Ecological consequences of global climate change for freshwater ecosystems in South Africa

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Freshwater resources in South Africa are under severe pressure from existing anthropogenic impacts and global climate change is likely to exacerbate this stress. This review outlines the abiotic drivers of climate change, focusing on predicted changes in temperature and precipitation. The consequences of global climate change for freshwater ecosystems are reviewed, with effects grouped into those related to water quantity, water quality, habitat and aquatic biological assemblages. Several guiding principles aimed at minimising the potential impact of climate change on freshwater ecosystems are discussed. These guidelines include those focused on water quantity and the maintenance of appropriate environmental flows, integration of global climate change into water quality management, conservation planning for freshwater biodiversity, the promotion of ecosystem resilience, and extending climate change science into policy and public discourse. Proactive assessment and monitoring are seen as key as these will allow for the identification of ecological triggers and thresholds, including thresholds of vulnerability, which may be used to monitor and inform decisions, as well as to improve the ability to forecast based on this knowledge.

Introduction

Freshwater ecosystems are considered to be among the ecosystems most vulnerable to global climate change.[1] Observational records and climate projections provide abundant evidence that freshwater resources have the potential to be strongly impacted by climate change, with wide-ranging consequences for human societies and ecosystems.[1] Observed global trends in precipitation, humidity, drought and run-off indicate that southern Africa is on a negative trajectory with respect to changes associated with climate change.[2] South Africa is a water-stressed country with a mean annual precipitation (MAP) of 500 mm per annum (approximately 60% of the world average[3]), with 65% of the country, especially the arid and semi-arid interior and western regions, receiving on average <500 mm per annum. The eastern half of the country receives between 500 mm and 1000 mm per annum, while a narrow region along the southeastern coastline receives rainfall of 1000 mm to 2000 mm per annum.[3] Southern Africa has been identified as a 'critical region' of water stress, based on an indicator using the ratio of annual withdrawals-to-availability, with more than half of the water management areas in South Africa currently in deficit.[4] The relative dryness of the region, expressed as an aridity index (i.e. the ratio between mean annual potential evaporation and MAP) varies from 1 in the east to >10 in the arid west.[5] Given the most probable scenario of a growing economy and population, climate change has major implications for aquatic ecosystems and for their ability to deliver ecosystem services.

Global and regional climate change models[5-9] predict likely trends in the magnitude and amplitude of event-driven systems, primarily rainfall and air temperature. Changes include shifts in mean condition, variance and frequency of extremes of climatic variables, which result in changes in water quantity, especially in arid and semi-arid regions.[5] Historically, focus on the consequences of global climate change trends has tended to be on terrestrial ecosystems, with less attention given to aquatic ecosystems. In the last decade, focus has shifted to freshwater ecosystems and the number of studies published annually has increased dramatically.[10] This shift follows the recognition that freshwater ecosystems are vulnerable to climate change, that aquatic organisms are highly sensitive to climate change[11,12] and that climate change is expected to worsen freshwater conditions, especially in Mediterranean regions[13]. Several climate model projections warn of widespread biological invasions, extinctions and the redistribution and loss of critical ecosystem functions.[14,15]

This review explores the likely impacts of climate change on freshwater ecosystems, focusing on lotic (rivers) ecosystems, although several issues are also relevant for lentic (lakes, wetlands) systems. It builds on information gleaned during an interactive workshop of climate change and freshwater specialists[16,17] and aims to summarise key issues related to climate change and freshwater ecosystems within the context of South Africa, but with reference to international research. The review discusses the abiotic drivers of climate change and the ecological consequences of climate change to freshwater ecosystems. These consequences are separated into those affecting water quantity, water quality, physical habitat and aquatic biological assemblages. Several guiding principles aimed at minimising the potential impact of climate change on freshwater ecosystems are discussed, including those focused on water quantity and the maintenance of appropriate environmental flows, integration of global climate change into water quality management, conservation planning for freshwater biodiversity, and the promotion of ecosystem resilience. Although specific scientific literature on climate change and freshwater ecosystems in South Africa is limited, relevant studies have been consulted and links have been made to the potential ecological consequences of climate change.

Setting the stage – abiotic drivers of global climate change

General circulation models (GCMs) are a class of computer-driven models for weather forecasting; those that project climate change are commonly called global climate models. GCMs are the core tool for simulating the coupled climate system using physical representations of the atmosphere, land and ocean surface.[6] GCMs simulate the most important features of the climate (i.e. air temperature and rainfall) reliably at a large scale, although, as uncertainties are inherent in CGMs, predictions for rainfall intensity, frequency and spatial distribution have a lower confidence.[5] CGMs are commonly downscaled to enable their outputs to be made relevant to regional- or local-scale climate change scenarios.[8,18]

In South Africa, regional models have developed to a stage where pattern changes at a sub-national scale are made with confidence, while confidence for the magnitude of change is weaker.[18] According to these models, predictions are not uniform within South Africa and climate change is likely to impact most strongly on the western regions, with less of an impact as one moves eastwards. Certain areas are likely to become 'winners' in light of certain projected changes, while other areas are likely to become 'losers' as more water-related stresses are experienced.[19] 'Hotspots' of concern are the southwest of the country, the west coast and, to a lesser extent, the extreme north of South Africa.[19,20] The responses of rainfall and temperature as predicted by global climate change models are summarised in Table 1, with summer and winter rainfall regions given separately where relevant.

Ecological consequences of global climate change

Primary climate change drivers are precipitation, air temperature and evaporative demand. Ecological consequences of global climate change on freshwater ecosystems may be grouped into effects that relate to water quantity, water quality, habitat and biological assemblages (Table 2). Often stressors act in synergistic ways with effects exacerbated through the interaction of two or more effects such as the combined effect of reduced run-off and elevated water temperature. Consequences for biological assemblages are thus often the result of several climate change drivers acting in synergy. In addition, climate change may cause changes in land-use patterns, which in turn may impact on, for example, volumes of fine sediment delivered to river channels. Such feedbacks need to be considered when trying to determine the potential effects of climate change on aquatic ecosystems.

Table 1: Responses of rainfall and air temperature for the summer and winter rainfall regions of South Africa as predicted by global climate change models[5,8,9,119]

<table>
<tr><th colspan="2">Predicted change in climatic factors</th></tr>
<tr><th>Summer rainfall region (central, north, east)</th><th>Winter rainfall region (southwest)</th></tr>
<tr><th colspan="2">Rainfall</th></tr>
<tr><td>Increase in mean annual precipitation (MAP) of 40 mm to 80 mm per decade in the east, particularly the mountainous areas. Northern and eastern regions likely to become wetter in summer and autumn, especially over regions of steep topography around the escarpment and Drakensberg.</td><td>Decrease in MAP of 20 mm to 40 mm per decade. Shorter winter rainfall season, weaker winter pressure gradients, more summer rainfall from January onwards, especially inland and towards the east.</td></tr>
<tr><td>Increase in year-to-year absolute variability of MAP in the east (from 30% up to double).</td><td>Decrease in year-to-year absolute variability of annual precipitation.</td></tr>
<tr><td>Wetting trend of varying intensity and distribution, particularly in the east and transitional region. Drying trend in the middle and towards the end of the wet season (i.e. January, April) in northern areas.</td><td>Drying trend in the west, mainly in the middle of the rainy season (July) and towards the end of the rainy season (October). Mountainous regions predicted to be relatively stable, while coastal regions likely to become drier.</td></tr>
<tr><td>Greater interannual variability, intensifying in autumn.</td><td>Greater interannual variability, more irregular rainfall events.</td></tr>
<tr><td>Increase in intensity of rainfall events.</td><td>Increase in the frequency of extreme events, including drought as a result of the predicted poleward retreat of rain-bearing frontal systems.</td></tr>
<tr><th colspan="2">Air temperature</th></tr>
<tr><td colspan="2">Into the IF mean annual temperatures are projected to increase by 1.5–2.5 °C along the coast and by 3.0–3.5 °C in the far interior.</td></tr>
<tr><td colspan="2">Into the MDF mean annual temperatures are projected to increase by 3.0–5.0 °C along the coast and by more than 6.0 °C in the interior.</td></tr>
<tr><td colspan="2">Interannual variability (standard deviation of the annual mean) of temperature is projected to increase by ~10% over much of South Africa, with increases in excess of 30% in the north. Variability in mountainous areas in the south and west not projected to change (i.e. January, April).</td></tr>
<tr><td colspan="2">July (winter) minimum temperatures are projected to increase by a wider range from <2 °C to >6 °C, but with essentially a south to north gradient from the coast to the interior.</td></tr>
<tr><td>January (summer) maximum temperature is projected to increase by 2–4 °C.</td><td>January (summer) maximum temperature is projected to increase by 4–6 °C.</td></tr>
<tr><td>In KwaZulu-Natal, mean daily air temperature is likely to increase by approximately 2.5 °C.</td><td>Increase in days with hot, berg winds during December/January/February.</td></tr>
</table>

IF, intermediate future (2046–2065); MDF, more distant future (2081–2100).[5]

Note: model predictions are more in agreement for temperature than for rainfall.

Water quantity

Global climate change drivers directly affect the quantity of water in freshwater ecosystems by changing run-off patterns (e.g. mean values, flow variability, duration and timing), increasing the frequency and intensity of extreme events (droughts and floods), and changing groundwater recharge rates (Table 2). A substantial amount of research has been undertaken in South Africa on the likely consequences of climate change on water resources.[5,9] Hydrologically, South Africa has a high-risk climate with a low conversion of rainfall to run-off and very high year-to-year variability (e.g. a 10% change in rainfall can result in up to a 20–30% change in run-off).[19] In addition, run-off response to rainfall is non-linear, with a larger proportion of rainfall being converted to run-off when a catchment is wetter, either because a region is in a high rainfall zone or because the soil water content is high as a result of previous rainfall.[5]

Projected impacts of climate change on hydrological responses have been determined using the Agricultural Catchments Research Unit's (ACRU) agrohydrological modelling system.[5] These impacts were determined using output from one to five GCMs, empirically downscaled to climate station level and adjusted to the 5838 quinary catchments[5]; a quinary is a statistically defined region of uniform topography falling within a quaternary catchment. Quaternary catchments are the principal water management units and have been defined according to a standardised run-off measure per unit area, i.e. drier regions have larger quaternary catchments than areas with higher run-off.[21] Quinary catchments are considered to be physiographically more homogenous than quaternaries and relatively homogeneous hydrologically.[5] Climate values are used as input to the ACRU model based on daily values of rainfall, maximum and minimum temperatures, solar radiation and a reference potential evaporation available for three 20-year climate time slices: the present (1971–1990), the intermediate future (IF: 2046–2065) and the more distant future (MDF: 2081–2100).[5] Predicted hydrological responses include changes in run-off patterns, in the frequency and intensity of extreme events and in groundwater recharge rates.

Table 2: Global climate change drivers and ecological consequences of global climate change in freshwater ecosystems.

Ecological consequence	
Water quantity	Change in run-off patterns (flow variability, duration, timing)
	Increase in frequency and intensity of extreme events (droughts and floods)
	Change in groundwater recharge rate
Water quality	Increase in water temperature
	Increase in organic matter decomposition
	Decrease in the concentration of dissolved oxygen
	Changes in nutrient cycles (and carbon cycling) and loads
	Increase in algal growth and change in eutrophic condition*
	Increase in the incidence of cyanotoxins*
	Increase in sedimentation and turbidity
	Mobilisation of adsorbed pollutants such as metals and phosphorus from the riverbed
	Increase in transport of dissolved pollutants such as pesticides and pathogens
	Increased salinisation in semi-arid and arid areas (shallow groundwater and surface water)
Physical habitat	Change in channel geomorphology
	Decrease in longitudinal and lateral connectivity
	Change or reduction in aquatic habitat
Biological	Change in aquatic biodiversity
	Change in phenology and life-history patterns
	Change in communities
	Change in species distribution and range
	Extinction of vulnerable species
	Increase in the number and spread of invasive and pest species
	Increase in waterborne and vector-borne diseases

**Consequence is also biological.*

Run-off patterns (flow variability, duration and timing)

Much of South Africa is projected to have increases in annual streamflows by 20% to 30%, regardless of whether it is a year of median flows or a year with the 1:10 year low or high flows.[5] The exception is the southwestern Cape which will have reduced streamflows especially in the wet years. Flow reductions are projected to occur, especially in the 35 years making up the time period between the IF and the MDF (i.e. 2081–2100). Interannual variability is projected to increase (20–30%) in most of the country, with the exception of the southwestern Cape where variability is projected to decrease. Whilst no specific studies exist for South African rivers, and given what is known about the hydroclimatic factors governing run-off, it seems likely that a reduction in streamflow would result in a change in perenniality (rivers) or permanence of inundation (wetlands), with perennial rivers becoming non-perennial and permanent wetlands becoming seasonal or temporary. Further, rivers that are mainly flowing because of surface run-off would be more susceptible to changes in climate compared to rivers with high baseflow indices which would be groundwater fed.

Frequency and intensity of extreme events (droughts and floods)

Researchers have projected that most parts of South Africa are likely to experience reduced frequency, duration and intensity of droughts, with the exception being the west coast and northwest, which will exhibit marked increases in annual droughts.[5] In these regions, an increase in the frequency of extreme events, including drought, is likely as a result of the predicted poleward retreat of rain-bearing frontal systems. Floods and stormflow, i.e. water generated from a specific rainfall event, are projected to increase across South Africa, particularly in the central west where both magnitude and variability of stormflow will increase.[5] An increase in flood frequency is likely to markedly alter many river ecosystems, although the extent to which this happens will depend on deviation from background conditions (e.g. degree of canalisation and catchment hardening) and on how humans respond to the increased flooding, for example through non-structural flood management.[22]

Groundwater recharge rate

Changes in the amplitude, frequency and timing of extreme events may affect groundwater recharge. Projected changes in recharge into groundwater stores are different for median, dry and wet years.[5] Under median conditions into the IF, recharge is projected to increase in a wide band stretching from northeast to southwest (covering over 80% of South Africa), with a small area in the extreme southwest displaying decreases in discharge.[5] In dry year conditions, a northeast to southwest line divides the country, with projected decreases north of the line and increases south of the line. In wet year conditions, a general decrease is projected for the west coast and an increase is projected for 95% of the country.[5] Groundwater is critical for maintenance of 'low flows' and aquatic habitats during the drier periods.

Water quality

Higher water temperatures, increased precipitation intensity, and longer periods of low flows are projected to exacerbate many forms of water pollution, including sediments, nutrients, dissolved organic carbon, pathogens, pesticides, salt and thermal pollution.[1] The quality of water in many South African rivers and wetlands is already widely compromised and climatic drivers therefore act as additional stresses on these ecosystems. Water quality changes, including water temperature, affect the solubility of oxygen and other gases, chemical reaction rates and toxicity, and microbial activity.[23,24] A reduction in the concentration of dissolved oxygen, particularly under the combined effects of high temperature and low flows, is particularly deleterious to aquatic organisms.[23] The effects of water quality variables on aquatic ecosystems have been widely documented[23], with specific studies focusing on particular variables, including water temperature[24]. Recent studies on the link between air and water temperature[25] and the effect of elevated water temperature on aquatic organisms have included experimental laboratory work[26,27] which together with field-based studies[25,28], has allowed for the development of tools for assessing water temperature in river ecosystems[25-30] and scenario prediction for elevated temperatures[31]. Estimating the likely increase in water temperature from predicted changes in air temperature is, however, complex and dependent on insulators and buffers such as solar radiation, groundwater input and shading. One of the key issues is how lapse rates (change in water temperature degrees with every 100 m altitude) will change.

Other water quality variables likely to increase in response to more intense rainfall events (Table 2) include turbidity and nutrients, with sediment washed in from the catchment or, in the case of nutrients, mobilised from the riverbed (e.g. phosphorus). A review paper on the potential impacts of climate change on surface water quality through the lens of UK surface water provides an excellent overview of key issues discussed in this section.[32] Average phosphorus concentration (as orthophosphate) and chemical oxygen demand values indicate that South Africa's freshwater resources are already excessively enriched and are considered to be moderately to highly eutrophic.[32] Further changes in nutrient loads and nutrient cycles (and carbon cycling) may result in increased algal growth, changes in eutrophic condition, as well as increased incidences of cyanotoxins, which affect human health negatively. Most eutrophic rivers and reservoirs in South Africa have as the dominant phytoplankton genera the cyanobacteria *Microcystis* sp. and *Anabaena* sp.[33,34] Other adsorbed pollutants such as metals may also be mobilised, together with increased transport of dissolved pollutants such as pesticides and pathogens. In semi-arid and arid areas salinity may increase as a result of increased evaporation from shallow ground and surface water. Several river systems already have high levels of salinity, for example, the Berg River in the Western Cape.[35] In comparison, salinity levels in the headwaters of the Murray–Darling Basin in Australia are expected to increase by 13–19% by 2050,[36] a situation that may be mimicked in some southern African regions, indicating that under predicted climate change for this region, salinisation would be exacerbated. The synergistic and antagonistic interactions of several water quality variables make it especially difficult to predict the likely consequences of climate change on receiving water bodies, suffice it to say that these consequences are likely to be significant given the levels of stress already imposed on these systems.

Physical habitat

Changes in the amount, seasonal distribution and intensity of rainfall may affect channel geomorphology, longitudinal and lateral connectivity, and aquatic habitat, through changes in run-off. Likely consequences of changes in flow on the geomorphology of river systems depend on the direction of change with increased discharge (e.g. in the eastern region) potentially resulting in channel enlargement and incision, greater channel instability and sinuosity, and increased bank erosion, while decreased discharge (e.g. in the western region) may result in channel shrinkage, greater channel stability, vegetation encroachment, and sedimentation in side channels.[37] Sensitive systems such as fine-grained alluvial streams are likely to be more affected than bedrock channels and armoured stream beds.[37] While local geomorphological studies have not focused specifically on climate change, observations elsewhere are likely to be applicable, with many effects similar to those already observed following the construction of impoundments and abstraction of water.[38]

Loss of longitudinal and lateral connectivity can lead to isolation of populations, failed recruitment and local extinction; the maintenance of natural connectivity patterns is thus essential to the viability of populations of many riverine species and for maintaining instream integrity.[39] Connectivity is typically reduced through flow regulation by dams and is often compounded by other structural modifications such as channelisation.[40] With respect to fish, researchers suggest that functional habitat units (FHU, i.e. 'natural partitions within the river system that contain all the necessary habitat elements to support all life-history stages'[41]) in South African rivers need to be identified, mapped and their connectivities to other FHUs identified and efforts made to protect them in conservation and water allocation strategies.[41]

Flow is a major determinant of physical habitat in streams, which in turn is a major determinant of biotic composition.[39] In South Africa, research has focused on the flow-related dynamics of hydraulic biotopes.[42] A study of four perennial upper rivers of the southwestern Cape, South Africa, revealed that natural and, particularly, manipulated low flows, resulted in consistent, marked declines in physical habitat availability for aquatic invertebrates, with increased habitat fragmentation, hydraulic biotope isolation and dominance by low-velocity shallow biotopes.[43] Invertebrate responses to low-flow disturbances, in contrast, were often river specific, subtle or inconsistent, and required multi-scale lines of evidence for their elucidation.[43] Regions predicted to have decreased flow will therefore likely exhibit increased fragmentation of existing instream and riparian habitats, and resultant loss of habitat and connectivity.

Biological

Thermal and hydrological regimes are master variables driving river ecosystems.[44] Temperature is a primary climate change driver, while flow has been shown to change substantially in response to changes in rainfall patterns.[5] It is therefore likely that climate change will affect aquatic assemblages with biological consequences of climate change acting at several levels, including that of the individual and community. Susceptibility of aquatic organisms to climate change is likely to vary between species and will in part depend on their biological traits. Those species with specialised habitat and/or microhabitat requirements, narrow environmental tolerances or thresholds that are likely to be exceeded at any stage in the life cycle, dependence on specific environmental triggers, dependence on interspecific interactions, and poor ability to disperse to or colonise a new or more suitable area, are likely to be more susceptible.[45] Potential biological consequences of climate change (Table 2) include changes in aquatic biodiversity, changes in individual life-history patterns, changes in communities, changes in species distribution and range, extinction of vulnerable species, increase in the number and spread of invasive and pest species, and an increase in waterborne and vector-borne diseases.

Aquatic biodiversity

Biodiversity in freshwater ecosystems shows substantial impacts from land use, biotic exchange and climate.[46] In the USA, for example, freshwater biodiversity is declining at far greater rates than most affected terrestrial ecosystems.[47] Threats to global freshwater biodiversity can be grouped under five interacting categories: (1) overexploitation, (2) water pollution, (3) flow modification, (4) destruction or degradation of habitat and (5) invasion by exotic species.[48] The inland waters of southern Africa support a high diversity of aquatic species with high levels of endemism, many of which provide direct (e.g. fisheries) and indirect (e.g. water purification) benefits to people.[49] The level of threat to species in South Africa is higher than in other African countries (for which it is about 7%) and 57% of river and 75% of wetland ecosystems are highly threatened,[49-51] while tributaries are in a better condition than main rivers. Researchers have highlighted the substantial threats to riverine biodiversity in South Africa and challenges faced in conserving species and habitats.[52] It has been noted that for every 10% of altered catchment land use, a correlative 6% loss in freshwater biodiversity occurs.[53] The amount of natural vegetation at catchment scale has been found to be a good predictor of river habitat integrity[54], which, in agricultural catchments declines as agriculture exceeds 30–50%[55]. Further, small dams within a catchment impact on water quality and quantity and hence biodiversity.

These existing anthropogenic threats are likely to be further exacerbated by predicted global climate change, leading to greater loss of aquatic biodiversity. For example, dams create discontinuities and downstream water temperature changes that in turn may alter chemical processes that drive energy flows in rivers. This in turn could differentially affect competitive abilities of different species and functional feeding groups, changing the composition of aquatic communities. Potential also exists for reduction or changes to genetic diversity. We see two possible reasons driving this reduction in genetic diversity: reduced flows of individuals within metapopulations because of decreased catchment connectivity, and increased homogenisation of communities because of environmental conditions favouring generalist or opportunist species.[56]

Phenology and life-history patterns

Individual species have life-history parameters that allow them to successfully inhabit aquatic ecosystems; changes in abiotic parameters such as temperature and flow may affect the growth, reproduction and survival of instream species. Data from South Africa, where detailed life-history data has been collected, are limited.[57,58] However, a recent study has provided the first detailed information on the responses of aquatic insect life histories to water temperature and flow, and data on egg development, nymphal growth and oviposition.[59] The study showed that water temperature regimes in rivers of the Western Cape have a measurable impact on aquatic macroinvertebrate life histories. Through a combination of field surveys and laboratory experiments, it was shown that life histories of three target macroinvertebrate species showed differing degrees of flexibility in life-history responses – from subtle changes in the timing of emergence and egg hatching to more extreme differences involving the production of additional generations within a year given differing environmental conditions.[25]

Several studies have examined the reproductive biology of fishes in South Africa and have shown that temperature is an important factor triggering spawning, with temperatures of 18–19 °C triggering spawning of several of South Africa's indigenous fish species.[24] Gonadal development and spawning may also be triggered by water level or flooding. In the Western Cape, the endangered Clanwilliam sawfin, *Barbus serra*, depends on certain key components of the annual flow and temperature regime.[41] Sawfin spawned over a period of about 100 days between November and January, and peak recruitment events were associated with a temperature of ~19 °C and continuously rising temperatures over 7 days or more.[41]

Communities

Aquatic species have had to adapt to variable flows and cope with daily and seasonal ranges of water temperatures.[60] Current community patterns are likely to be in dynamic equilibrium with such abiotic regimes. Consequently, any changes to these regimes in response to climate change would differentially affect different species, which would ultimately be reflected in species patterns. A combination of temperature and the onset and cessation of floods was shown to influence the seasonal pattern of change in an invertebrate community assemblage in a Western Cape river.[58] Under future climate change scenarios, one might therefore anticipate shifts in communities in response to elevated temperatures and changes in frequency, duration and intensity of rainfall events. Certain species are likely to be more or less resilient to changes associated with climate change, with certain species increasing in abundance (winners), while others decrease in abundance (losers). This difference will result in a shift in community structure and possibly lead to a change in trophic status. Thermal tolerances of individual taxa,[26,27] and their ability to withstand changes in water temperatures, may ultimately translate into shifts evident at community levels. Montane stream assemblages are considered to be most vulnerable to climate change because their distribution is most responsive to climatic factors, and elevated sites are isolated from one another, which reduces the scope for altitudinal migration.[61] Changes in flow, particularly flood events, may also lead to changes in riparian vegetation such as reduction in cover and a loss or shift of species, with non-riparian species increasing in abundance as flow decreases. These changes in turn impact on water temperature regimes, particularly in smaller streams in upper reaches.

Species distribution and range

Various studies have reported shifts in distributional ranges of aquatic species[62] with effects being typically species specific, where cold-water organisms are generally negatively affected and warm-water organisms positively affected. Much of this research appears to relate to migratory fish species of economic importance (notably trout[63]) with very few studies on aquatic macroinvertebrates, and virtually no studies applicable to southern Africa. One such example is for range shifts in stoneflies (Plecoptera), in which logistic multiple regression models were developed to predict stonefly responses to temperature change.[64] These models showed mixed success for different species, although predictions broadly agreed with data that the species considered already showed uphill altitudinal shifts of 100–140 m over a 30-year period between 1977 and 2006.[64] Knowledge of species thermophily and rheophily have been used to predict distributional changes associated with climate change.[65] It was hypothesised that thermophobic (i.e. those that favour cool water) taxa and rheophilous (i.e. those that prefer fast water) taxa would have range contractions, being least able to cope with rising temperatures and declines in stream flow, and, conversely, thermophilic taxa (i.e. those that favour warm water) and rheophobous taxa (i.e. those that prefer still water) would expand their ranges, being best placed to take advantage of warmer and more sluggish streams.[65] The study concluded that:

> *Trait analysis has potential for predicting which species will expand their ranges and which will contract, but it needs to be coupled with assessment of how the landscape provides each species with opportunities to track or avoid climate change. Improved quantification of climatically relevant traits and integration of trait analysis with species distribution modelling are likely to be beneficial.*[65]

In a southern African study, researchers demonstrated that a cold-water Western Cape stenotherm could experience a 30% habitat loss in response to a 2 °C increase in mean daily water temperatures.[31] However, predicting changes in species distribution and range is not an exact science, because different taxonomic groups may show different responses to climate change. This is partly a function of dispersal ability and strategy[62], but also because different species show different tolerances to thermal stress, and have different behavioural mechanisms to avoid thermal stress[14].

Extinction of vulnerable species

Freshwater aquatic ecosystems appear to have the highest proportion of species threatened with extinction by global climate change.[66] Recent studies have shown the disproportionate risk of extinctions in mountain ecosystems and, in particular, among endemic species, with rare and stenothermic species likely to become at least locally extinct.[67,68] For example, of the 27 currently recognised indigenous freshwater fish species in the Cape Floristic Region of South Africa, 24 (89%) are endemic to the region and 19 (70%, all endemics) are listed as threatened in the *IUCN Red List of Threatened Species*.[69] Temperature rises will be especially deleterious in high-altitude, fast-flowing streams in which cold stenotherms could lose their thermal refuges.[70] Similar risks exist for the mountainous regions of South Africa that have many of the Gondwanan species.[31] Identifying highly vulnerable species and understanding why they are vulnerable[71] is seen as critical to developing climate change adaptation strategies and reducing biodiversity loss in the coming decades.[72]

Invasive and pest species

Climate change and invasive aquatic species are considered to be two of the most pervasive aspects of global environmental change.[73] As climate change proceeds, aquatic systems may become more vulnerable to invasion[74], and the key climate change drivers – temperature and flow – are likely to determine the invasion and success of exotic and introduced species in rivers.[39,73] Given potential disaggregation in aquatic ecological communities resulting from likely concomitant changes in flow and water temperature regimes, community equilibria are likely to shift. This shift makes communities more vulnerable to invasion by alien species, particularly in species-poor systems where niche space is more open, and as a consequence of increased interbasin transfer schemes. Typically, alien species may out-compete indigenous species; similarly warm-water species may have an advantage over cold-water species as temperature increases. Changes in species patterns could also lead to development of indigenous pest species, as has happened with pest blackfly (Diptera: Simuliidae), which is a threat to livestock, in the Great Fish River (Eastern Cape Province).[75] Invasive aquatic species, including both plants and fish, are already a major threat in many parts of South Africa and one of the greatest threats to biodiversity in the Western Cape is the spread of invasive fish species.[76] Virtually no information is available on the thermal tolerance of indigenous fish species in South Africa, although tolerances are known for several alien species,[77] especially those of aquacultural importance.

Waterborne and vector-borne diseases

Rising temperatures, heavy rainfall and increased flooding are likely to increase the burden of infectious waterborne (e.g. microbial pathogens) and vector-borne (e.g. malaria, bilharzia) diseases, especially for vulnerable populations.[1,78] Heavy rainfall leading to flooding has been associated with increased risk of infection, particularly in developing countries, while temperature affects both the distribution of vectors such as mosquitoes and snails and the effectiveness of pathogen transmission through the vector.[78,79] The incubation period for malaria parasites within the mosquito is strongly temperature sensitive, such that temperature is a major determinant of malaria risk.[79] Malaria transmission in Africa is projected to increase by 16–28% in person-months of exposure by 2100 as a result of projected climate scenarios.[80] This projected increase is related to an increase in distribution (mainly altitudinal) and season length, and, in the Limpopo Province of South Africa, a substantial latitudinal extension.

Discussion

Global climate change is recognised as an additional, amplifying driver of system variability and cannot therefore be viewed in isolation from other stressors.[17,81] Many non-climatic drivers affect freshwater resources at a global scale and the quantity and quality of resources are influenced by, for example, land-use change, construction and management of reservoirs, pollutant emissions, and water and wastewater treatment.[2] South Africa is fortunate in having established widely recognised approaches for determining the 'ecological reserve' – a South African term used to describe what are globally referred to as environmental water requirements. However, there is widespread agreement among scientists that South Africa's aquatic ecosystems have significantly deteriorated since the revision of the *National Water Act (Act 36 0f 1998)*.[82] A key reason given for this deterioration is the widespread failure to operationalise, monitor and enforce ecological reserves – a legislated framework for securing water quality and quantity for the environment.[82] Understanding the likely consequences of climate change for freshwater ecosystems is therefore of critical importance to the future well-being of the resource and society. Several guiding principles, or proactive response options, aimed at minimising the potential impact of climate change on freshwater ecosystems, were formulated during a workshop.[17] These guiding principles include those focused on water quantity and the maintenance of appropriate environmental flows, integration of global climate change into water quality management, conservation planning for freshwater biodiversity, the promotion of ecosystem resilience, and extending climate change science into policy and public discourse. The adoption of a proactive, 'no-regrets' policy with respect to climate change has been widely endorsed in South Africa and elsewhere[17]; such a policy calls for proactive management which includes actions such as restoration, land purchases, and measures that can be taken now to maintain or increase the resilience of rivers.[81] The alternative – reactive management – which involves responding to problems as they arise by repairing damage or mitigating ongoing impacts, has been shown to be inadequate and short-sighted and results in considerable ecological, social and economic consequences and costs in the longer term.[81]

Maintaining appropriate environmental flows

Flow is one of the master variables controlling river ecosystems[44] and it is recognised that a naturally variable flow regime, rather than a static minimum low flow, is required to sustain freshwater ecosystems.[39,83,84] South Africa has been at the forefront of environmental flow research and the DRIFT (Downstream Response to Imposed Flow Transformation) method has been widely applied.[85-87] DRIFT is a scenario-based approach that predicts the bio-physical and socio-economic impacts of proposed water-resource developments on rivers.[82] The maintenance of appropriate environmental flows is considered to be a critical aspect in promoting ecological integrity and reducing ecological consequences of global climate change.[88] In a global analysis of the potential effect of climate change on river basins, it was shown that rivers impacted by dams or with extensive development will require more management interventions to protect ecosystems and people than will catchments with free-flowing rivers.[89] Catchments that are modified have limited ability to absorb disturbances, such as changes in discharge. In contrast, healthy, free-flowing rivers respond to changes in land use and climate through dynamic movements and flow adjustments that buffer against impacts, and are thus more resilient.[89] The rate and magnitude of change relative to historical and recent thermal and flow regimes for each catchment will also determine the impacts of climate change on river ecosystems[81], and changes outside the natural range of flow or temperature variability may have drastic consequences for ecosystem structure and function depending on the rate of change in temperature or discharge relative to the adaptive capacity of species[90].

South Africa has 62 large free-flowing rivers, representing just 4% of South Africa's river length,[50] with the remaining rivers dammed. The approximately 600 large dams and more than 500 000 small dams[91] that regulate South African rivers significantly affect their discharge and hydrological regimes.[75,92-97] Dams, interbasin water transfers[98] and abstraction of water threaten the maintenance of appropriate environmental flows in our rivers. Worldwide management actions have been recommended for dammed river systems.[89] Consideration should be given to undertaking a review of the justification and viability of existing water infrastructure, including opportunities to re-engineer such infrastructure to incorporate better environmental and social performance measures. Use should be made of infrastructure management as an opportunity to retrofit dams to build ecological resilience, for example, retrofit outlet valves to allow environmental flows to be released and install fishways[99] to facilitate passage of fish – although in some instances this may be inadvisable (e.g. the Western Cape) as it would facilitate invasion of alien fish. In addition, an evaluation should be undertaken of the appropriateness of interbasin water transfers and vulnerability of donor and recipient riverine biota to climate change.

Integrating global climate change into water quality management

In recognising that climate change would be a further contributing factor to existing water quality problems, management options for reducing these effects need to be examined. Water quality issues in South Africa are a major cause for concern, with contributing sources including mines, sewage effluent discharges, industrial effluents, non-point source pollution from agricultural sources, acid atmospheric depositions, over-abstraction of groundwater, and excessive soil losses and sedimentation.[100,101] Water quality impacts could be ameliorated or decreased through application and implementation of the ecological reserve and Water Resources Classification processes, and identification of a dynamic baseline that incorporates climate change. The actual mechanism for achieving these objectives is through the determination of resource quality objectives (RQOs) per Water Management Area, which relate to the quality of water resources in terms of their quantity, quality, habitat and biota, as provided for in South Africa's *Water Act of 1998*. RQOs may be established for priority 'resource units' (i.e. river reaches identified as having value to society; for example, presence of a unique community of aquatic macroinvertebrates). Each priority resource unit will have associated indicators linked to numerical limits (which should also incorporate thresholds of potential concern that inform river managers of a problematic trend before the system state changes). These are defined based on a narrative vision (for example, that the water quality be suitable to maintain a Gondwanan relict macroinvertebrate community of conservation importance), and provide the yardsticks from which to develop a monitoring programme. RQOs are determined based on a seven-step process,[102] and are gazetted together with their associated classification and ecological reserve. In theory, RQOs should be updated every five years. While there is no explicit provision for integrating global climate change into water quality management, the five-yearly revisions make this a possibility. Thus, in practice, an RQO could be set for water temperatures, with an indicator chosen that reflects changes in water temperatures, such as a thermally sensitive aquatic macroinvertebrate species. This species could be monitored over the succeeding five years, until the time to review the RQOs applies. Should it be found that the numerical limits were repeatedly exceeded, i.e. that a downward trend was observed, then questions should be raised in connection with how to enhance system resilience. Potentially, increasing river connectivity increases the adaptive capacity of the river in question by better enabling river biota to undergo range shifts to avoid habitat stress.

Conservation planning for freshwater biodiversity

The principles of conservation planning[103] can be applied to identify biodiversity threats. In South Africa, recent approaches to systematic conservation planning for freshwater biodiversity have shifted from 'representation' to 'representation and persistence'.[104,105] These approaches present four key principles to consider when planning for the persistence of freshwater biodiversity: (1) selecting ecosystems of high ecological integrity, (2) incorporating connectivity, (3) incorporating areas important to population persistence and (4) identifying additional natural processes that can be mapped.[104,105] A critical assumption in conservation planning is that a conservation target (such as percentage species area) is the minimum area needed to ensure representivity and persistence. In South African freshwater conservation planning, 20% targets are typically used for both species occurrences and freshwater types.[106] However, conserving river systems continues to present challenges because a river reach cannot be assumed to be protected by virtue of its being within a protected area, as it is affected by cumulative upstream influences as well as downstream connections.

Recently, biodiversity conservation has also shifted from a species to a landscape approach,[107] which has resulted in a number of implications for conservation planning. The first is a move away from individual species targets (although these still play a role in conservation plans) and a move towards river types as surrogates for freshwater biotic communities. The second is the need to recognise and incorporate differential rates of turnover of species and communities with downstream distance, with implications for setting higher targets in upstream areas where turnover rates are higher.[108]

Planning for climate change is, however, in its infancy. Global climate change causes changes in the spatial configuration of habitats, and static conservation planning approaches are not adequate to deal with such changing environmental gradients.[70] The question arises as to whether protected areas are an effective conservation strategy in the face of climate change. Ideally, reserves should be planned around biomes which are expected to have reduced representation. In the absence of data, this planning requires either individual species models that may be simplistic in complex community landscapes, or species models that inevitably include uncertainties because of difficulties in accounting for stochastic events, synergies and interactions between multiple species. For reserve design to be resilient, corridors and connectivity are required.[109] Connectivity must be planned in spatial and temporal dimensions, to counter disrupted hydrological and thermal time-series signatures (changes in frequency, duration, magnitude and timing of flow or thermal events) resulting from, for example, dam construction, water abstractions and land-use changes.[110,111] Connectivity in stream channels and riparian corridors becomes critical as species distributions change relative to protected area boundaries. Restoring freshwater ecosystem connectivity (e.g. with fish passages) could be a key mechanism to enable freshwater biota to move to new areas. However, connectivity is not always a panacea; it sometimes is a double-edged sword because of the spread of aliens. Careful assessment of risks and advantages in establishing corridors is necessary.[109]

Connectivity includes maintaining flow signatures (the magnitude, timing, frequency and duration of flow events), which are linked to life-history cues, and may be lost because of increased construction of dams and disrupted hydrological and thermal regimes.[110,111] It has been recommended that the integration of environmental flow assessment and systematic conservation planning would be mutually beneficial and provide an ideal platform for integrated water resource management.[112] Changes to the flow regime under various climate change scenarios[5] may be used in environmental flow assessment to examine the likely impacts of development and conservation within a changing climate. There will be increased difficulty in meeting sufficient flows to maintain the character of all systems, leading to difficult dilemmas in choosing one system over another.[109]

There is also growing consensus amongst freshwater scientists that water temperatures should be incorporated into environmental flow guidelines.[113] Increases in water temperatures have more severe consequences for the higher-altitude, stenothermic cold-water species, whose distributions are expected to shrink as water temperatures increase. These consequences should be of particular concern to conservation planners as the upper zones of river systems are typically where species turnover, ecotones and taxonomic diversity are highest. It therefore becomes imperative to maintain river connectivity in these upper reaches to facilitate system adaptation and species range shifts.

Promoting ecosystem resilience

Resilience is the capacity of reduced or impacted populations or communities to recover after a disturbance.[114] The resilience approach is founded on the understanding that the natural state of a system is one of change rather than one of equilibrium, even though the magnitude and type of change is not always predictable.[115] It is the ecological concept that reflects the capacity of natural systems to recover from environmental change and thus persist into the future. Systems that are more resilient are better able to adapt to changes in climate[116] and ecosystem resilience is seen as key to reducing the consequences of global climate change on aquatic ecosystems. Stressed ecosystems have lower resilience. To enhance the resilience of freshwater ecosystems and minimise impacts, specific, proactive restoration, rehabilitation, and management actions are recommended.[89] Ways to promote ecosystem resilience include, for example, maintaining environmental flows,[117] restoring habitat and connectivity, and recognising the link between catchment condition and freshwater ecosystem health. As mentioned, free-flowing rivers in largely undeveloped catchments are expected to be resilient in the face of climate change, while the need for restoration/rehabilitation and proactive management may be quite high in dammed and developed river systems.[89] The resilience of a catchment may also, for example, be influenced by the intactness of its tributaries, which often act as refuges for aquatic biota.[118]

Enhancing resilience of freshwater ecosystems in South Africa requires the application and implementation of the Resource Directed Measures, which consist of three main elements: classification and the reserve and resource quality objectives.[17,82] It is therefore very important that the water resources status and the ecological flow requirements of these resources be determined for an effective national scale allocation process (National Water Resources Strategy) and resource protection. Rehabilitation of riparian zones and landscapes are considered important.[17] Global climate change increases the urgency to institute the freshwater conservation measures that are already desirable, to increase resilience.

Extending climate change science into policy and public discourse

Ultimately, the vulnerability of freshwater systems to climate change depends on national water management and the desire and ability to instigate management options that have the potential to lessen its consequences.[1] Governance and integration of plans and policies in a holistic manner that incorporates all levels of governance, especially to avoid conflicts between climate, energy and water policies, is recommended.[17] Engaging top level leadership is important, with potential economic savings linked to adaptation more likely to receive reaction and support from government, whose decisions are often not driven by issues such as biodiversity and conservation.[17] Engagement at a local scale, which in reality is the scale at which climate change is going to be felt, is as important as institutional support.

Conclusions

Proactive assessment and monitoring are key as these would allow for the identification of ecological triggers and thresholds, including thresholds of vulnerability, which may be used to monitor and inform decisions, as well to improve the ability to forecast based on this knowledge. Identification of ecological reference sites for long-term monitoring and routine monitoring of these and other impacted sites within a framework of established biomonitoring programmes are critical. This monitoring would facilitate detection of change, both in response to non-climate as well as climate change induced effects, although the ability of the various monitoring tools to facilitate this may still need to be validated. One of the key challenges facing freshwater ecologists is to develop a suite of tools for detecting the impacts of climate change in complex natural systems that can be applied across multiple spatio-temporal scales and levels of organisation.[12] Integration of long-term, empirical survey data with models and manipulative experiments will facilitate the development of mechanistic, and hence predictive, understanding of responses to future change.[12]

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Authors' contributions

H.D. is the project leader and researcher and wrote the manuscript; and N.R-M. is a researcher on the project and contributed to the manuscript.

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