

Fig. 8. (a) Dendrogram of relationships between reach types and **(b)** spatial arrangement of annual water quality reach types along surveyed section of the lower Waikato River. See Fig. 7 and Table 2 for characteristics of each reach type (W1-W11).

and c. 10–30% on the second axis (Fig. 10). The third PCO axis generally explained < 10%, except in autumn when variation was similar to the second axis (c. 25%). River reaches above the Waipara confluence (W1 and W2) grouped away from those below (W3 – W11) in PCO plots of annual measurements (Fig. 7), and in most seasons (Fig. 10), usually due to decreased transmittance and specific conductivity. This clustering of points was most

pronounced during high winter and spring flows, and reflected marked differences in water clarity, as suggested by SIMPER analyses and Spearman correlation coefficients (Table 3). Reach types immediately below the Waipara confluence tended to reflect a decrease in specific conductivity and water temperature, as water from the Waipara mixed with the main flow (Figs. 6 & 7). Except during winter, reach types typical of the tidally influenced

Table 3. Summary characteristics of seasonal water quality clusters identified using SIMPROF routines (with a Euclidean distance of < 1) for Summer (SM), Autumn (AT), Winter (WT) and Spring (SP).

Cluster	n	Temperature (°C)	Specific conductance (µS/cm)	Chlorophyll fluorescence (relative fluorescence units)	Light transmittance (%)
SM1	41	21.01 (0.06)	140.62 (1.17)	9.99 (0.55)	55.1 (2.45)
SM2	10	21.28 (0.12)	145.33 (1.57)	10.02 (1.22)	47.24 (1.91)
SM3	11	20.6 (0.19)	146.05 (0.84)	9.38 (0.4)	46.9 (3.06)
SM4	18	19.82 (0.1)	144.44 (1.63)	9.01 (0.43)	51.19 (2.51)
SM5	2	21.03 (0.01)	147.94 (0.05)	13.39 (0.44)	23.41 (0.15)
SM6	18	20.79 (0.12)	147.29 (0.44)	10.58 (1.05)	31.16 (1.73)
SM7	5	20.42 (0.13)	146.7 (0.5)	11.69 (1.98)	35.49 (2.1)
SM8	16	20.34 (0.07)	142.62 (0.43)	16.05 (1.35)	32.84 (2.44)
SM9	6	20.16 (0.08)	143.26 (0.22)	20.71 (1.36)	37.06 (1.61)
SM10	5	20.15 (0.06)	142.9 (0.09)	25.36 (1.3)	28.75 (3.64)
SM11	1	19.88 (0)	157.54 (0)	27.2 (0)	19.71 (0)
SM12	1	19.72 (0)	206.66 (0)	28.83 (0)	18.38 (0)
Total	134	20.62 (0.47)	144.22 (6.18)	12.05 (4.52)	43.91 (10.88)
AT1	17	15.7 (0.03)	179.99 (1.05)	10.15 (0.23)	60.68 (1.68)
AT2	36	15.6 (0.05)	180.71 (2.52)	9.5 (0.56)	49.32 (3.68)
AT3	35	15.64 (0.22)	176.28 (1.96)	11.06 (0.71)	39.53 (3.26)
AT4	1	15.85 (0)	179.57 (0)	12.81 (0)	22.13 (0)
AT5	13	15.59 (0.03)	180.02 (1.36)	14.03 (0.45)	30.89 (1.09)
AT6	15	15.38 (0.1)	181.92 (1.86)	15.42 (0.69)	32.71 (2.15)
AT7	9	15.52 (0.1)	167.03 (4.33)	8.77 (0.51)	44.69 (3.71)
AT8	4	16.44 (0.12)	177.47 (0.93)	12.08 (0.45)	41.07 (2.05)
AT9	4	16.89 (0.52)	177.37 (1.03)	11.62 (0.16)	35.76 (0.67)
Total	134	15.66 (0.31)	178.41 (4.23)	11.21 (2.12)	43.39 (9.66)
WT1	48	11.8 (0.06)	147.23 (0.79)	47.03 (3.28)	10.95 (0.75)
WT2	4	12.54 (0.11)	127.46 (4.35)	2.54 (1.64)	8.22 (0.74)
WT3	3	12.45 (0.15)	134.12 (2.17)	12.29 (11.9)	11.6 (0.81)
WT4	33	12.75 (0.21)	140.11 (2)	13.23 (2.29)	10.58 (0.83)
WT5	7	12.58 (0.15)	138.1 (2.53)	14.63 (1.98)	7.15 (0.35)
WT6	32	12.71 (0.15)	139.09 (1.47)	12.64 (1.75)	8.56 (0.49)
WT7	6	12.47 (0.07)	146.07 (4.84)	8.04 (0.89)	13.47 (1.54)
WT8	1	12.77 (0)	118.7 (0)	0.21 (0)	11.91 (0)
Total	134	12.37 (0.45)	141.9 (5.43)	10.14 (1.61)	24.6 (17.22)
SP1	1	17.88 (0)	156.7 (0)	19.59 (0)	39.43 (0)
SP2	22	18 (0.07)	157.64 (0.5)	17.75 (1.27)	35.2 (1.48)
SP3	14	18.2 (0.09)	159.43 (0.44)	18.5 (0.61)	31.56 (0.8)
SP4	11	18.39 (0.1)	162.98 (1.04)	19.45 (0.42)	28.67 (1.05)
SP5	14	19.47 (0.38)	155.25 (1.54)	17.32 (1.53)	22.64 (1.31)
SP6	3	19.93 (0.43)	158.71 (2.62)	23.19 (1.2)	19.42 (0.26)
SP7	1	19.77 (0)	158.57 (0)	24.94 (0)	21.06 (0)
Total	66	18.53 (0.69)	158.45 (2.67)	18.48 (1.86)	29.81 (5.54)

Table 3. cont.

Cluster	n	Temperature (°C)	Specific conductance (µS/cm)	Chlorophyll fluorescence (relative fluorescence units)	Light transmittance (%)
SP8	8	21 (0.09)	152.87 (1.9)	9.49 (0.93)	44.96 (1.81)
SP9	11	21.22 (0.17)	156.28 (0.56)	11.74 (1.25)	41.17 (2.44)
SP10	2	21.6 (0.26)	158.33 (0.24)	9.3 (0.08)	38.33 (1.12)
SP11	28	22.44 (0.21)	159.9 (1.08)	13.76 (2.32)	34.03 (2.26)
SP12	10	21.93 (0.12)	160.09 (0.35)	14.02 (1.16)	27.15 (1.44)
SP13	22	22.39 (0.14)	161.54 (1.31)	19.17 (1.83)	27.41 (2.99)
SP14	1	23.06 (0)	165.52 (0)	30.95 (0)	20.4 (0)
SP15	3	22.68 (0.18)	162.59 (0.41)	26.65 (1.73)	22.83 (0.48)
SP16	1	23.24 (0)	181.64 (0)	31.38 (0)	19.72 (0)
Total	87	22.08 (0.59)	159.6 (3.79)	15.27 (4.9)	32.85 (6.92)

section of river grouped away from most of those upstream (Fig. 10), apparently due to increasing fluorescence (Fig. 6), and occasionally due to higher specific conductivity at river reach 140 km during summer (see group SM12 in Fig. 10). The upstream extent of tidal influence on groups appeared to vary with flow conditions, and during low autumn flows two sites at the downstream end of the fluvial section aligned more closely with tidally influenced river reaches (Fig. 10). This indicates that the effect on water quality of the upstream amplitude of the tidal cycle is likely to vary between seasons and in response to flow conditions upstream. During high winter flows, however, there appears to be little effect of the tidal cycle on water quality measurements at the downstream end of the surveyed section of river, 140 km from Kariro dam. Higher water temperatures were evident immediately downstream of Huntly at low flows (Fig. 10) and subsequently these reaches were characterised as significant groups in CLUSTER analyses (Fig. 9). Conversely, tributaries appeared to contribute cooler water to the main stem during summer and autumn (Fig. 6c).

Cluster groups above the Waipa confluence were most closely related to each other than they were to those below and were unique to that part of the river based on the annual average (Fig. 8a), a pattern generally supported in each season (Fig. 9). SIMPER analyses indicated that clusters of river reaches above the Waipa River could generally be distinguished from those immediately below, as they were associated with higher water clarity and specific conductivity (Table 2; Table 3). However, at lower autumn flows some clusters downstream of the Waipa were also closely related to those above, and some water quality reach types occurred both above and below the Waipa confluence (Fig. 8b). This was most apparent when the Waipa contributed a relatively small volume to the

main stem flow. At this time reaches immediately downstream of the confluence belonged to a distinct cluster group, and the dominant cluster type from above the confluence reappeared further downstream. Conversely, during winter and spring when flows from the Waipa were high, groups above the confluence did not persist downstream (Figs. 9c, d).

Cluster groupings were often present downstream of tributary confluences, most notably the Waipa (driven by low water clarity and specific conductance as described above), but also for smaller tributaries such as the Mangawara Stream (Fig. 9). Tributary confluences other than the Waipa tended to belong to groups characterised by increased chlorophyll fluorescence and conductivity (Figs. 6 and 9). Unique groups did exist in the tidal freshwater section of the lower river, generally reflecting higher fluorescence measurements, and the upstream extent of groups unique to the tidally influenced region was greatest at low autumn flows.


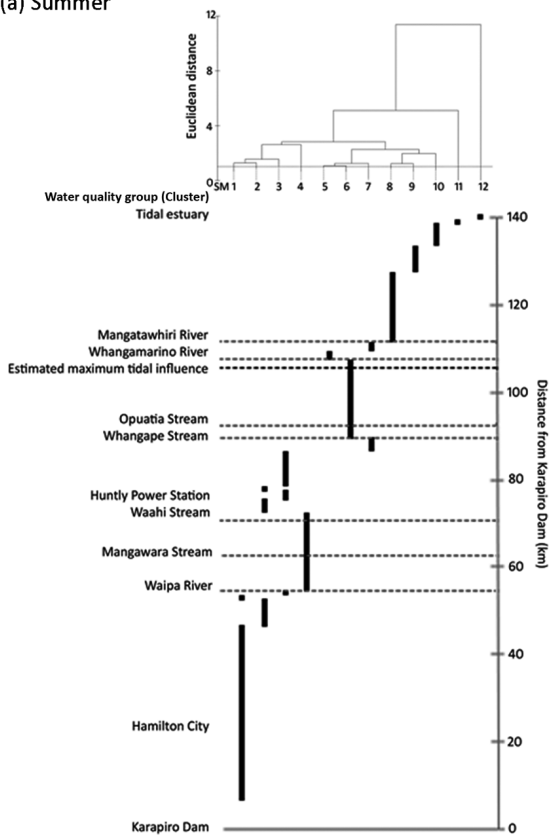
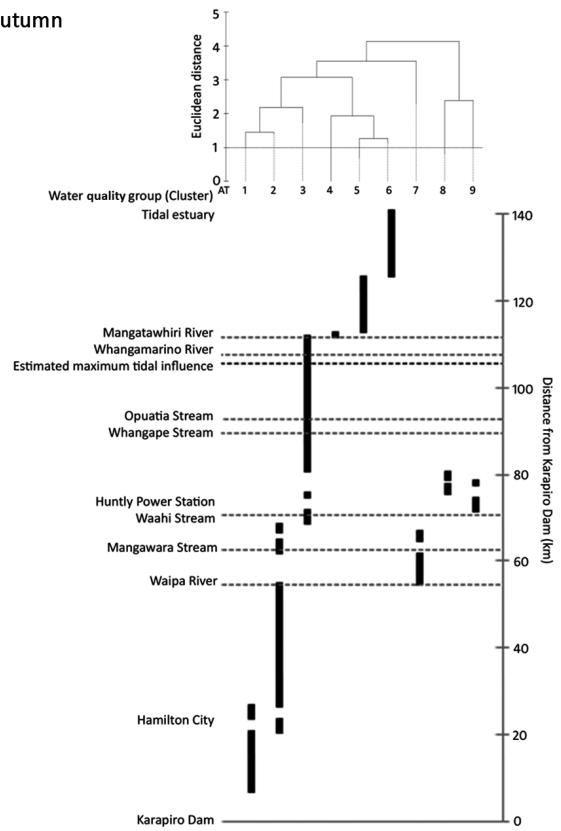


Fig. 9. Dendrogram and spatial arrangement of significant groups identified by PRIMER SIMPROF and CLUSTER routines for surface water quality measurements collected using the Biofish during (a) Summer (March 2010), (b) Autumn (May 2010), (c) Winter (August 2010) and (d) Spring (November/December 2010, separated by black line). Dotted red lines represent locations of major tributaries to the lower Waikato River.

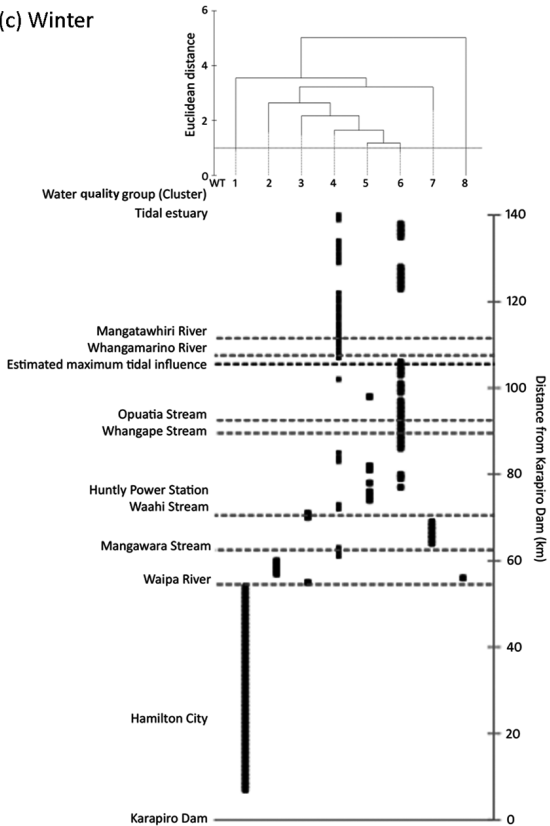
(a) Summer



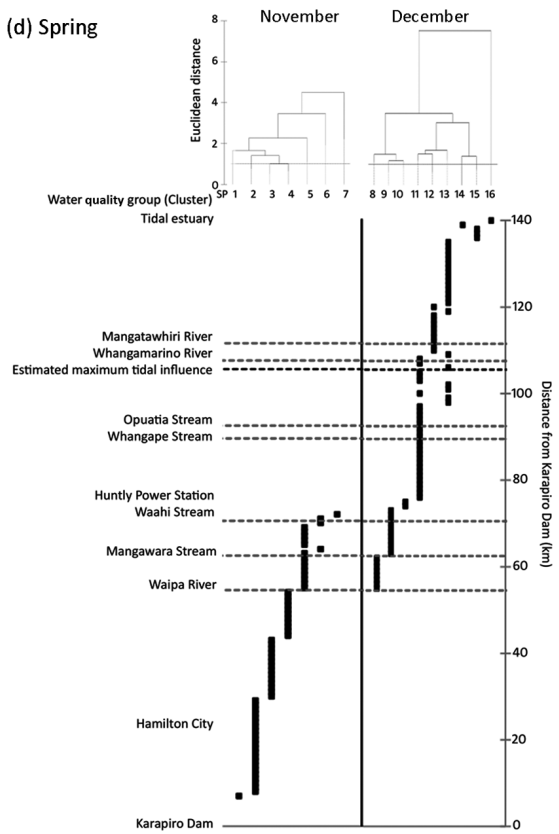
(b) Autumn



(c) Winter



(d) Spring



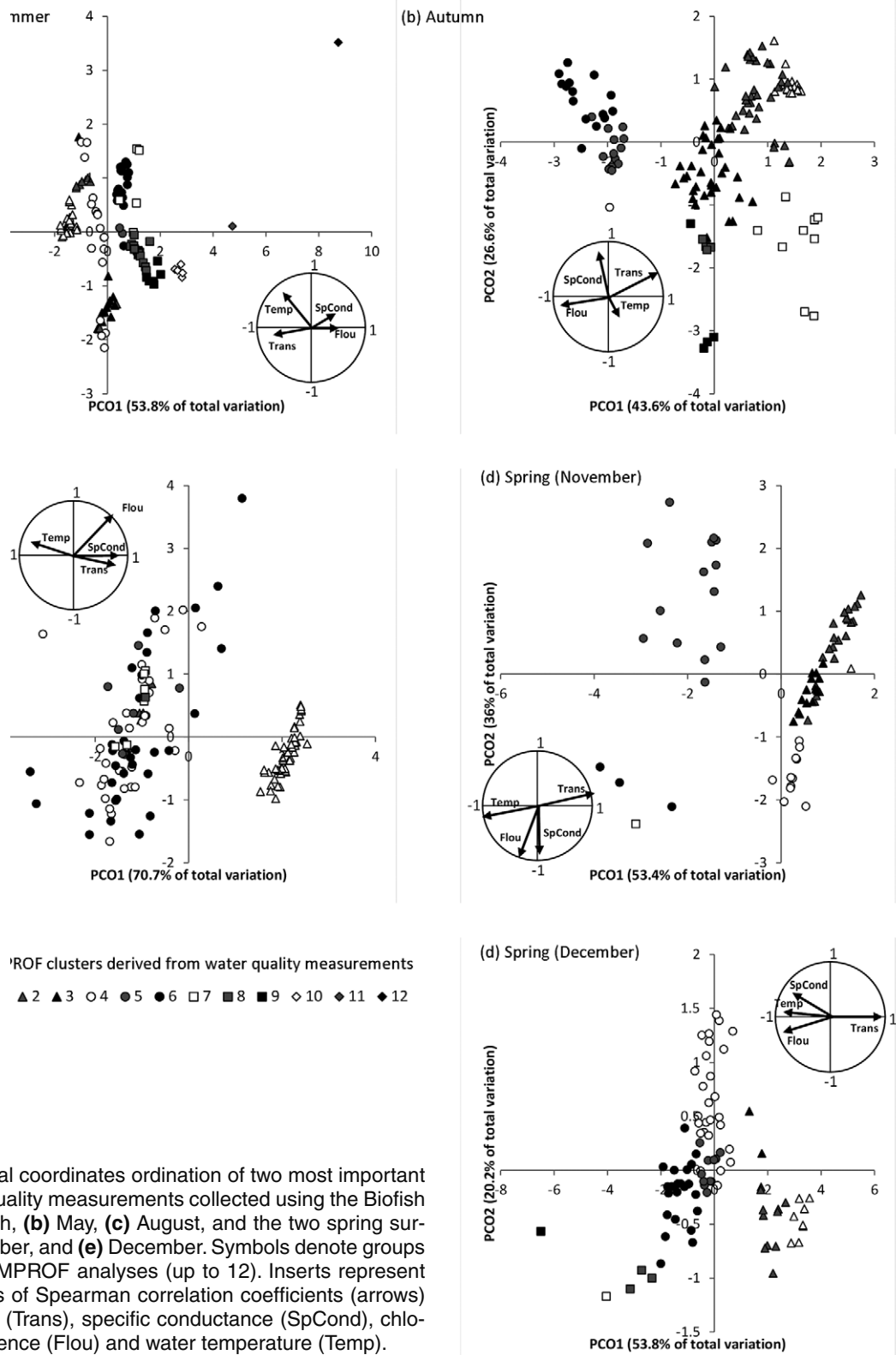


Fig. 10. Principal coordinates ordination of two most important axes of water quality measurements collected using the Biofish during (a) March, (b) May, (c) August, and the two spring surveys (d) November, and (e) December. Symbols denote groups identified by SIMPROF analyses (up to 12). Inserts represent vector diagrams of Spearman correlation coefficients (arrows) for water clarity (Trans), specific conductance (SpCond), chlorophyll fluorescence (Flou) and water temperature (Temp).

Discussion

Definition of spatial units

Multivariate statistical approaches are useful for interpreting and evaluating complex datasets (Varol et al. 2011), and were successful in our study for discriminating spatial units with similar environmental character along the lower Waikato River. Using this framework to analyse high intensity data from physical measurements of 1-km long polygons and from sensor arrays measuring seasonal water quality every 25 seconds resolved 7 or 11 spatial units, respectively. Water quality patterns were represented by differences in clarity, chlorophyll fluorescence and specific conductance driven by tributary inflows in the mid-section of the river and tidal cycles in the lower section. The identified water quality patterns support those documented by previous measurements of turbidity and concentrations of nitrogen, phosphorus, water column chlorophyll *a* and dissolved colour (Vant 2010), and also patterns in phytoplankton biomass observed by Lam (1981) which peaked in the tidal freshwater section of the river and decreased immediately below the Waipa River. Patterns of channel character were largely shaped by the depth and lateral complexity of constituent river reaches, with boundaries partly reflecting geomorphic features constraining the main channel (e.g., Taupiri Gap). However, longitudinal changes in environmental pattern were not necessarily abrupt and some reflected a transition in geomorphology or, for water quality, prevailing flow conditions. Tributary inflows to the lower Waikato River also tend to be enriched in nutrients and sediment from the surrounding agricultural catchment, especially those draining lakes which tend to be highly eutrophic and can drive localised patterns in main stem chlorophyll *a* (Hamilton et al. 2010).

Large rivers provide an interface with coastal environments and are therefore strongly influenced by tidal fluctuations in their lower reaches, adding hydrological complexity that can affect both the morphology of the river channel and biological production (Ensign et al. 2012). These sections of river, where water flow is affected by the tidal cycle but remains fresh, can extend upstream for tens to hundreds of kilometres (e.g. Howarth et al. 1996). Similar to studies of smaller coastal rivers (Ensign et al. 2012), a significant divergence in river morphology began around one-third of the way into the tidally influenced freshwater section. Moreover, flood control works and channel modification in the lower Waikato River may have led to an increase in the upstream extent of the tidal influence by around 10 km, with historical tidal influence previously closer to the delta (Van Kampen 2010). The effect of tidal cycles was evident on the freshwater section of the lower Waikato River, both in terms of physical

complexity and water quality measurements, with greater river width, depth and shoreline complexity, and elevated seasonal mean chlorophyll fluorescence indicating greater phytoplankton abundance. Phytoplankton biomass is strongly dependent on fluvial discharge and the residence time available for community development in tidally influenced freshwater sections of rivers (Neal et al. 2006). High biomass often occurs at low flows (Bennett et al. 1986) when water travel times can be many times greater than in non-tidal river sections (Ensign et al. 2012). Production is also closely linked to channel form, with broad channels and extensive shallow lateral areas, such as those in the delta, providing favourable light and flow retention conditions for algal growth (Bukaveckas et al. 2011a), which in turn can enhance zooplankton growth in tidal systems (Müller-Solger et al. 2002). These findings highlight interactions between hydrology, water quality and the physical structure of channels in tidal river sections, supporting their identification as discrete spatial units for management. Boundaries between strictly fluvial and tidal freshwater sections are likely to be transitional, variable and sometimes indistinct due to the nature and strength of daily tidal cycles, and flow conditions.

Although seasonal averages were used to define spatial units based on water quality measurements, the number of units and location of boundaries differed between seasons. Substantial increases in sediment loads supplied by major tributaries may occur with seasonal high flows, while high flows in the main channel can also overwhelm the contributions of smaller tributaries (Boyer et al. 2010). Water temperature also plays an important role in primary production, with increased seasonal temperature and light availability linked to elevated rates of photosynthesis, respiration and metabolism in other large lowland rivers (Descy et al. 1987). In our study and that of Lam (1981), measurements of phytoplankton biomass (chlorophyll fluorescence in our study) were recorded during summer and spring when water temperatures were warmest, particularly in the tidal freshwater zone. The discontinuity between the river sections dominated by clear, dam-fed water of the Waikato River and the Waipa River, which contributes significant amounts of flow and sediment at high flows (Brown 2010), was most distinct during winter and spring (high flows) and less so during summer and autumn (low flows). High river flows in the main channel can also have a dampening effect on tidal cycles and upstream extent of saline intrusion into freshwater sections of lowland rivers (Anderson & Lockaby 2012). Tidal cycle fluctuations at Tuakau (Fig. 1a) were greatest during months of lower fluvial flows (Fig. 1d), and this is reflected in the transition from fluvial to tidal water quality reach types being shortest and furthest upstream during summer and autumn (Fig. 9). Conversely

during high winter flows a transition was undetectable and daily water level fluctuations were also small (Fig. 1d).

The identified channel units correspond to some extent to known variations in biological patterns within the lower river. Collier et al. (2014) reported an abrupt decrease in benthic macroinvertebrate biodiversity at Huntly downstream of the geomorphic channel constriction at Taupiri, and hypothesised that this reflected deposition of sediment delivered to the main channel from the Waipa River. Increases in suspended sediment are also likely to affect downstream food webs (Henley et al. 2000), and it has been suggested that lower invertebrate densities below the Waipa confluence during winter and spring may be a result of less suitable flow and growth conditions (Collier et al. 2011), while the growth and food assimilation of key primary consumers in the lower Waikato River, such as *Potamopyrgus antipodarum*, can be adversely affected by high sediment to food ratios (Broekhuizen et al. 2001). Similarly, changes in stable isotope signatures and differences in carbon utilisation by aquatic biota have been observed between sites from different sections of the lower Waikato River (i.e. fluvial reaches above the Waipa confluence, those below, and tidal freshwater reaches) (Pingram et al. 2014). Littoral macroinvertebrate communities have also been reported to respond to localised effects of organic matter, sediment and thermal discharges but not to clinal gradients, suggesting that physical heterogeneity of river edges is not a key factor structuring community composition (Collier et al. 2014). Physical channel complexity may be more relevant for riverine fish which use lateral habitats during various life-cycle stages (Górski et al. 2014), and as lateral habitats can represent a key location for carbon transfer through food webs (Pingram et al. 2014). Laterally complex river zones are likely to have a greater array of habitats where abiotic characteristics and biotic function are driven by the frequency, magnitude and duration of main channel flow and flood pulses (Schiemer & Hein 2007; Thorp et al. 2008). Reduced flow velocities and increased water retention in these habitats are important factors in the processing of nutrients and organic carbon by plankton before transfer to other parts of the food web (Schiemer et al. 2001; Górski et al. 2013). Smaller retention zones can be created by changes in shoreline configuration, with increasing shoreline complexity (e.g., length, sinuosity) leading to reduced current velocities and longer retention times that benefit some littoral organisms (Schiemer et al. 2001; Schiemer & Hein 2007).

Role of discontinuities

Our Waikato River case study has highlighted the importance of network, geomorphic and anthropogenic discontinuities to the spatial structure of river sections. While geomorphic constrictions defined the boundaries of some physical units, adjoining tributaries from the wider river network often interrupted broader spatial patterns of water quality units and in one instance defined a boundary in the main stem between reaches above and below the tributary inflow. Tributary junctions can create additional complexity in the main river, with a complex range of associated effects on woody debris abundance, substrate heterogeneity, consumer abundance, water volume, nutrient availability, sediment loading, and bed particle shape and size that can in turn create nodes of high habitat complexity, biological diversity and productivity (Kiffney et al. 2006; Rice et al. 2006; Rosales et al. 2007). The relative impact and extent of discontinuities and complexity in the main river caused by tributary junctions will depend on temporal and spatial flow variability. For example, the distribution and intensity of rainfall in the catchments of large tributaries can mediate the delivery of sediment, allochthonous carbon sources and woody debris to rivers (Rice et al. 2006).

In our study there was a clear discontinuity between river reaches above and below the confluence of the largest tributary, the 5th order Waipa River, for all water quality measurements taken, particularly at high flows (winter and spring). Depending on the relative flow conditions in the main stem, minor discontinuities were also apparent around smaller tributaries, usually denoted by increased chlorophyll fluorescence or specific conductivity. Lake- and wetland-fed tributaries in particular tended to have localised positive effects on phytoplankton biomass in the main stem, while the Waipa tended to reduce chlorophyll fluorescence. The differential effects of tributaries on main stems, dependent on donor concentrations of algae and magnitude of flow, have also been noted by other workers in terms of positive (Bukaveckas et al. 2011b) or negative (Descy et al. 1987; Bukaveckas et al. 2011b) effects on main stem phytoplankton biomass. The downstream extent of tributary influence on water quality will likely depend on flow volumes and velocities of both the contributing source and the receiving main channel (Rice et al. 2008). Direct human influences were also noted around a thermal discharge (at Huntly; Fig. 1a), which measurably increased water temperature, leading to a distinct group of reaches immediately downstream of the discharge. However, these smaller network and anthropogenic discontinuities did not have an over-riding effect on spatial clustering, and reaches further downstream tended to belong to the predominant group upstream of the minor

discontinuity. Such localised changes can be considered as ‘noise’ within a given river ‘link’, as defined by Rice et al. (2001), since they do not lead to a significant shift in main stem character. Nevertheless, major discontinuities caused by significant tributary contributions of flow and sediment can significantly affect spatial patterns of biological communities (Collier et al. 2014).

Large dams also represent significant discontinuities along large rivers, leading to marked downstream changes in ecosystem function, including reduced flow pulses and transported sediments, increased channel incision leading to disconnection of lateral habitats, changes in water temperature and releases of lake-derived plankton (Ward & Stanford 1983; Górski et al. 2011). Moreover, fluctuations as a result of diurnal hydro-power generation can have impacts on the species richness, abundance and behaviour of macroinvertebrates and fish (Bunn & Arthington 2002). The rate of downstream recovery from these effects will be dependent on the magnitude of regulation (Cortez et al. 2012) and the presence of large unregulated downstream tributaries (Stanford & Ward 2001), such as the Waipa River in this study. Flow variability above the Waipa confluence is regulated by the dam at Karapiro (Fig. 1b) and high water clarity partly reflects the retention of suspended solids in the series of eight upstream hydro lakes, which has also led to increased bed incision downstream, although the river channel maintains its natural shape (Hicks & Hill 2010).

Conclusions

Multivariate statistical approaches and geographic tools provided a powerful means for condensing our spatially intensive dataset and guided identification of river units for future ecological management and research. Channel units were distinguished by both riverscape features and physico-chemical parameters which did not necessarily align and sometimes had indistinct boundaries. Lateral channel complexity and depth played an important role in shaping physical patterns, while features such as large tributaries and tidal influences had substantial roles in shaping water quality patterns. The boundaries of potential zones may have been different in the past and could change again as a result of improvements to current land management practices or rising sea levels. As aerial and high resolution satellite photos become more widely available during different seasons and flow conditions, further analyses could be conducted to quantify temporal variability in physical complexity metrics, as recommended by the authors of the RCCR (O’Neill & Thorp 2011). Our results can also be seen in the context of a developed river whereby the anthropogenic impacts such as

large dams (increased water clarity and incision), thermal power stations (heated discharges), and land clearance for pastoral grazing (increased suspended sediments and hydrological extremes) can affect the ecological integrity of a fluvial system and the composition of contemporary management units. Management objectives should reflect the dynamic spatial and temporal nature of rivers (Elosegi et al. 2010) which can create fuzzy or shifting boundaries between hydrogeomorphic units. The scale of potential units identified in this case study, generally more than several kilometres in length, is relevant for management because these units integrate an ecologically meaningful combination of properties likely to shape ecosystem processes such as energy transfer in food webs. Given that actions and targets may differ between physical channel and water quality management, spatial units (reach types) identified for each of these do not necessarily need to directly coincide from a management or research perspective, although both should be considered in decision making and experimental design.

Acknowledgements

The authors acknowledge funding provided by the University of Waikato Strategic Investment Fund for the costs of sample collection. We thank Warrick Powrie and Dudley Bell for driving boats, and Mathew Allan and Chris McBride for assistance with GIS and Biofish, respectively. The University of Waikato provided a doctoral student scholarship. We thank Professor James Thorp and two anonymous reviewers who provided comments that helped improve this manuscript.

References

- Anderson, C.J. & Lockaby, B.G. (2012): Seasonal patterns of river connectivity and saltwater intrusion in tidal freshwater forested wetlands. – *River Res. Appl.* 28: 814–826.
- Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008): PERMANOVA+ for PRIMER: guide to software and statistical methods. – In: *Primer-e*, Plymouth, UK, pp. 214.
- Bennett, J.P., Woodward, J.W. & Shultz, D.J. (1986): Effect of discharge on the chlorophyll *a* distribution in the tidally-influenced Potomac River. – *Estuaries* 9: 250–260.
- Boyer, C., Verhaar, P.M., Roy, A.G., Biron, P.M. & Morin, J. (2010): Impacts of environmental changes on the hydrology and sedimentary processes at the confluence of St. Lawrence tributaries: potential effects on fluvial ecosystems. – *Hydrobiologia* 647: 163–183.
- Broekhuizen, N., Parkyn, S. & Miller, D. (2001): Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and

- Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). – *Hydrobiologia* 457: 125–132.
- Brown, E.J. (2010): Flow regime and water use. – In: Collier, K.J., Hamilton, D.P., Vant, W.N. & Howard-Williams, C. (eds.): *The Waters of the Waikato: Ecology of New Zealand's longest river*. – *Environ. Waikato and Centre Biodivers. Ecol. Res.* (The University of Waikato). Hamilton, pp. 29–46.
- Bukaveckas, P., Barry, L., Beckwith, M., David, V. & Lederer, B. (2011a): Factors determining the location of the chlorophyll maximum and the fate of algal production within the tidal freshwater James River. – *Estuaries Coasts* 34: 569–582.
- Bukaveckas, P., MacDonald, A., Aufdenkampe, A., Chick, J., Havel, J., Schultz, R., Angradi, T., Bolgrien, D., Jicha, T. & Taylor, D. (2011b): Phytoplankton abundance and contributions to suspended particulate matter in the Ohio, Upper Mississippi and Missouri Rivers. – *Aquat. Sci.* 73: 419–436.
- Bunn, S.E. & Arthington, A.H. (2002): Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. – *Environ. Manage.* 30: 492–507.
- Chang, H. (2008): Spatial analysis of water quality trends in the Han River basin, South Korea. – *Water Research* 42: 3285–3304.
- Collier, K.J., Watene-Rawiri, E.M. & McCraw, J.D. (2010): Geography and history. – In: Collier, K.J., Hamilton, D.P., Vant, W.N. & Howard-Williams, C. (eds.): *The Waters of the Waikato: Ecology of New Zealand's longest river*. – *Environ. Waikato and Centre Biodivers. Ecol. Res.* (The University of Waikato), pp. 1–12.
- Collier, K.J., Hamer, M.P. & Davenport, M.W. (2011): Artificial substrate monitoring of macroinvertebrates in the Waikato River: 25 years on. – *Waikato Regional Council Technical Report 2011/25*.
- Collier, K.J., Clapcott, J.E., David, B.O., Death, R.G., Kelly, D., Leathwick, J.R. & Young, R.G. (2012): Macroinvertebrate pressure relationships in boatable New Zealand rivers: Influence of underlying environment and sampling substrate. – *River Res. Appl.* 29: 645–659.
- Collier, K.J., Hamer, M.P. & Moore, S.C. (2014): Littoral and benthic macroinvertebrate community responses to contrasting stressors in a large New Zealand river. – *N. Z. J. Mar. Freshw.* (in press)
- Cortez, D.P., Growns, I.O., Mitrovic, S.M. & Lim, R.P. (2012): Effects of a gradient in river regulation on the longitudinal trends in water quality and benthic algal and macroinvertebrate assemblages in the Hunter River, Australia. – *Mar. Freshw. Res.* 63: 494–504.
- Descy, J.P., Servais, P., Smits, J.S., Billen, G. & Everbecq, E. (1987): Phytoplankton biomass and production in the river meuse (Belgium). – *Water Research* 21: 1557–1566.
- Dolédéc, S., Phillips, N. & Townsend, C. (2011): Invertebrate community responses to land use at a broad spatial scale: trait and taxonomic measures compared in New Zealand rivers. – *Freshwat. Biol.* 56: 1670–1688.
- Elosegi, A., Díez, J. & Mutz, M. (2010): Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. – *Hydrobiologia* 657: 199–215.
- Ensign, S.H., Doyle, M.W. & Piehler, M.F. (2012): Tidal geomorphology affects phytoplankton at the transition from forested streams to tidal rivers. – *Freshwat. Biol.* 57: 2141–2155.
- Eyre, B.D. & Pepperell, P. (1999): A spatially intensive approach to water quality monitoring in the Rous River catchment, NSW, Australia. – *J. Environ. Manage.* 56: 97–118.
- Górski, K., van den Bosch, L.V., van de Wolfshaar, K.E., Middekoop, H., Nagelkerke, L.A.J., Filippov, O.V., Zolotarev, D.V., Yakovlev, S.V., Minin, A.E., Winter, H.V., De Leeuw, J.J., Buijse, A.D. & Verreth, J.A.J. (2011): Post-damming flow regime development in a large lowland river (Volga, Russian Federation): Implications for floodplain inundation and fisheries. – *River Res. Appl.* 28: 1121–1134.
- Górski, K., Collier, K.J., Duggan, I.C., Taylor, C.M. & Hamilton, D.P. (2013): Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. – *Freshwat. Biol.* 58: 1458–1470.
- Górski, K., Collier, K.J., Hamilton, D.P. & Hicks, B.J. (2014): Effects of flow on lateral interactions of fish and shrimps with off-channel habitats in a large river-floodplain system. – *Hydrobiologia* 729: 161–174.
- Hadwen, W.L., Fellows, C.S., Westhorpe, D.P., Rees, G.N., Mitrovic, S.M., Taylor, B., Baldwin, D.S., Silvester, E. & Croome, R. (2010): Longitudinal trends in river functioning: patterns of nutrient and carbon processing in three Australian rivers. – *River Res. Appl.* 26: 1129–1152.
- Hamilton, D.P., Vant, W.N. & Neilson, K.A. (2010): Lowland lakes. – In: Collier, K.J., Hamilton, D.P., Vant, W.N. & Howard-Williams, C. (eds.): *The Waters of the Waikato: Ecology of New Zealand's longest river*. – *Environ. Waikato and Centre Biodivers. Ecol. Res.* (The University of Waikato), pp. 245–264.
- Henley, W.F., Patterson, M.A., Neves, R.J. & Lemly, A.D. (2000): Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. – *Rev. Fish. Sci.* 8: 125–139.
- Hicks, D.M. & Hill, R.B. (2010): Sediment regime: sources, transport and changes in the riverbed. – In: Collier, K.J., Hamilton, D.P., Vant, W.N. & Howard-Williams, C. (eds.): *The Waters of the Waikato: Ecology of New Zealand's longest river*. – *Environ. Waikato and Centre Biodivers. Ecol. Res.* (The University of Waikato). Hamilton, pp. 71–92.
- Howarth, R.W., Schneider, R. & Swaney, D. (1996): Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. – *Estuaries Coasts* 19: 848–865.
- Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989): The flood pulse concept in river-floodplain systems. – In Dodge, D.P. (ed.): *Proceedings of the International Large River Symposium*. – *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 110–127.
- Kiffney, P.M., Greene, C.M., Hall, J.E. & Davies, J.R. (2006): Tributary streams create serial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. – *Can. J. Fish. Aquat. Sci.* 63: 2518–2530.
- Lam, C.W.Y. (1981): Ecological studies of phytoplankton in the Waikato River and its catchment. – *N. Z. J. Mar. Freshw.* 15: 95–103.

- McBride, C., Hamilton, D., Gibbs, M., White, P. & Stewart, L. (2008): BioFish survey of Lake Taupo, 2006. – CBER Contract Report 68. University of Waikato, Hamilton.
- Müller-Solger, A.B., Jassby, A.D. & Müller-Navarra, D.C. (2002): Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). – *Limnol. Oceanogr.* 47: 1468–1476.
- Mulholland, W.M. (2010): Box 2.2: History of the lower Waikato Flood Protection Scheme. – In: Collier, K.J., Hamilton, D.P., Vant, W.N. & Howard-Williams, C. (eds.): *The Waters of the Waikato: Ecology of New Zealand's longest river.* – Environ. Waikato and Centre Biodivers. Ecol. Res. (The University of Waikato). Hamilton, pp. 16.
- Neal, C., Hilton, J., Wade, A.J., Neal, M. & Wickham, H. (2006): Chlorophyll-*a* in the rivers of eastern England. – *Sci. Total Environ.* 365: 84–104.
- Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005): Fragmentation and flow regulation of the world's large river systems. – *Science* 308: 405–408.
- O'Neill, B.J. & Thorp, J.H. (2011): A simple channel complexity metric for analyzing river ecosystem responses. – *River Systems* 19: 327–335.
- Parsons, M. & Thoms, M.C. (2007): Hierarchical patterns of physical – biological associations in river ecosystems. – *Geomorphology* 89: 127–146.
- Pingram, M.A., Collier, K.J., Hamilton, D.P., Hicks, B.J. & David, B.O. (2014): Spatial and temporal patterns of carbon flow in a temperate, large river food web. – *Hydrobiologia* 729: 107–131
- Power, M.E. & Dietrich, W.E. (2002): Food webs in river networks. – *Ecol. Res.* 17: 451–471.
- Rice, S.P., Greenwood, M.T. & Joyce, C.B. (2001): Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. – *Can. J. Fish. Aquat. Sci.* 58: 824–840.
- Rice, S.P., Fergusson, R.I. & Hoey, T.B. (2006): Tributary control of physical heterogeneity and biological diversity at river confluences. – *Can. J. Fish. Aquat. Sci.* 63: 2553–2566.
- Rice, S.P., Kiffney, P., Correigh, G. & Pess, G.R. (2008): The ecological importance of tributaries and confluences. – In: Rice, S.P., Roy, A.G. & Rhoads, B.L. (eds.): *River Confluences, Tributaries and the Fluvial Network.* – John Wiley & Sons Ltd., Chichester, pp. 209–242.
- Rosales, J., Blanco-Belmonte, L. & Bradley, C. (2007): Hydrogeomorphological and ecological interactions in tropical floodplains: The significance of confluence zones in the Orinoco Basin, Venezuela. – In: P.J. Wood, D.M. Hannah & J.P. Sadler (eds.): *Hydroecology and Ecohydrology: Past, present and future.* – John Wiley & Sons Ltd., Chichester, pp. 295–316.
- Schiemer, F., Keckeis, H., Reckendorfer, W. & Winkler, G. (2001): The “inshore retention concept” and its significance for large rivers. – *Large Rivers* 12: 509–516.
- Schiemer, F. & Hein, T. (2007): The ecological significance of hydraulic retention zones. – In: Wood, P.J., Hannah, D.M. & Sadler, J.P. (eds.): *Hydroecology and Ecohydrology: Past, present and future.* – John Wiley & Sons Ltd., Chichester, pp. 405–420.
- Speirs, D.A., Allen, D.G., Kelleher, R.M., Lake, M.D., Marchant, A.N., Mayes, K.A., Watene-Rawiri, E.M. & Wilson, B.J. (2010): River management. – In: Collier, K.J., Hamilton, D.P., Vant, W.N. & Howard-Williams, C. (eds.): *The Waters of the Waikato: Ecology of New Zealand's longest river.* – Environ. Waikato and Centre Biodivers. Ecol. Res. (The University of Waikato). Hamilton, pp. 13–26.
- Stanford, J.A. & Ward, J.V. (2001): Revisiting the serial discontinuity concept. – *Regul. Rivers: Res. Manage.* 17: 303–310.
- Thorp, J.H., Thoms, M.C. & Delong, M.D. (2006): The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. – *River Res. Appl.* 22: 123–147.
- Thorp, J.H., Thoms, M.C. & Delong, M.D. (2008): *The Riverine Ecosystem Synthesis: Towards conceptual cohesiveness in river science.* – Elsevier, 208 pp.
- Van Kampen, J. (2010): Flow river flow. – Jack Van Kampen, Manukau, 72 pp.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980): The river continuum concept. – *Can. J. Fish. Aquat. Sci.* 37: 130–137.
- Vant, W.N. (2010): Water quality. – In: Collier, K.J., Hamilton, D.P., Vant, W.N. & Howard-Williams, C. (eds.): *The Waters of the Waikato: Ecology of New Zealand's longest river.* – Environ. Waikato and Centre Biodivers. Ecol. Res. (The University of Waikato). Hamilton, pp. 93–114.
- Varol, M., Gökot, B., Bekleyen, A. & Şen, B. (2011): Water quality assessment and apportionment of pollution sources of Tigris River (Turkey) using multivariate statistical techniques – a case study. – *River Res. Appl.* 28: 1428–1438.
- Ward, J.V. & Stanford, J.A. (1983): The serial discontinuity concept of lotic ecosystems. – In: Fontaine, T.D. & Bartell, S.M. (eds.): *Dynamics of lotic ecosystems.* – Ann Arbor Scientific Publishers, Ann Arbor, MI, pp. 29–42.
- Ward, J.V. (1989): The four-dimensional nature of lotic ecosystems. – *J. N. Am. Benthol. Soc.* 8: 2–8.
- Woodward, G. & Hildrew, A.G. (2002): Food web structure in riverine landscapes. – *Freshwat. Biol.* 47: 777–798.

Received 1 February 2013

Modified version received 28 April 2014

Accepted 30 June 2014