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Major flood disturbance alters river ecosystem evolution

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Comment [AU1]: Should be revision 2?

Floods, major formative drivers of channel and floodplain structure and associated riparian and instream communities[1,2], are increasing in intensity and magnitude with climate change in many regions of the world [3,4]. However, predicting how floods will affect stream channels and their communities as climate changes~~,~~ is limited by a lack of long-term pre-flood baseline datasets across different organismal groups. Here we show salmon, macroinvertebrate and meiofauna communities, monitored for 30 years in a system evolving due to glacier retreat, were modified significantly by a major rainfall event that caused substantial geomorphic change to the stream channel. Pink salmon, reduced to one tenth of pre-flood spawner densities, recovered within two generations. Macroinvertebrate community structure was significantly different after the flood as some pioneer taxa, which had become locally extinct, recolonized while some later colonizers were eliminated. The trajectory of the macroinvertebrate succession was reset toward the community structure of 15 years earlier. Meiofaunal abundance recovered rapidly and richness increased post flood with some previously unrecorded taxa colonizing. ~~Our findings demonstrate~~ ~~m~~Markedly different responses to ~~a~~ this major flood event according to the organismal group suggest a need for caution when applying general aquatic ecosystem theories and concepts. A better understanding of the response of different groups to floods is thus essential for developing appropriate strategies for river ecosystem management under changing climatic regimes.

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Comment [L2]: Think we need to say something like this to give it the 4* REF global significance up front, rather than sounding like a one-river case study??

Hopefully still in word limit!

The projected increase of high magnitude rainfall events with climate change in many regions of the world[3,4] will ~~increase~~ alter the role of floods in structuring riverine habitat and their communities. However, a full understanding of the effects of floods across a range of organismal groups has been hindered by the lack of long-term pre-disturbance data which would permit insights into the interaction of community dynamics, successional processes and stream channel geomorphology. Changing flow regimes influence channel development[5]~~,~~ and, ~~geomorphological complexity~~ in new channels evolving after deglaciation, geomorphological complexity reaches a maximum in streams 120 to 160 years old[6]. The colonization and subsequent succession of biological communities in such ecosystems is typically considered a directional process[7] driven by biotic (e.g. facilitation, inhibition, dispersal) and/or abiotic (e.g. temperature, moisture, pH) processes[8]. While glacier retreat driven by climate warming is clearly a strong driver of ecological succession[9], predicted changes in precipitation can be expected to introduce more stochastic events into flow regimes, the effects of which will be harder to predict. Some impacts of changing flow regimes on floodplain vegetation succession are understood[10], but effects of floods on instream community succession in evolving stream channels have largely been ignored. In addition, the effects of floods, in the absence of anthropogenic modifications to flow or other stressors, have rarely been studied[1,11].

Biotic responses to flood events are dependent on the resistance (ability to withstand a disturbance) and resilience (ability to recover from disturbance) of organisms. Flood timing is also of major importance in the context of organism life histories. For example, large floods during autumn and winter can cause high mortality of anadromous salmonids by scouring eggs from redds[12]. Among invertebrates, small body size, streamlined shape and substrate attachment may convey resistance, while rapid life cycles and generalist resource use convey resilience[13]. Studies of how different organismal groups respond to flood disturbances are lacking though, despite comparative understanding being essential for the development of balanced river flow and floodplain management strategies under changing climate regimes.

In 1978, a study was initiated at Wolf Point Creek (WPC), a newly formed stream system sourced from a basin with ~70% glacial ice cover (58º59'49.84"N, 136º9'57.05"W) in Glacier Bay, southeast Alaska. Primary succession has been ongoing following subsequent glacial

Comment [L3]: Should we reference the flood pulse concept here?

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retreat, with permanent ice being absent since 2004. We examined this unique record that has continued to the present day to evaluate the degree to which a major rain on snow event and associated flood, which occurred in November 2005, influenced the directional trend of stream ecosystem development and primary successional processes in the evolving channel. Over 400 mm of rain fell over a four day period (Nov 21-24) including over 130 mm on a single day. Intensity of rainfall over 24 h indicated this event was > 1-in-a-100 year occurrence (Supplementary Figure 1); its severity was compounded by storm duration (xx h) and the existence of catchment snow cover. A comparison of river channel cross-sections before and after the flood indicated width decreased from 12.4 to 7.8 m and incised by a maximum of 1.2 m from the active channel surface. Up to 0.7 m depth of sediment was deposited where water flowed originally (Figure 1a and b). Cross section measurements in subsequent years indicate continued channel deepening and no recovery to its previous profile (Supplementary Figure 2).

Comment [L4]: Quantify?

The deepening of the channel and deposition of sediment caused considerable mortality to incubating pink salmon eggs, such that estimates of returning pink salmon (*Oncorhynchus gorbuscha*) spawners in 2007 (i.e. 2-year life cycle) were <500 compared to the >14,000 in late summer 2005 before the flood (Figure 2). However, in 2011 (i.e. within two generations) the number of pink salmon spawners had recovered to pre-flood levels (>14,000; Figure 2). Juvenile coho (*Oncorhynchus kisutch*) salmon densities were also reduced significantly from a mean Catch Per Unit Effort (CPUE) of 9.3 (2003-2005) to 0.6 in 2006 after the flood. Densities remained low in 2007 but recovered to a mean CPUE of 12.4 juvenile coho for the years 2008-2010. These findings illustrate the rapidity with which Pacific salmon populations are able to recover, and demonstrates their resilience to high magnitude flow disturbances in the absence of direct anthropogenic stressors.

Changes in abundance and addition/loss of taxa within the macroinvertebrate community over the 30 year period were evident from a Non Metric Multidimensional Scaling (NMDS) analysis (Figure 3a). Two clear pre-flood successional ~~trajectories~~ groupings were notable: (i) years 1978 to 1994 as richness increased, and; (ii) years 1996 to 2005 due to the loss of early colonizing taxa and the addition of larger bodied forms. A distinct ‘reset’ of the macroinvertebrate successional community was evident in the years immediately after the flood (2006 to 2008) with these years on axis 1 lying between the two pre-flood- groupings. Community composition was significantly different after the flood (ANOSIM, $r^2 = 0.63$; $P < 0.01$) even though overall numbers of taxa were similar.

Comment [L5]: Basically just because in previous sentence we say pre-flood successional trajectories then in this one say pre-flood groupings?

Immediate post-flood changes involved the Chironomidae (non-biting midge) community. *Tanytarsus,* typical of more stable habitats, was markedly reduced. *Paratrichocladius,* the only chironomid present throughout the successional sequence[14], was the most resistant taxon with similar abundance both pre- and post-flood and was dominant in the post-flood community. *Diamesa* spp., typically considered fugitive species and poor competitors[15], became extinct in 1992 but recolonized in 2006 and 2007 following the post-flood reduction in abundance of potential competitors (e.g. *Pagastia partica*) and predators. As macroinvertebrate abundance increased, *Diamesa* were absent from the community in 2008. The occurrence of these fugitive taxa depends upon flow disturbances at the reach scale and this finding illustrates the role of major flood events in enhancing some aspects of stream biodiversity. Although overall taxa richness was not influenced markedly by the flood (Figure 4a), the relatively large bodied Dytiscidae beetles, the freshwater shrimp *Gammarus* and the caddis fly *Ecclisomyia*, which colonized post 1996, were lost from the community and had not recolonized by 2008.

Comment [AU6]: Should be an s here??

Total macroinvertebrate abundance post-flood was reduced by 78-92 % (mean abundance 3990 m^{-2} for 2001 to 2004, to 330 and 898 m^{-2} in the spring and summer of 2006, respectively). Recovery of abundance was not evident by 2008 attaining only 1082 m^{-2} (Figure 4a). Similar reductions in abundance have been reported in other studies following floods but rapid recovery to pre-flood levels abundances have typically occurred[16,17]. Blackflies (Simuliidae) showed the highest reduction in abundance, from 5454 m^{-2} in 2005, to 80 m^{-2} by 2006. By 2008 blackfly densities were still only 123 m^{-2}.

The meiofaunal response differed from the macroinvertebrates, with taxonomic richness showing a reduction during successional development from 1994 to 2004 (Figure 4b) but increasing significantly post-flood when several taxa were collected for the first time. New colonisers included the harpacticoid copepod *Bryocamptus zschokkei* and the chydorid cladocerans *Chydorus* and *Pleuroxus*. Other taxa collected post-flood had been absent from the WPC meiofaunal assemblage for some time (e.g. the harpacticoid *Maraenobiotus brucei* for six years previously). Post flood meiofaunal abundance in summer 2006 and 2007 (5896 m^{-2} and 8780 m^{-2} respectively) was similar to pre-flood (mean 5830 m^{-2} in summer 2003-4 potentially explained by a combination of resistance (utilisation of in-stream refugia) and resilience (rapid reproduction) traits[18,19].

Changes across the entire meiofaunal assemblage were evident from the NMDS analysis (Fig. 3b). The pre-flood successional trajectory along axis 1 was reset with post-flood points (2006-2008) lying towards the centre of the previous trajectory. Unlike the macroinvertebrate community, ANOSIM did not show significant changes in meiofaunal assemblage composition pre- and post- flood consistent with our suggestion that most meiofauna exhibited high resistance and resilience to this major flood event. Nevertheless, the post-flood meiofaunal assemblage included previously unrecorded species. This colonization may result from the removal of fine sediments during the flood. Previous work in Glacier Bay indicated copepod species richness increased as the range of particle sizes within the stream bed decreased, likely due to more open interstitial spaces[18]. Fine glacial sediments are unlikely to accumulate again in the substrate of WPC as their major source, the remnant ice, has now ablated.

This study has provided novel insights into the resistance and resilience of riverine communities to major flood events, demonstrating different responses between taxonomic groups with body size considered a major contributing factor. Larger bodied juvenile salmonids and some macroinvertebrates demonstrated lower resistance but high resilience, whereas smaller bodied meiofauna showed both high resistance and resilience. Foraging habit also appeared a factor in resistance, with blackfly larvae that inhabit the surface of rocks, the most affected macroinvertebrate group despite their relatively small body size/mass. Most groups demonstrated high resilience to disturbance by recovering within three years although the abundance of some common macroinvertebrate taxa remained low. Black flies in particular had not recovered to high pre-flood abundances by 2008, perhaps because of the altered hydraulics (deeper channel, swifter flow, less stable substrate). The persistence of lower macroinvertebrate abundance may have wider implications in terms of food availability for juvenile salmonids and other predators.

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Marked reductions in salmonid populations due to floods have been reported elsewhere[20,21] and most studies report recovery within five years following a pulse disturbance[17]. Timing of the flood relative to the spawning season influences recovery times[17] as does its effect on habitat complexity[22]. Although juvenile coho salmon were markedly reduced, ocean adults from previous year classes spawned to rebuild populations despite lower habitat complexity. ~~With~~ For pink salmon, the timing of the flood ~~clearly~~ would have eliminated a large number of eggs reducing markedly the numbers of returning adults in 2007. However if a small population of pink salmon can survive to return as spawning adults, this study has illustrated that numbers can increase rapidly, providing habitat conditions are suitable and no additional stressors are acting on the ecosystem. This ability appears to be a function of the evolutionary history of Pacific salmon, which allows them to survive in dynamic environments[12]. These findings have significant positive implications for the conservation of threatened Pacific salmon populations ~~and~~ given their ~~relationship~~ ability to recover from~~to~~ catastrophic events[23].

A major ~~flood~~ effect of the flood on the macroinvertebrate community was reduced abundance of potential competitors enabling previously extinct pioneer taxa to recolonize. Clearly this successional reset would have differed had the flood occurred earlier in the stream's development, when the community was principally dominated by pioneer Chironomidae. Interestingly, the major channel changes observed immediately post flood were associated with clear changes to the biota, but the channel has continued to deepen (Supplementary Figure 2). This has not influenced the recovery of the majority of the meiofauna, macroinvertebrates and fish species in this system indicating a large degree of biological independence from geomorphological recovery. However, the continued post-flood absence of a number of macroinvertebrate taxa (e.g. beetles, freshwater shrimp and a caddisfly) can be attributed to the loss of slower flowing habitats, some of which had been created by large-wood accumulations which were removed or repositioned by the flood. These taxa may take a considerable time to recover either because development of this habitat is a long term process and/or dispersal constraints limit colonization potential[24]. Floods can have a major influence in recruiting wood into stream channels[12] but in streams with immature riparian forests, such as WPC, the small size and lack of complexity of ~~coarse~~ large wood ~~y debris~~ accumulations limits its hydrogeomorphic influence[6]. The low abundance and complexity of instream wood and other roughness elements, plus the relatively unconsolidated bed, is likely to account for the post-flood deepening and constriction compared to widening that might be expected in more developed channels[25]. If

Comment [L7]: Is this the message you want to convey?

Negative short term but positive long term recovery?

Comment [L8]: Cant help thinking we should be making more of this – how many studies are out there suggesting strong geomorph-biotic links which seemingly don't apply here?

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Comment [AU9]: Should change this also to 'large-wood accumulations' to answer reviewer 1?

climate change causes the expected increase in the frequency of high magnitude rainfall and associated flood events[4] then this may constrain ecosystem development in evolving stream channels.

Maintaining and increasing the resistance and resilience of freshwater organisms and protection of riverine ecosystem ~~functions~~ functioning in the face of projected climate change is a key global challenge. This study of how an anthropogenically unimpaired system has recovered from a major flood provides some key insights for river managers. The implementation of mitigation strategies such as maintaining habitat heterogeneity, preserving remnant population refuges and proximal colonizing sources, and the removal of migratory obstructions (e.g. for salmonids) can maximise the resilience of aquatic biota to changing flow regimes associated with climate change.

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Methods

The mouth of WPC was uncovered by ice retreat in the mid-1940s and the stream, fed from Lake Lawrence, is now approximately 2 km in length and flows over glacial moraine, till, and outwash deposits. Dolly Varden (*Salvelinus malma*) were the first fish to colonize in 1987, followed by pink and coho salmon in 1989. The continued decrease in glacial ice cover after this time is associated with significant increases in stream temperature and decreases in turbidity. By 1997 (<10% glacierization), alder and willow were dominant with riparian plants exceeding 3 m in height and pink salmon numbering >12,000 individuals[24]. In 2004, glacial ice had almost completely disappeared and the upper terraces supported increasing numbers of cottonwood trees (*Populus trichocarpa*) along with the occasional Sitka spruce (*Picea sitchensis*).

From 1978, macroinvertebrates (animals > 1 mm) were collected in August or early September from a representative sampling station located 0.75 km from the stream mouth using a Surber net (ten replicates; 330-µm mesh) with the exception of 1979-1985, 1987, 1995 and 2003. From 1994 meiofauna (animals > 63 µm < 100 µm) were collected in summer (June – August) with the exception of 1995 and 1999 (collected mid-May) and 2005 (no sample). Samples were collected from the same sampling station with a Surber net (five replicates; 63-µm mesh). Invertebrates were preserved in 70% ethanol and later separated in the laboratory from detritus and inorganic matter. Macroinvertebrates were identified using Merritt and Cummins[26] and Chironomidae larvae were identified using methods outlined in Milner et al.[27]. Meiofauna were identified using Thorp and Covich[28] and Smith[29]. Adult pink salmon spawners were estimated using the average of counts by two observers walking the length of the stream, and juvenile coho salmon densities with minnow traps baited with salmon eggs and fished for 2h[27].

All statistical tests were undertaken using Minitab v15. Non Metric Multidimensional Scaling was undertaken using PRIMER v6. Each year was included in an ordination using Non Metric Multidimensional Scaling (NMDS). Analyses were run with arcsin transformed macroinvertebrate and meiofauna log10 (abundance+1) data. Both analyses were conducted using Bray-Curtis dissimilarity matrices and 2000 restarts. One-way analysis of similarity (ANOSIM) tested the null hypothesis that differences in stream meiofauna and macroinvertebrate community composition between year groups before and after the flood (i.e. 1999-2004 v 2006-2008 for meiofauna, and 1996-2005 v 2006-2008 for macroinvertebrates) were not different to those within year groups. ANOSIM was undertaken on $\log_{10}(x+1)$ transformed taxon abundance (mean) per year because temporal dynamics were the key focus of this analysis. Analyses were run using Bray–Curtis (BC) dissimilarity scores, with 10 000 permutations and Bonferroni corrections using ~~past~~ Past 2.05[30].

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Author Contributions

AMM initiated the study of WPC and collected many of the pre-flood samples. AMM, ALR, and LEB were responsible for the funding application to study the post flood ecosystem, research design and planning, data collection and analysis, and writing the manuscript. MM~~.~~ assisted with the field work and analysed the post-flood samples in the laboratory. MJK undertook fieldwork, analysed the channel profile data and assisted with writing the manuscript.

Additional Information

The authors declare no competing financial interests.

Figure legends

Figure 1 (a) ~~Photographs of t~~The pre-flood channel ~~before~~ (August 2004) changed markedly ~~and~~ after (May 2006) the ~~November~~ flood in November 2005. Although ~~at~~ discharge~~s~~ ~~are~~ is normally higher in May the dramatic reduction in channel width is illustrated and supported by, (b) ~~Cross~~ cross sections of the ~~representative~~ ~~sample~~ sampling reach in Wolf Point Creek before and after the flood. Broken line~~s~~ illustrates ~~comparative~~ water level~~s~~.

Figure 2 Adult pink salmon spawner estimates in Wolf Point Creek from 1978 to 2011 showed a marked post-flood reduction but a rapid recovery.

Figure 3 NMDS plots for (a) macroinvertebrates from 1978 to 2008 using mean numbers from 10 replicates collected in August/early September, and (b) meiofauna from 1994 to 2008 using mean numbers from five replicates collected in summer (or occasionally mid-May). The post-flood years are highlighted ~~with~~in ~~the~~ boxes and the arrows ~~indicate~~ highlight marked shifts in community structure between groups of years.

Figure 4 ~~Taxa~~ Taxon richness and ~~log~~ total abundance for (a) macroinvertebrates from 1978 to 2008 using mean numbers from 10 replicates collected in August/early September, (b) meiofauna from 1994 to 2008 using mean numbers from five replicates collected in summer (or occasionally mid-May).

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Comment [AU11]: There is only one broken line so it can't be comparative?

Comment [L12]: Water level is dynamic so pretty meaningless to include it?

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Comment [AU13]: Reviewer 3 suggests 'The arrow from pre-flood to post-flood could be differentiated somehow (colour) from the other arrow.' I think we should leave as it is – multiple colours etc would make this already busy fig more confusing.

Comment [L14]: Agree leave arrow as is

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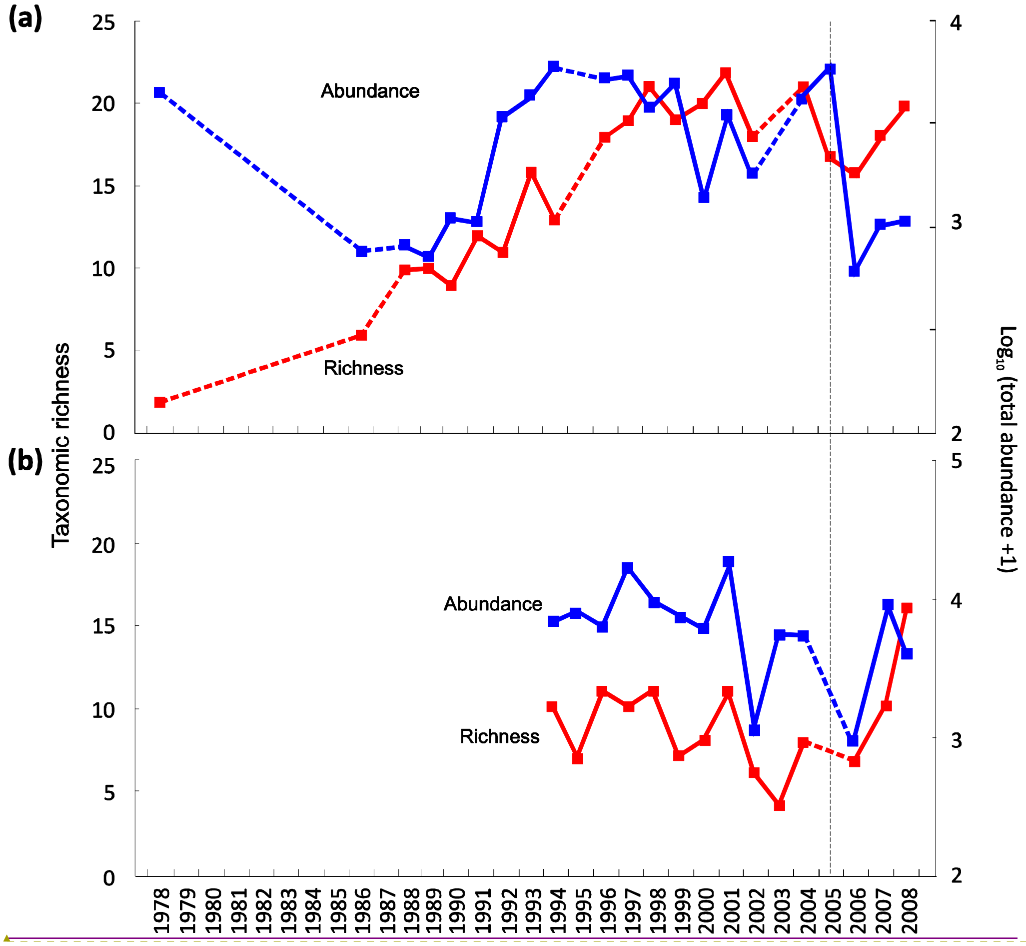
Comment [AU15]: I guess we could add extra tick marks but it is v. Minor point

Comment [L16]: c

Comment [L17]: changed below – but strange that the reviewer would contemplate scanning data from a figure: this is playing with fire! Figures are always just artisitic representations of the data – a few pixels here and there is not perceptible by eye but would introduce errors into a dataset.



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