

DYNAMIC PROCESSES IN NEW ZEALAND LAND-WATER ECOTONES*

Summary: This paper reviews current knowledge of dynamic processes in New Zealand land-water ecotones drawing on published quantitative data wherever possible. Basic ecosystem processes in forested and natural unforested land-water ecotones are compared, and dynamic processes are discussed under the following headings: time scales of change; water movement; sediment trapping and transport; dissolved nutrient dynamics; dissolved oxygen; trophic interactions. Environmental "resetting" agents such as floods, fires and storms have been shown to be important regulators of change at the land-water interface. However, an element of stability is imparted by continuous allochthonous inputs from evergreen vegetation into the water at the interface, as well as an important contribution from terrestrial insects. Stable isotope studies have shown that such inputs are translated as a carbon source through aquatic food chains in some New Zealand streams. Dynamics of sediment movement and nutrients are governed by the complex patterns of water movement along the ecotone. Patterns of water movement at this interface are controlled by obstructions to flow providing eddies and "dead zones". Manning's coefficient of drag is a convenient measure of the degree of obstruction by aquatic vegetation, fallen branches etc. Nutrient dynamics along the land-water interface of lakes and streams are affected not only in moving surface water, but also in groundwater. New Zealand studies have, in recent years, concentrated on nitrogen pathways in ground waters at the interface where denitrification is shown to be an important N sink. This is controlled largely by dissolved oxygen and prevailing redox conditions. Implications for management of New Zealand land-water ecotones where ecosystem dynamics are governed by periodic physical disruptions such as floods, fires or dry-wet cycles are discussed.

Keywords: Aquatic vegetation; benthic invertebrates; fish; avifauna; cyclic change; succession; trophic interactions; water movement; sediment movement; groundwater; nitrogen; phosphorus; oxygen; redox.

Introduction

The land-water interface is an area that shares ecological properties of both terrestrial and aquatic (flowing and standing water) systems, but ecosystem processes within this ecotone are in many ways unique.

In non-forested areas, the natural land-water ecotone is usually occupied by wetland vegetation (Johnson and Brooke, 1989) but in forested areas, deep shade frequently prevents stream bank or wetland vegetation from developing along stream margins (Fig. 1). Superficially, the non-forested land-water ecotone appears to be very different from that along small forested streams. However, a closer look at the basic ecosystem processes at these two types of land-water ecotone reveals enough similarities for them to be treated together. In both cases light reaching the water is trapped by an autotrophic canopy in the air to the extent that in the water phase, ecosystem processes are dominated by

heterotrophs. Litter is deposited into the water, and plants (or plant remains in the form of fallen branches) obstruct or divert water flow and impart a complex physical structure to the system. In both types of ecotone saturated soils extend back for varying distances from the open water, and nitrogen, phosphorus and oxygen dynamics in the root zone and the groundwater flows of the ecotone are governed by the extent of this saturation (Fig. 1). The land-water ecotone is often characterised by sharp environmental gradients relative to adjacent ecosystems, and high biological diversity frequently occurs at this interface with marked species zonation associated with these gradients.

New Zealand's mountainous terrain and relatively high rainfall is reflected by a large network of generally short shallow swift rivers (Duncan, 1987). Considering its small size the country has a high number and wide variety of lake types (Viner, 1987). This abundance and complex network of waterways means that ecotones at the land-water interface cover extensive areas of the country. However, large scale modifications to New Zealand's landscape and waterways that have occurred in the

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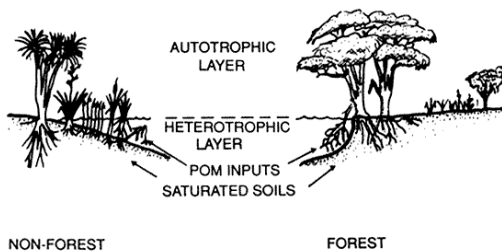


Figure 1: Diagrammatic representation of non-forested and forested land-water ecotones. POM = Particulate Organic Matter.

last century (McColl and Ward, 1987) mean that these ecotones themselves are continually changing. As an example, McColl and Ward (1987) point out that examples of indigenous lowland riparian vegetation are almost impossible to find because this native lowland river landscape is now characterised by willows.

This paper reviews current knowledge of dynamic processes in New Zealand land-water ecotones drawing on published quantitative data whenever possible. Rather than adopting a hierarchical or an energy flow approach to reviewing these ecosystems the information is arranged into subheadings which emphasise dynamics. The sub-headings are: time scales of change, water movement, sediment trapping and transport, dissolved nutrients, dissolved oxygen, and trophic interactions. These topics are then integrated in a final discussion where an attempt is made to relate these to management of land-water interface areas.

Time scales of change

The growth of aquatic vegetation is very responsive to small changes in water level and the quantitative wetland ecological studies of Walker and Coupland (1968) showed clearly the logarithmic nature of the response to water level at the land-water interface where a given change in level has a very much greater effect on vegetation in shallow water than the same change in deep water. Exposure to air, aeration, increased temperature variability, sensitivity to wave action and related factors are more likely to occur in shallow water than in deep water and the community dynamics of the vegetation on the land-water interface are affected by these.

For instance, a very interesting dynamic process in a shallow lake littoral zone is shown for Lake Rotoiti by Chapman, Coffey and Brown (1971) where a constantly changing siltation and erosion process causes shifting vegetation mounds in the shallow

water on the lake edge. Part of this process is illustrated in Fig. 2. The process of vegetated mound buildup has a time scale of 12-18 months, while the time scale of erosion is very dependent on water depth and the frequency of storm events and wave energy on the shallow lake littoral. The cycle shown in Fig. 2 may have a time scale of up to 3 years with severe wave action acting as a "resetting" agent to complete the cycle. .

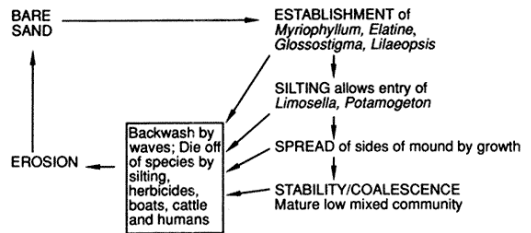


Figure 2: "Pattern and process" vegetation dynamics in a wave-washed lake littoral zone. Time scale of the complete cycle is ca. 3 years. (Redrawn from Chapman et al. 1971).

A different and perhaps more frequently observed pattern of cyclical change in vegetation of the land-water interface is shown in Fig. 3 which describes the seasonality of events at a North Island stream near Taupo (Howard-Williams, Davies and Pickmere, 1982). Plant growth (in this case, watercress) on the streambank is triggered in spring by changes in day length. The plants grow out over the water causing hydraulic drag and physical blockage of the stream channel. The water level consequently rises and floods new areas providing new aquatic habitat along the land-water interface, for further growth (Fig. 3). Towards winter, frosts kill off the vegetation with a resulting collapse of the community. The shrinking of the land-water interface zone follows rapidly once the central stream channel is opened up. In this case the "resetting agent" is winter frost conditions.

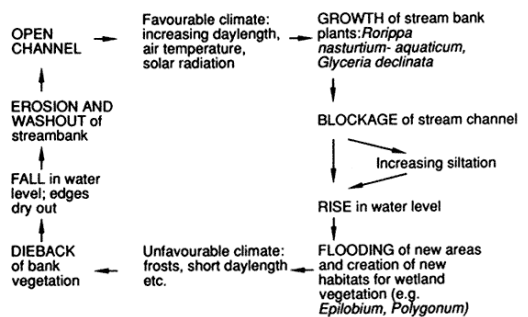


Figure 3: Annual cyclic process of growth and dieback of streambank vegetation in the Whangamata stream, Lake Taupo. (Adapted from data in Howard-Williams et al., 1982).

At a very different time scale, the dynamics of primary succession from pakihi bog to mixed beech-podocarp have been studied in south Westland by Mark and Smith (1975). The deeper parts of the bog indicate an age of ca. $10^3 - 10^4$ years with an extremely slow progression from bog to woodland. This slow progression was thought to be caused by the unfavourable soil conditions of the pakihi particularly the low pH of 4.1. However, growth rates of young manuka in the relatively narrow ecotone (Fig. 4) were found to be quite rapid in spite of the low pH. The dynamics of succession at this site are thought to be controlled by occasional fires which periodically destroy the woody vegetation on the edge of the bog. Fires in this case, and large floods in other areas, which destroy marginal vegetation act as "resetting" agents in long term succession.

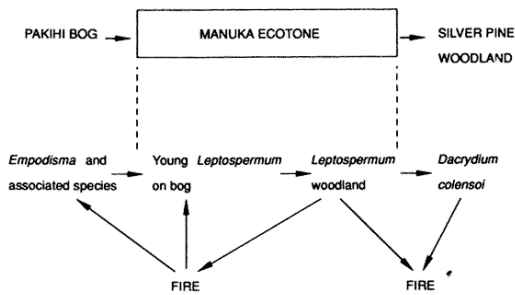


Figure 4: Long term (decades) vegetation changes at the land-water interface of a pakahi bog, Westland. (Adapted from data in Mark and Smith, 1975).

Water movement

All processes at the land-water ecotone are governed by water movement. This may be as ground water or surface flow and may be parallel to the land or perpendicular to it. However, the single most important feature at the ecotone is that water movement is slowed down. This reduction in movement can take place on a catchment-wide basis or at a small scale at specific sites on the edge of a river. Objects in the path of flow such as aquatic vegetation, fallen tree branches or roots obstruct the flow imparting a drag which can be measured. This is usually expressed as Manning's coefficient 'n' which is a measure of "roughness" in the path of the flow (Ogrosky and Mockus, 1964). Drag increases rapidly with increasing vegetation height and cover but is also a function of discharge (Fig. 5). As the water is obstructed by increasing instream plant biomass, the water level rises and velocity decreases as shown for the Whangamata stream at Taupo (Fig. 6).

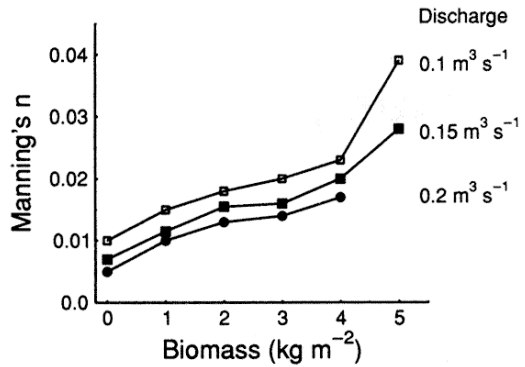


Figure 5: Roughness coefficient (Manning's n) as a function of instream plant biomass at different discharges. (Adapted from data in Watson, 1987).

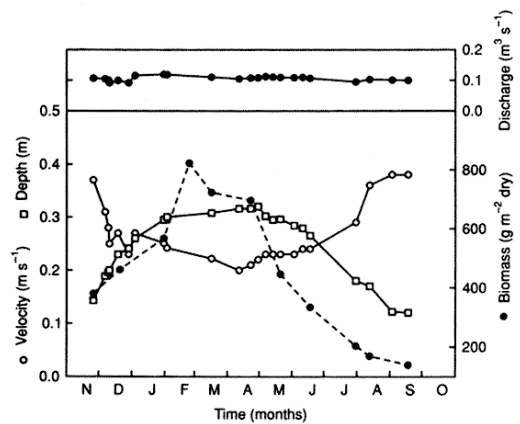


Figure 6: Seasonal changes in stream vegetation biomass (solid circles and dotted line), stream velocity (open circles) and channel depth (squares) at baseflow discharge in the Whangamata stream, Lake Taupo. Baseflow discharge is shown in the upper panel, indicating the constant year round baseflow in this spring fed stream. (Adapted from data in Howard-Williams et al., 1982).

Retardation of water flow along stream banks or lake shores (Fig. 7a) prevents shoreline erosion. Indeed, design criteria are available for minimising channel edge erosion by planting vegetation at varying densities and heights depending on channel shape and other hydraulic characteristics (Ogrosky and Mockus, 1964; Watson, 1987).

A further effect of vegetation (alive, or dead in the case of woody debris) at the land-water ecotone is to create system "structure" and habitat diversity with a complex range of velocities and eddies along the interface.

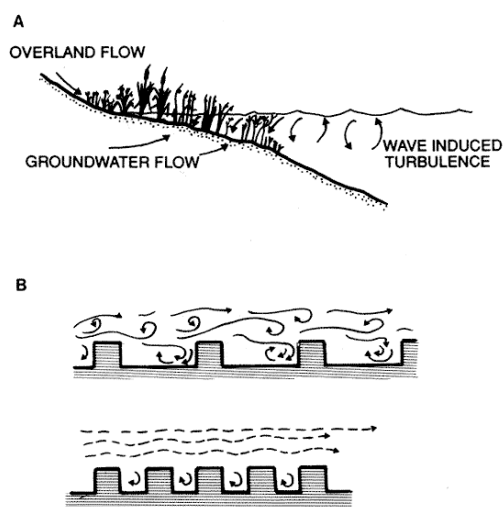


Figure 7: A) Wetland vegetation intercepts overland and groundwater flow, and dampens wave energy and water movement. B) Water flow patterns associated with two scales of stream edge or bottom roughness. (Redrawn from Chow, 1959).

The actual path length a parcel of water travels, when moving downslope from land to lake or downstream in a river, will be greatly enhanced by physical barriers set up by aquatic vegetation or debris from woody riparian vegetation. Thus in a water flow context the land-water ecotone includes a large "dead zone" component (Fig. 7b). Dead zones¹ are regions of stagnant water that occur along the line of flow such as backwaters or holes in the stream bed (Valentine, 1982). These dead zones or "roughness elements" have the effect of increasing dispersion (and hence path length) and will therefore reduce mean water velocity further (Davis and Barmuta, 1989). By influencing water movement, vegetation and woody debris on the land-water ecotone have a number of secondary effects including:

- enhanced sedimentation and trapping of suspended particulate organic material;
- enhanced trapping of dissolved nutrients as complex relationships exist between flow and solute uptake by organisms;
- an increase in habitats for aquatic organisms, and others (e.g., birds) that depend on aquatic vegetation for feeding, cover, nesting, roosting etc.

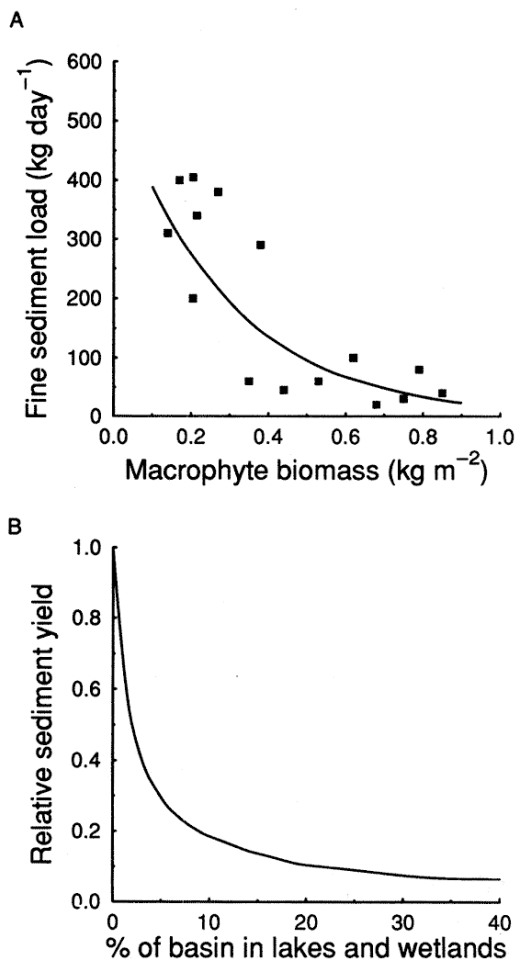


Figure 8: A) Suspended sediment load in the Whangamata stream at base flow discharge as a function of macrophyte biomass (after Howard-Williams, 1983). B) Sediment yield (relative scale) as a function of the proportion of a catchment occupied by lakes and wetlands (after Novitski, 1978).

Sediment trapping and transport

As water velocities are decreased by aquatic vegetation, either on the edges or beds of streams, rivers or lakes (Figs. 6, 7), suspended particles are sedimented out. An example is shown for the Whangamata Stream, Taupo (Fig. 8a). Here, as the

stream bank macrophyte biomass increased, the output of suspended sediment from the stream decreased. The data were best fitted by a logarithmic transformation of fine sediment load indicating that for a given flow, changes in the aquatic vegetation of the stream bank at low biomass levels have a proportionately greater effect on stream sediment transport than do equivalent changes at high biomass.

On a catchment wide scale, a clear log relationship exists (Fig. 8b), so that small increases in the number of wetlands where few exist have a major effect on catchment sediment yield (Novitski, 1978).

McColl (1979) found that phosphorus runoff to a stream where the land-water interface had been grazed to the water edge, was considerably less than that of an adjacent stream which had marsh and scrub vegetation along the banks. He suggested that when widespread runoff occurs the vegetation of the stream channel acts as a reservoir area, ponding the runoff. This allowed particulate matter to settle and for more intimate contact of the dissolved components with the vegetation to enhance removal of those fractions. In Scotsman Valley, near Hamilton a comparison was made between sediment loads entering the stream from protected (with riparian vegetation) and unprotected (grazed) areas. Stream protection by retirement from grazing substantially reduced the sediment loads on the stream (Smith, 1989; Smith, Williamson and Cooper, 1989). These reductions were attributed to sediment deposition within the riparian pasture strip because of both declining runoff velocities and physical trapping by the riparian vegetation.

Dissolved nutrient dynamics

Vegetation at the land-water interface intercepts nutrients running from land to water in either surface runoff or in groundwater where this percolates through the root zone. Vegetation at the land-water interface also affects nutrients travelling downstream or along lake margins.

The dynamics of nutrient cycling at the land-water interface have received considerable attention in New Zealand (e.g., see review by Rutherford, Williamson and Cooper, 1987, and Cooper, 1990). Nitrogen cycling in particular has been well documented, as this element has been identified as being of low availability in New Zealand fresh waters (White, 1983). Howard-Williams, Pickmere and Davies (1986) and Cooke (1980) pointed out that as nitrate leaches readily through soils and moves with groundwater, standard soil conservation and farm management practices geared to controlling surface runoff were often not applicable to the control of nitrate. In such cases this form of nitrogen may only

be controlled where groundwaters emerge as seeps and springs and headwater streams; in other words, along the land-water interface.

Reasons for enhanced nutrient cycling at the land-water interface are complex, but New Zealand studies have shown that the aquatic vegetation and organic matter in this zone perform a number of functions which influence the dynamics of nutrient cycling. These are:

- (a) Decrease direct channelisation of water, and therefore throughflow, and increase path lengths for a parcel of water. This results in greater contact with biological material for a given downstream distance.
- (b) Provision of a high nutrient demand to support macrophyte growth and biomass assisting in removal of dissolved nutrients from the water.
- (c) Provision of oxygen to sediments by radial oxygen loss from roots. This enhances the processes of decomposition, nitrification, and phosphorus precipitation.
- (d) Provision of a substrate for mycorrhizae which may enhance nutrient uptake.
- (e) Provision of organic matter for decomposition which enhances nutrient release and provides a mosaic of low oxygen environments for denitrifying bacteria and methane producers.

Recent work by Cooper (1990) and Schipper *et al.* (1989) has shown the importance of wet soils in the riparian zone of New Zealand streams as a sink for nitrogen. Denitrification rates in these soils can be high, with maximal rates in the upper part of the riparian zone at some distance (2-20 m) from the stream channel. Studies on the dynamics of nitrate reduction by denitrifying bacteria indicate that rate limitation is due to nitrate concentrations in the groundwater and the availability of organic substrates. Schipper, Cooper and Dyck (*in press*) report a decrease in denitrification rates across a riparian zone (Fig. 9) where water soluble carbon remained constant. They inferred that this decrease was due to a measure~ decrease in nitrate concentration (Fig. 9). Howard-Williams and Downes (1984) showed the effects of varied $\text{NO}_3\text{-N}$ concentrations on natural riparian zone denitrifiers from a Taupo stream. During the first two hours the rates of denitrification were not limited by nitrate concentration anywhere within the range 800-6400 mg m^{-3} of $\text{NO}_3\text{-N}$. It was only after longer time intervals that nitrate at the lower concentration treatments became depleted, causing a reduction in denitrification rates (Fig. 10). However, in most natural land-water interface areas continuous nitrate resupply occurs as the water moves through the system. In such cases availability of reducing sites and organic carbon rather than nitrate are likely to be the prime limiting factors. This is supported by the work of Cooper (1990) who found

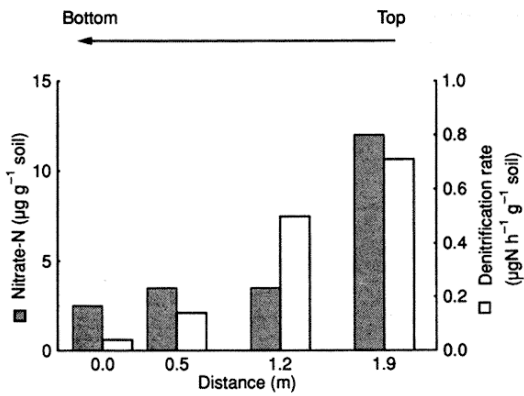


Figure 9: Nitrate concentration and denitrification rates in soil cores in a transect from the top to the bottom (stream edge) of an organic riparian zone (Tairua Forest). (Modified from Schipper et al., in press).

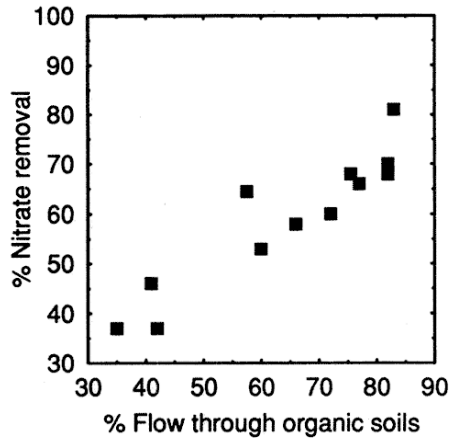


Figure 11: Nitrate removal (denitrification) as a function of the proportion of groundwater flow through organic rich soils. (After Schipper et al., in press).

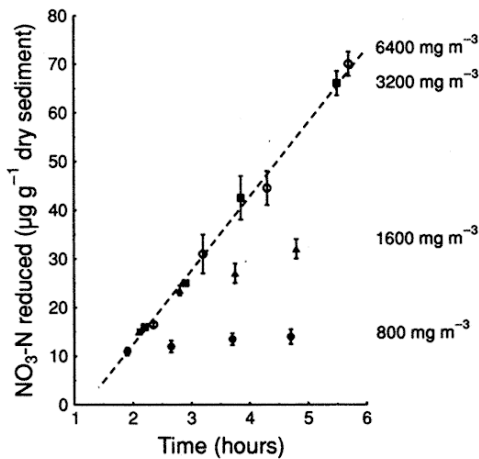


Figure 10: Time course of nitrate reduction in stream bank soils from the Whangamata stream at 4 concentrations of added nitrate; 800, 1600, 3200, 6400 mg m⁻³. Dotted line = rate with no nitrate limitation; vertical bars = Standard Error; n=4. (From Howard-Williams and Downes, 1984).

that the amount of nitrate removed in a riparian zone soil near Cambridge was dependent on the proportion of the flow which passed through soils which were organically enriched (Fig. 11).

Riparian vegetation can provide a sink for dissolved nitrogen that has reached a stream channel, and several New Zealand studies have been conducted which compare bacterial denitrification rates with macrophyte uptake rates (Howard-Williams and

Downes, 1984; Cooper and Cooke, 1984; Cooke and Cooper, 1988). In these studies uptake by stream bank aquatic plants (*Rorippa nasturtium-aquaticum* L. (Hayek) and *Glyceria* (R.Br.) spp.) accounted for 80-90% of the observed nitrogen removal from the stream.

Likewise, Vincent and Downes (1980) showed that of the 70-80 mg m⁻³ of dissolved reactive phosphorus that entered the Whangamata stream, 95% was removed by summer growths of streambank vegetation. The sink was only temporary and phosphorus from this compartment was washed out as particulate-P following vegetation die-off or in floods (Howard-Williams and Pickmere, unpublished data). Cooke's (1988) work at Scotsman Valley in the Waikato showed that the seepage areas of the riparian zone along the stream edges were an important trap for phosphorus from pasture runoff. In all except extreme storm events, the stream system acted as a net sink for phosphorus.

Dissolved oxygen

The element of biological importance that shows the highest variability in the land-water interface zone is dissolved oxygen (DO). Dissolved oxygen concentrations affect inorganic chemical reactions (e.g., P-Fe reactions which affect phosphorus solubility) and almost every bacteria-mediated process in the nitrogen cycle. The activity of invertebrates and many vertebrates at the land-water interface is also affected by changes in dissolved oxygen. These can

occur on broad or microscale spatial patterns, and on short (hours) to long (seasonal) time periods. Stream water, or littoral lake water is usually oxygenated, as is surface runoff water and some groundwater. In the interface zone, however, conditions for deoxygenation are common. These include slower water movement and respiration in excess of production in the heterotrophic (see Fig. 1) environment there.

Wetland plants lose oxygen from roots by a process known as radial oxygen loss (ROL) so that a high redox potential can exist at the immediate vicinity of the root (Etherington, 1983). A few millimetres away in a reducing sediment the oxygen can be depleted by bacterial activity so that micro-scale patches of oxidised and reduced sediment coexist where, for instance, populations of nitrifying bacteria producing nitrate can occur close to denitrifiers which reduce it.

Clumps of roots or clumps of decaying matter can result in larger (i.e., scales of cm) mosaic effects of oxygenation or deoxygenation (Fig. 12); and stagnant backwaters or swamps with little throughflow can have large areas of deoxygenated conditions. Floods and widespread surface runoff can result in increased oxygenation of the interface zone (Howard-Williams and Lenton, 1975).

There is therefore a large temporal and spatial range in dissolved oxygen conditions, which allows for a varied and complex set of bacterial mineral cycling reactions.

Where water flows are turbulent and oxygenated, the invertebrate fauna is characterised by a wide range of insect species adapted to processing detritus as well as browsing on organic layers on stones, with

little evidence of food partitioning (Winterbourn, Rounick and Cowie, 1981). However, where marginal vegetation causes reduced flows, and fine sediment is trapped, the fauna changes from insect-dominated to one where oligochaetes and gastropods form the major component of invertebrate biomass (Marshall and Winterbourn, 1979).

Where fluctuating water levels at the land-water interface occur those species which can move rapidly and colonise rapidly have an advantage. One of the few studies to consider this was the work of Town (1981) on the Whangamarino Swamp. Here, the black mudfish (*Neochanna diversus* Stokell) was deemed to be the only obligate swamp dweller as it has an ability to tolerate both low dissolved oxygen concentrations and seasonally dry conditions. Other native fish with an ability to "breathe" air such as eels can also tolerate low oxygen conditions in waters and can make use of temporary flooding to move inland to feed (Chisnall, 1987; Jelliman, 1989). Of the invertebrates, backswimmers (*Anisops* Spinola) and waterboatmen (*Sigara* Fabricius), as well as several beetles can migrate by flying and make use of temporary pools at the land-water interface. Oxygen tolerance ranges of New Zealand invertebrates are not well studied (D.J. Forsyth, *pers. comm.*).

Trophic interactions

Fringes of marginal vegetation were found to greatly extend the amount of habitat available for insects, molluscs, crustaceans and fish in Canterbury streams (Carpenter, 1982). Winterbourn (1987) pointed out that in rivers like the Waikato and the upper Clutha,

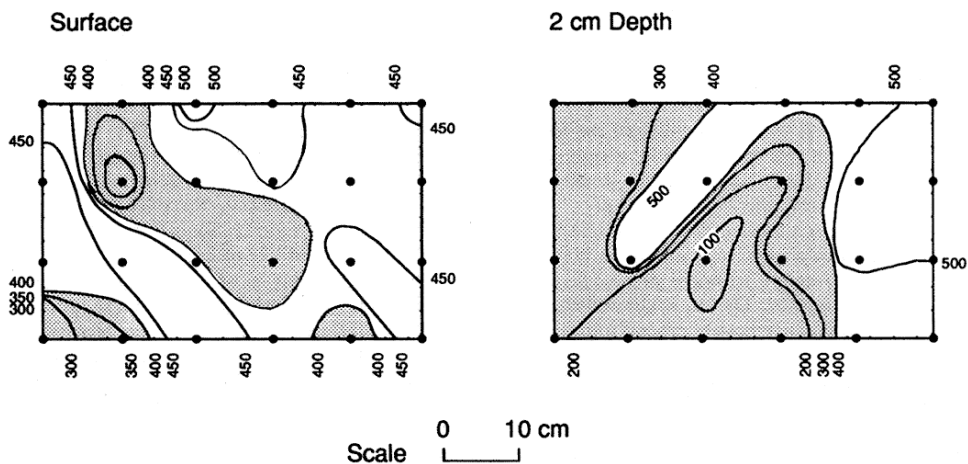


Figure 12: Mosaic of redox potentials (mV) at grid points in the Whangamata stream bank soil at two depths, surface and 2cm. Shaded areas show potential denitrification zones. Isolines are hand drawn.

productive vegetated backwaters may constitute significant sources of animals that colonise the mainstream. Thus in terms of open water population dynamics, marginal vegetation can provide a continuous population inoculum. It is of interest that the benthos from New Zealand streams shows a remarkably low seasonal variation in species composition (Towns, 1985), and a lack of synchrony in life history patterns. Winterbourn (1987) discusses some reasons for this, one of which is the year-round availability of food in the form of fine particulate organic matter originating from the native evergreen trees of the land-water ecotone. A further contributing factor is the unpredictability of the physical environment of New Zealand streams (Winterbourn *et al.*, 1981).

Trophic studies on the caddis *Zelandopsyche ingens* Tillyard in Canterbury have shown that it, and several other large particle detritivores, are absent from highly unstable streams with little wood debris, but occur continuously in nearby similarly unstable streams where wood debris accumulates (Rounick and Winterbourn, 1983). Wood debris, predominantly from trees at the stream margin, helps retain leaf litter which is a food source and provides a habitat by forming so called "debris" dams. The wood itself also provides an additional habitat for invertebrates, particularly the tipulid *Limonia nigrescens* (Hutton) and the chironomid *Harrissius pallidus* (Freeman) which burrow into rotting logs.

Further examples of trophic dynamic interactions of the land water interface are given by the work of Rounick, Winterbourn and Lyon (1982) on carbon dynamics in Middle Bush stream. These authors used the ratio of the stable isotope ^{13}C to that of ^{12}C in potential aquatic foods in streams, and in the stream invertebrates to trace the food sources. Terrestrial plant material is enriched with ^{13}C relative to aquatic autotrophs (Rau, 1980) because HCO_3^- carbon source in water is depleted in ^{13}C . As the ratio of $^{13}\text{C}/^{12}\text{C}$ in animals is only slightly enriched relative to the food source, an analysis of this ratio provides a summary of the food that is actually used in tissue growth. These authors compared the food sources of invertebrates living in a shaded stream (Middle Bush stream) flowing through stands of mountain beech with an unshaded stream (Grasmere stream) flowing through tussock grassland. The study showed that most of the non-predatory aquatic insects appeared to be dependent on carbon of terrestrial origin for food and tissue development, and that this was reflected further up in the food chain. In contrast, a high depletion in ^{13}C is shown for the organisms of Grasmere stream (Table 1) where the food chain is dependent on in-stream aquatic autotrophs. Depletion was much less in the food chain of Middle Bush stream with its predominantly terrestrial inputs (Table

Table 1: ^{13}C values of potential invertebrate foods and of invertebrates from Middle Bush stream (forested with dense riparian cover) and Grasmere stream (open with little riparian cover). Aquatic plants are sparse in Middle Bush and abundant in Grasmere streams. The less negative the ^{13}C value the more enriched the sample is with the isotope and the more likely it is to have a terrestrial origin. Data condensed from Rounick *et al.* (1982).

	Middle Bush	Grasmere
Potential food		
Beech leaves in stream	-27.3	
Beech wood in stream	-25.0	
Fine particulate organic matter	-27.2	-29.1
Stone organic layer	-26.0	-33.2
Aquatic primary producers	-29.8	-31.0
Invertebrates		
Oligochaetes	-24.7	-29.3
Gastropods		-34.5
Ephemeroptera	-29.5	-34.4
Plecoptera	-25.2	-31.1
Trichoptera	-25.7	
Diptera	-23.9	-29.2
Coleoptera	-25.9	-31.5

1) and illustrated a strong dependence on terrestrial food (i.e., the vegetation of the land-water interface).

Close trophic coupling between land and water ecosystems is demonstrated by the presence, in Westland brown water streams and lakes, of several galaxid fish species (kokopu) which appear to feed on terrestrial insects which fall onto the surface film. These fish (*Galaxias fasciatus* Gray, *G. argenteus* Gmelin, *G. postvectis* Clarke) are frequently absent from Westland streams which lack riparian forest vegetation (Winterbourn, 1987). Swales and West (University of Waikato, unpublished data) have more recently demonstrated a strong preponderance of terrestrial food items in the diets of the kokopu (*Galaxias argenteus* and *G. fasciatus*) in the North Island. The studies of Williamson, Smith and Quinn (1990) on the effect of riparian zone management on invertebrate communities in Southland indicates that shading of stream riparian zones reduced invertebrate abundance. I would like to speculate that this reduction is made up, in terms of food for higher trophic levels (e.g., trout), by an increase in terrestrial insects that fall into streams from the riparian cover. The value of this food source needs further study.

On a New Zealand wide basis only four species of native freshwater fish can be described as "open living" (McDowall, 1987) and most are associated in some way with the land-water ecotone. Many species take cover in rocks, boulders, and forest debris in streams or under stream banks. Some are found in swampy habitats around emergent vegetation or fallen

trees or even in wetland areas which periodically dry out (e.g., the mudfish, *Neochanna* spp.). Indeed, the decline in wetlands in recent years in New Zealand has been suggested as the reason for the decline in the commercial whitebait and eel fisheries (McDowall, 1984). Close coupling between land and water systems is illustrated by eel (*Anguilla australis* Richardson and *A. dieffenbachii* Gray) feeding dynamics. Rounick and Hicks (1985) found that some eel stomachs contained 100% terrestrial invertebrates and BC analyses indicated that this food source was being incorporated into biomass. They were not able to identify the source of this food. However, recent studies in rivers (Chisnall, 1987) and lakes (Jellyman, 1989) have shown that at some times of the year these fish can make use of rising water levels to feed on the newly flooded river margins. When this happens, terrestrial organisms form 90% of the eel diet. Green, McPherson and Scott (1989) assessed the effects of riparian vegetation with particular reference to salmonids in New Zealand and concluded that removal of overhead cover from streams is likely to have a negative impact particularly on older fish.

While the value of the land-water interface as a habitat for avifauna is well documented (e.g. Ogle and Cheyne, 1981; Sagar, 1982) I have been unable to find much quantitative data which define dynamic interactions between birds and their environment at the land-water interface. However, it is clear that feeding and breeding of many birds are particularly responsive to very small changes in water level. Waders, for instance, are very susceptible to small water level changes. A rise of only a few centimetres can cause a loss in feeding grounds. However, even waterfowl (Grey duck - *Anas superciliosa* Buller, and Mallard duck *A. platyrhynchos* L.) have shown susceptibility to changes in water level. During the breeding season a water level rise of only 20-30cm has flooded nests at Pukepuke Lagoon, adversely affecting breeding success (Caithness and Pengelly, 1973). New Zealand waterfowl have the same requirements of the land-water interface as species elsewhere in the world. These are: cover (emergent vegetation) for nesting and hiding; open water for a secure moulting area (although the blue duck demands dense terrestrial riparian vegetation for this); and shallows for food. Reduction in anyone of these diminishes the ability of the land-water interface to support waterfowl.

Discussion

The system dynamics of the land water interface are dictated by the movement of water in stream and swamp channels, lake littoral zones or through the ground. When the interface is managed in any way these flows are directly affected, and hence an

understanding of the role of water movement through the land water interface is necessary for any predictions on how the system will respond.

Because the interface is a relatively narrow boundary it is likely to be less stable in space and time than adjacent systems, and in fluvial landscapes, in particular, ecotones may appear and disappear and may be displaced in lateral or downstream directions. Thus, the interface is likely to be in a continual state of flux, superimposed on which are the shorter term cyclic seasonal or "pattern and process" dynamics illustrated in Figs. 2 and 3, or "resetting" events such as fires (Fig. 4) or floods.

The dynamic nature of the land-water interface makes the formulation of management goals for these areas very difficult. Do we stop riverbanks from shifting or do we stabilise them? Do we stop floods and fires? An easy management option is the complete protection or "let alone" option. Even this has potential problems as recently illustrated by the Whangamata stream at Taupo. Over a 6 year period of complete riparian protection by fencing off riparian strips, the stream bank vegetation shifted in species composition from one which died back in winter (Fig. 3) to one dominated by perennials (e.g., *Mimulus guttatus*) which continuously blocked the stream channel. When this happened, spawning runs of trout in this locally important stream were severely curtailed. As one of the management goals of this stream is to allow its use for trout spawning, an active management policy of channel clearing in autumn is now practised within the confines of the protected riparian strip. In flood plain streams in Southland, Williamson *et al.* (1990) found that riparian protection (fencing to exclude grazing) by itself may not necessarily benefit stream bank stability. They speculated that in addition to riparian protection other management techniques such as tree or shrub plantings may be necessary.

Work to date on the New Zealand land-water interface shows two important features which distinguish this system from many ecotones in the Northern Hemisphere. These are the timing of input of organic matter to the heterotrophic layer, and the timing and periodicity of flood events.

The relatively mild climate caused by New Zealand's maritime position provides for an all year round input of allochthonous carbon from the evergreen forests (Winterbourn, 1987) and a reduced range in annual water temperatures. This may tend to enhance stability of the land water ecotone. However, steep slopes and high rainfall which occur in a non-seasonal pattern (Heine, 1985), produce floods at all times of the year in many areas. Flow regimes are thus highly variable and temporally unpredictable.

The combination of both these factors would tend to select for species with opportunistic behaviour

patterns rather than those with a well defined seasonal response.

New Zealand studies on the dynamics of ecological processes at the land-water interface have demonstrated:

1. The importance of terrestrial inputs of both plant litter and invertebrates to aquatic food webs.
2. Unusual patterns of animal behaviour and seasonality when compared with north temperate situations, particularly a lack of synchrony and long emergence periods in invertebrate populations.
3. The importance of denitrification in the interface groundwater and the importance of macrophytes along channel edges for nitrate removal.
4. High winds (which affect lake littoral zones) and high, variable rainfalls mean that ecosystem dynamics at the land-water interface are dominated by short term, often unpredictable, physical processes.

There is growing evidence that the maintenance of high productivity, biotic diversity and enhancement of some nutrient transformations at the land-water interface requires periodic physical disruptions such as floods, fires or drying-wetting cycles. The unpredictability of such events in New Zealand means that management goals for the land water interface which are based on concepts of homeostasis and stability could be disadvantageous.

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