined with the post-harvest changes in community structure from relatively impact-sensitive towards tolerant taxa (Stark, 1985; Quinn and Hickey, 1990), and then increased as communities recovered towards pre-harvest structures.

4.3. Management of riparian buffers and logging debris

Across all sites, the largest post-harvest divergences from pre-harvest QMCI and IBI values, and macroinvertebrate community structures occurred after harvesting of riparian vegetation. Previous studies have demonstrated that provision of buffers with intact riparian vegetation can greatly reduce the disturbances associated with forest harvesting, by stabilising stream banks, filtering sediment and nutrients in runoff, maintain a high level of shading, and contributing allochthonous detritus (e.g., Graynoth, 1979; Quinn et al., 2004; Davies and Nelson, 1994; Jackson et al., 2001). Both the longitudinal and lateral extents of buffers are important considerations for maximising ecological benefits. Quinn et al. (2004) found that protection of streams was greater where continuous buffers that extended from the source of permanent flow were provided than where ‘patch’ buffers were left along study reaches but upstream riparian vegetation was harvested. The most commonly recommended lateral riparian buffer width for protection of streams from forestry impacts is 30 m on both banks (e.g., Newbold et al., 1980; Clinnick, 1985; Davies and Nelson, 1994), but effective width varies with factors such as local climate, stream order and catchment slope. In some forestry catchments it may be possible to partially harvest riparian buffers without adversely influencing stream communities (Chizinski et al., 2010). The amount of area allocated to buffers will also be a trade-off between protection of stream ecosystems and use of land for timber production (Quinn et al., 2004). Further, although multiple important functions are provided to streams by setting aside continuous buffers (Quinn et al., 2004), protecting these buffers during harvesting may necessitate additional roading and/or log hauler sites, which are major sources of sediment in runoff (Graynoth, 1979; Fahey and Coker, 1992). Logging debris may perform the shading role of riparian vegetation, and therefore partially ameliorate post-harvest impacts, as observed at site WH3 during the present study and in previous studies in New Zealand (Collier et al., 1997; Thompson et al., 2009), but excess harvesting debris which falls into the water may impede flow and cause marked reductions in dissolved oxygen concentration as it decays (Bailie et al., 2005; Wright-Stow and Quinn, 2009). Ultimately, management of riparian vegetation involves compromises amongst maximising the ecological benefits, whilst also minimising both the loss of area for timber production and the mobilisation of extra sediment from land cleared for forestry infrastructure, and considering hydrological and landscape constraints within each plantation.

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Appendix A.

Fig. A.1. Multidimensional ordination (MDS) of macroinvertebrate community structure for all sites and years (stress = 0.21), based on Bray-Curtis similarities of log-transformed abundance data. The years over which surveys were conducted are shown in parentheses for each site. Stepwise multiple linear regressions between relative position of datapoints along either axis and cumulative percent harvest, epilithon biomass, temperature and percentage of fine sediment on the streambed indicated that: Axis 1 = cumulative harvest + epilithon biomass + temperature + fine sediment (P<0.001), whilst Axis 2 = epilithon biomass (P=0.042). To aid interpretations of relative magnitudes of impact and recovery rates of macroinvertebrate communities over time, in comparison to temporal variability at the native forest reference site (NR1), the datapoints of each site on this MDS are highlighted in Fig. 3.

References


