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Review Article

A Review of the Drawdown Zone in African Reservoirs: Current Knowledge, Understudied Areas and Recommendations for Future Research

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Drawdown zones in African freshwater reservoirs are pivotal for ecological, economic, religious, and cultural reasons, as well as in carbon dioxide emission dynamics. Hence, there is a need to elucidate their ecology, opportunities for their utilisation, and the various threats to their integrity. Littoral zones of freshwater reservoirs harbour diverse ecological communities and serve vital ecosystem functions, which are largely regulated by water drawdowns. Severe alteration of natural and artificial drawdowns exposes previously submerged areas in reservoirs. These exposed zones, termed 'drawdown zones,' although short-lived, serve vital ecological functions in reservoirs. Nonetheless, studies on the ecology and ecosystem functions of drawdown zones are few and fragmented in African reservoirs. This review aimed to (i) examine and provide critical insights into recent literature on the ecology of drawdown zones in African reservoirs, (ii) assess the delineation of drawdown and overlapping littoral zones and their ecosystem functions in reservoirs, (iii) synthesise research on human utilisation of drawdown zones in African reservoirs, and (iv) evaluate current knowledge and understudied aspects of drawdown zones in African reservoirs. Scoping surveys of literature on the ecology and utility of drawdown zones in African reservoirs were used for data collection. Examined literature indicated that aquatic ecologists delineated drawdown zones as transitional zones interlinking terrestrial and aquatic ecosystems. However, there is ambiguity regarding an acceptable definition and delineation of drawdown zones within the littoral zones of reservoirs. This leads to conflation of the ecology and ecosystem functions of drawdown and littoral zones, which does little to disentangle the influence of autochthonous and allochthonous inputs on drawdown zone productivity and its contribution to overall reservoir productivity. Humans utilise the drawdown zones for socioeconomic purposes, yet diminish their ecosystem services provision and value. This review highlights that a new paradigm on redefining and delineating the shoreline zone into the terrestrial, drawdown, overlap, and littoral zones is imperative for understanding shoreline ecology and the ecological and

socioeconomic roles of drawdown zones, an area that is currently missing in studies of African reservoirs.

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1. Introduction

Lake drawdowns occur naturally in response to moderate and severe climatic and hydrological changes (Abrahams, 2006) and in response to artificial withdrawal by humans for several purposes such as agriculture and hydroelectricity generation (Zohary and Ostrovsky, 2011). Natural and artificial drawdowns are necessary for ecological functions (Wantzen et al., 2008) and biodiversity conservation, although a stable lake can also function perfectly well (Semlitsch and Bodie, 2003). An exponential increase in human population has led to high water drawdown cycles in reservoirs (Hellsten et al., 2001, Strayer and Findlay, 2010). The short-term drawdown cycles in reservoirs impact nutrient dynamics, ecological integrity, productivity, and fauna and flora diversity (Bond et al., 2008). Most African reservoirs and rivers alike are located in the tropics and arid and semi-arid areas (see Appendix), implying that intermittent drawdowns are extensive and highly variable over temporal scales, enforcing sharp seasonal limnological conditions replete with adaptable organisms (White et al., 2008). Drawdowns are more pronounced in shallow lakes and determine overall diversity, the condition of shoreline physical habitat, littoral communities, and animal habitats (Van Oort et al., 2015).

Although drawdowns are critical for ecosystem structure and function, hydrologic drawdowns that exceed natural variability are detrimental to reservoir ecosystems as they alter shoreline geomorphology and modify some morphometric parameters, e.g., shoreline irregularity (Winfield, 2004; Peters and Lodge, 2009; Strayer and Findlay, 2010). Modification of shoreline habitats alters ecosystem functions and may lead to a loss of biodiversity in reservoirs (Stendera et al., 2012). Nonetheless, altered drawdown regimes that include frequent and extreme fluctuations and some periods of relative water level stabilization create novel environments that may attract adaptive organisms (Boschilia et al., 2012). Several studies related to both the negative and positive effects of drawdowns on reservoir integrity do not agree on the exact mechanisms of adaptation and detriment thresholds associated with a drawdown in a specific reservoir (Coops et al., 2003; Abrahams, 2006; Leira and Cantonati, 2008; Strayer and Findlay, 2010; Carmignani and Roy, 2017). This observation is even more complex to disentangle for tropical reservoirs, e.g., the Swakoppoort and Von Bach Dams in Namibia, located in arid and semi-arid areas, e.g., deserts, where the association between rainfall levels, drawdowns, system response, resilience, and productivity is unpredictable (Sirunda et al., 2021).

Littoral zones are hotspots for biodiversity, ecological processes, and human activity (Abrahams, 2006). The land-water interfaces in reservoirs promote the exchange of water, nutrients, and energy and provide habitats for organisms (Hofmann et al., 2008; Yuan et al., 2015). What this implies is that extreme drawdown beyond normal thresholds will reduce nearshore habitat complexity, modify biodiversity, and affect nutrient and energy exchange processes (Carmignani and Roy, 2017). The crucial aspect is that littoral habitat complexity tends to be diminished where drawdown has exposed previously inundated littoral habitat features, including outcropping trees and vegetation, snags, overhanging vegetation, and aquatic macrophytes. Carmignani and Roy (2017) indicated that near-shore terrestrial vegetation cover and complexity are typically low where increased drawdowns have increased the length of the exposed zones in reservoirs.

Previously submerged or currently exposed terrestrial points in the shoreline zones defined as littoral, eulittoral, or drawdown zones (Abrahams, 2006; 2008) serve vital ecological functions in reservoirs through ecosystem services such as nutrient filtration, exchange, and recycling (Furey et al., 2006), sediment aeration (Luken and Bezold, 2000), groundwater exchange, and spawning habitats for aquatic biota (Wantzen et al., 2008). Recent papers have focused on drawdowns and their effects on fisheries productivity in reservoirs (Kolding and Van Zwieten, 2012), with a few describing in detail the ecosystem functions of the drawdown zones with a bias towards the northern hemisphere, i.e., Europe and America (Abrahams, 2008; Strayer and Findlay, 2010; Carmignani and Roy, 2017). Inasmuch as the drawdown zones are exploited for various reasons in inland freshwater systems in Africa, there is not much knowledge and literature on some ecological, economic, religious, and cultural aspects associated with the zones. Hence, there is a need to elucidate their ecology, opportunities for their utilisation, and the various threats to their integrity using selected case studies where literature exists. In fact, a need, therefore, arises for a current review of the functions of the drawdown zones in African reservoirs, where there is a dearth of relevant literature.

This review provides insights into recent literature on drawdown zones in African reservoirs from an ecological perspective, and it describes drawdown and littoral shoreline overlapping zones and their ecosystem functions. It further reviews the utilisation of the drawdown zones by humans and outlines current knowledge and understudied aspects of drawdown zones in African reservoirs, with recommendations on pertinent areas for future research. This review aimed to (i) examine and provide critical insights into recent literature on the ecology of drawdown zones in African reservoirs, (ii) assess the delineation of drawdown and overlapping littoral zones and their ecosystem functions in reservoirs, (iii) synthesise research on human utilisation of drawdown zones in African reservoirs, and (iv) evaluate current knowledge and understudied aspects of drawdown zones in African reservoirs.

2. Materials and Methods

The research used a scoping review method following the four stages in the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flow diagram of: i) Identification of articles, ii) Screening of articles for review, iii) Eligibility using the inclusion and exclusion criteria for studies, and iv) Finalisation of the list of eligible or included studies. The scoping review method is a synthesis-based approach to build new knowledge on the drawdown zones in African reservoirs from rigorous analysis and examination of existing literature. The research started by formulating the question: What is the state of knowledge on the drawdown zone in African reservoirs? Afterwards, a protocol was generated, and a logical and systematic selection of relevant information, critical appraisal of results, data extraction, and contextual synthesis was done. Lastly, the findings were disseminated. Each step of the process is summarised below in Figure 1.

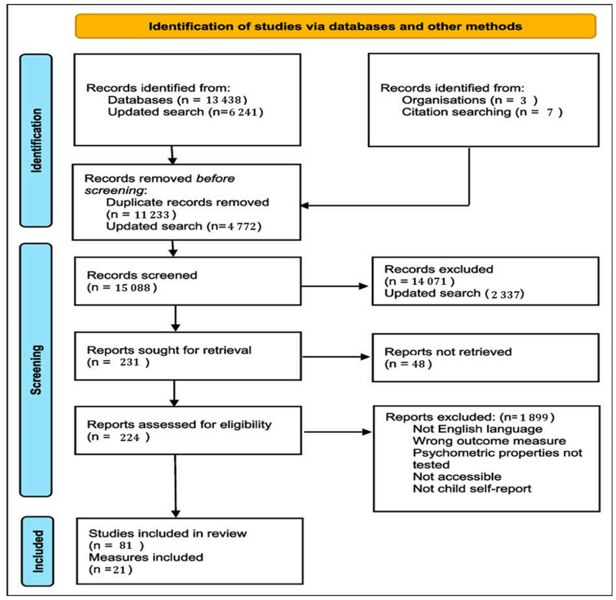

Figure 1. PRISMA flow diagram for assessing drawdown zones in inland African reservoirs.

2.1. Defining the search strategy and pre-document selection

After situating the study within the formulated main research question, the first exploratory search was conducted in Google Scholar, Scopus, Bing, and GiveWater, as well as the Boolean search engine, in order to combine the words AND, NOT, OR, and the commonly used ISI Web of Knowledge (ISI WoK) databases with no historical cut-off dates. This study explicitly searched for studies focusing on littoral zones, shorelines, drawdowns, drawdown zones, limnology, aquatic ecology, African reservoirs, lakes, and dams, with further searches for water research, human activity, and fisheries in all coupled (using AND, NOT, OR) subgroups comprising: “limnology-fisheries”, “water resources conservation-reservoirs”, “drawdowns-ecology”, “aquatic ecology-shorelines”, “aquatic resources-drawdowns”, “drawdown zones-limnology”, “drawdowns-lakes”, “littoral shorelines-African dams”, “littoral shorelines-African lakes”, “reservoir-African fisheries”, “human activity-African lakes”, and “littoral zones-African lakes”. However, some of the coupled terms, e.g., “water resources-African lakes”, “water resources-African dams”, “human activity-African lakes/dam/reservoirs”, and “water resources conservation-fisheries”, produced a lot of background noise and conjoined other non-relevant information for the study, which was subsequently removed from the analysis. In essence, there were no

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additional terms that related to drawdown zones in African reservoirs, lakes, or dams. The final search terms used were as follows: (((African reservoirs/lakes/dams, littoral zones, shoreline zones, drawdown zones, limnology, drawdowns, AND ("drawdown zones in African lakes/reservoirs/dams*"))).

2.1.1. Document selection

For item/document selection, the keyword search methods in the same search engines above were used, limited to the title, abstract, and keywords. From an initial list of 13,438 articles, the abstracts were screened for relevant items that could be classified as or mentioned drawdowns, drawdown zones, or littoral shorelines in African lakes/reservoirs/dams (Figure 1). The rationale was to screen the data set to manageable and relevant sizes. After thorough screening, a total of 81 items were used to reflect the breadth of the context citing drawdown zones in African reservoirs. An article was included if it met the following criteria: (a) It was published in a reputable journal, international organisation technical report, or a book; (b) relevant conference proceedings on the limnology of African lakes/dams/reservoirs; and (c) credible limnological reports in citable technical and scientific reports of reputable organisations.

3. Results and discussion

3.1. Definition and demarcation of drawdown zones in reservoirs

Extreme drawdowns in reservoirs, especially during drought years, the dry season, or in periods of excessive water abstraction, expose previously submerged littoral zones (Abrahams, 2006; 2008). This causes a directional shift from an aquatic habitat to a terrestrial or semi-terrestrial habitat in the littoral zone (Wantzen et al., 2008; Chen et al., 2009). The exposed reservoir area, termed the drawdown zone or eulittoral zone (Abrahams, 2006), is an ephemeral portion of the littoral zone (Strayer and Findlay, 2010). Drawdown zones serve various functional and integral roles, including nutrient exchange, ephemeral habitat and spawning refugia, and nutrient filtration (Abrahams, 2008; White et al., 2008; 2010). In some flora-, fauna-, and nutrient-depauperate lakes, drawdown zones serve as nutrient reflux zones that stimulate primary and secondary production (Abrahams, 2008). Despite their ecological significance, the actual contribution to the productivity of reservoirs by the drawdown zones has been overlooked in most limnological studies in inland African reservoirs (Utete et al., 2017). This is possibly due to the complexity of their demarcation and overlap with the moist littoral zone, which complicates actual measurements and quantification of the ecological contribution of the zone (Abrahams, 2006; 2008; Kolding and Van Zwieten, 2012).

Repeated drawdowns create pedestals or terraces in shallow and even in some relatively deeper reservoirs (Abrahams, 2006; Utete and Tsamba, 2016). These terraces, (shown in Figures 2 and 3) indicate the disjuncture of the last flooding level with the adjacent littoral upland and are termed littoral/shoreline contours or pedestals (Abrahams, 2008). Examination of the literature indicates that littoral pedestals are taken as part of the shoreline or littoral zone when submerged in reservoirs (Abrahams, 2008). The question is, what is the definition of the space between the exposed pedestals and the edge of the water? Or the name of the space between the pedestals (in between) and the start of the adjacent terrestrial zone? Further, a review of the literature indicated that most authors, e.g., Antenucci et al. (2003), Abrahams (2008), rightly pointed out that the pedestals or shoreline 'terraces,' as they called them, serve various ecological roles, more significantly as micro barriers to the upward and downward migration of benthic invertebrates as well as aquatic macrophytes when reservoir levels rise and fall (Abrahams, 2008). In reservoirs with pedestals or 'shoreline terraces,' benthic invertebrates (e.g., molluscs, amphibians, and crustaceans) have three choices: a.) migrate back into the water if they cannot climb up the pedestal, b.) adapt their locomotive systems to fossorial systems for digging and climbing up the vertical terraces of the littoral pedestals, and c.) synchronise their migration with upwelling in water levels in reservoirs. As such, shoreline terraces are temporary spawning habitats and dormancy, and even evolutionary sites for some organisms, such that drawdown cycles support flora and fauna in African reservoirs (Skarpe, 1997). However, for all their limnological significance, the ecology of littoral pedestals or terraces and the drawdown zones is scarcely known, especially for shallow and even deeper reservoirs in Sub-Saharan African countries (Taylor, 1989; Skarpe, 1997; Furey et al., 2006; Utete and Tsamba, 2016).

The key question remains of defining the drawdown zone as a part of the littoral shoreline zone. For this review, Figure 4 can be an illustrative definition of the physical aspects of the drawdown zone with no ecological connotations to the definition (Monteith et al., 2006). For a working definition, this study defines a drawdown zone as a heterogeneous zone in between the terrestrial and littoral zones, characterised by the formation of new habitats and unique microhabitats, with high dissipation of wave energy and mixed sediment characteristics and nutrient composition, and a dispersal and migration corridor supporting specialised and, in some cases, economically valuable hydrobionts. The drawdown zone includes and, in fact, overlaps with the littoral zone (Furey et al., 2006; Abrahams, 2006; 2008; Utete and Tsamba, 2016) as illustrated in Figure 4. The terrestrial zone represents the dry, soil-dominated section, normally in the adjacent catchment, whereas the drawdown zone represents the zone immediately after the terrestrial zone and is interlinked or is part of the overlap zone which connects the drawdown zone and the aquatic zone (Monteith et al., 2006).

The salient point in this physical definition is that the drawdown zone is the direct link with the adjacent terrestrial zone and mediates allochthonous organic and inorganic matter input into the adjacent aquatic system (Monteith et al., 2006). Within the drawdown zone, there is the overlap zone which interlinks the portion of the littoral zone section with the portion close to the terrestrial zone (Figure 4). The overlap zone represents a mixed or transient horizontal and vertical continuum with characteristics of the terrestrial zone in edaphic factors, e.g., soil texture, dissolved oxygen amounts, pH levels, and drainage capacity (Wetzel, 2001; Monteith et al., 2006). The littoral zone represents the immediate section before delving deeper into the pelagic section (Wetzel, 2001) and largely consists of characteristics (e.g., conductivity and redox potential) similar to the aquatic zone. However, some parameters, e.g., total dissolved solids and total suspended matter, indicate a continuum or overlap with the terrestrial part and, in fact, indicate the overlap zone characteristics (Wetzel, 2001; Monteith et al., 2006). The interlinkage of the two zones, i.e., drawdown and littoral, is universal for all reservoirs and has several limnological implications (Furey et al., 2006). What is imperative is for the linkage between drawdown and littoral zones to be disentangled in physical and ecological aspects in order for limnologists to establish the clear roles rather than the current lumping together as the littoral zone for reservoirs (Ostendorp, 2004; Thomaz et al., 2006).

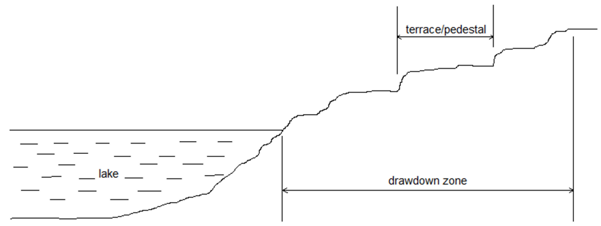

Figure 2. Sideways illustration of the drawdown zone and the pedestal contours or terraces sampled in Manjirenji Dam, Zimbabwe. Adapted from Utete and Tsamba (2016).

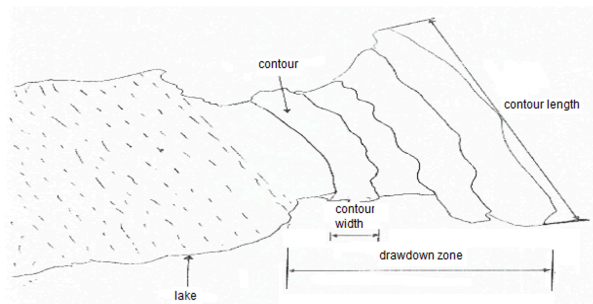

Figure 3. Aerial illustration of the pedestal contours or terraces and its overlap with the littoral zone. Adapted from Utete and Tsamba (2016).

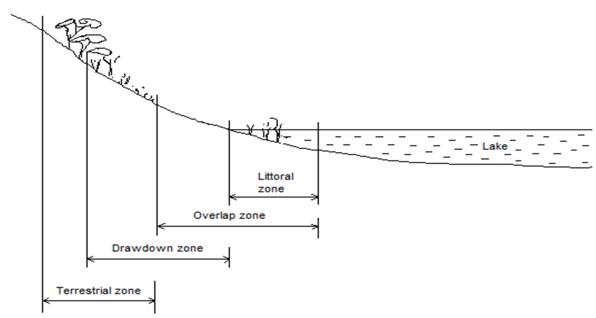

Figure 4. Cross section of a reservoir indicating the drawdown and littoral shoreline overlap zone, and related zones adapted from Monteith et al. (2006).

3.2. Ecology and productivity of drawdown zones in African reservoirs

Drawdown zones contain organic matter like macrophytes that have high decomposition potential (Wetzel, 2001). Decomposing organic matter adds

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nutrients to the drawdown zone and the adjacent littoral zone (Wilson and Baldwin, 2008). This may lead to nutrient pulses and high primary productivity during the inundation stages in drawdown zones (Furey et al., 2006; Wilson and Baldwin, 2008; Zohary and Ostrovsky, 2011). Several studies on phytoplankton, zooplankton, benthic macroinvertebrates, molluscs, potamodromous fish, and water birds have indicated high productivity in the drawdown zone, especially during the inundation phase (Furey et al., 2006; Wilson and Baldwin, 2008; Zohary and Ostrovsky, 2011; Utete et al., 2017). This section examines the ecology and productivity of African reservoirs using available literature.

In Lake Kainji, Nigeria, Obot (1989) indicated different floristic compositions in the drawdown zone arising from the shifting of the ecotone. Obot (1989) asserted that differences in the macrophyte community composition along the drawdown, littoral, and pelagic zones were caused by significant differences in elevational gradients, nutrient types, and amounts among the zones. This observation by Obot (1989) merely highlighted the ecological implications of constant shifts in the drawdown zone during drawdown cycles (Van Geest et al., 2005; Abrahams, 2006; 2008; Utete and Tsamba, 2016). In reservoirs, there is a re-emergence of macrophytes and macroinvertebrates in the inundation phase in the mud edges after a prolonged drying phase (Utete et al., 2017). The recolonisation of the drawdown zone substratum by adaptive macrophytes and macroinvertebrates is attributed to the disparity of nutrients and particle aggregation of the drawdown zone relative to the aquatic and terrestrial phases (McLachlan, 1970a, b, 1971; Utete et al., 2017).

Differences in edaphic factors in the terrestrial, drawdown, overlap, and littoral zones due to underlying geology, topographical, and elevational gradients (Obot, 1989), moisture holding capacity, soil particle aggregation, and infiltration and percolation capacity of each zone (McLachlan, 1971; Gaudet, 1979; Gaudet and Muthuri, 1981) cause differences in macrophyte composition in reservoirs and even natural lakes. Significantly, these studies by McLachlan (1970a, b, 1971), Harper (1982), and Obot (1989) indicated that in the lumped-together littoral or shoreline zones, there are totally different zones which must be clearly identified and assessed in reservoirs and natural lakes in order to fully understand shoreline ecology. The succession of macrophytes, macroinvertebrates, and fish species in reservoirs with clear drawdown cycles implies a need to isolate different stimulants in different zones in the shorelines (Wilson and Baldwin, 2008). Differences in transportation and sedimentation rates in different zones and the presence/absence of littoral pedestals lead to different plant succession and colonisation and spawning rates in the zones, even within the same reservoir (Watts, 2000; Weatherhead and James, 2001; Wetzel, 2001; Furey et al., 2006; Abrahams, 2008; Yamanaka, 2013; Utete et al., 2017). Thus, there is succession and different mosaics of macrophyte life forms at finer spatial scales along different zones in reservoirs.

3.3. Ecological implications of overlapping drawdown and littoral zones in African reservoirs

3.3.1. Sediment and nutrient dynamics

The littoral zone is the most likely to be affected by drawdowns in reservoirs, with fundamental processes such as productivity, sedimentation, remineralisation, denitrification, decomposition, and trophic interactions affected (Furey et al., 2006; Taljaard et al., 2018). Overlapping of drawdown and littoral zones due to drawdown alterations will change sediment characteristics, organic matter decomposition rates, predator-prey relations, flow of energy and matter, and biodiversity in both zones. Systematic analysis of studies in African reservoirs revealed that sediment biogeochemistry differs between the littoral and drawdown zones (Thornton, 1986; Boschilia et al., 2012). Within drawdown zones, there is microstratification of trace elements in sediments because of continuous exposure to oxygen, which leads to the aggregation of particles (Baldwin, 1996). In littoral zones, the aerobic-anaerobic cyclic exposure of trace elements leads to the agglomeration of particles, especially clay, creating a semi-solid mass of sediments (Baldwin, 1996). Consequently, the differences in nutrient aggregation or particle angular orientation lead to variations in mineral bioavailability, with nutrients in the semi-solid phase readily available in the moist littoral zone (Baldwin, 1996; Baldwin and Mitchell, 2000). Loss of fine sediment from the littoral zone to either the drawdown or the pelagic zone decreases nutrient availability over time, but desiccation in drawdown zones may promote a temporary nutrient pulse upon re-inundation (Watts, 2000; Strayer and Findlay, 2010). What is critical from these studies is that drawdowns result in overlaps of drawdown and littoral zones, leading to disequilibria in sedimentation, mineralisation, decomposition, and nutrient retention and distribution in the two zones.

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Research on the nutrient dynamics and stoichiometry in African reservoirs concentrates on assessing the trophic states of the littoral zones and the influence of nitrogen and phosphorus on primary productivity, especially that of phytoplankton and vegetation, e.g., Thornton (1986); Skarpe (1997); Utete and Tsamba (2017). However, the diffusion coefficients, nutrient reflux, and advection rates of nutrients from littoral to drawdown zones are less studied aspects in African reservoirs. A simple insight shows that most of the studies concentrate on the nutrient stoichiometry, particularly the N: P ratio, in the drawdown and littoral zones in relation to its effects on macrophytes (Botschillia et al., 2012), phytoplankton (Carney et al., 1993), macroinvertebrates, and fish productivity (Winfield, 2004; Kolding and Van Zwieten, 2012). This bias towards assessing the N: P ratio in the littoral zone, although justifiable, has been challenged by some researchers, e.g., Utete and Tsamba (2017) and Utete et al. (2017), who indicated that in reservoirs with frequent drawdowns and clear-cut drawdown zones, carbon is a key driver in phytoplankton productivity. Nevertheless, most limnological studies of reservoirs did not investigate the effect of shifting and overlapping drawdown and littoral zones and the key nutrients involved in primary and secondary productivity at each drawdown cycle (Carney et al., 1993; Diaz et al., 2007; Strelin et al., 2014). The type and composition of nutrients differ for each pulse at any phase in the drawdown cycle (Furey et al., 2006; Abrahams, 2008). Thus, there is a need to clearly identify the different zones in the shorelines and then institute stoichiometry studies for comparability of results (Utete and Tsamba, 2017). As it is, most studies (e.g., Carney et al., 1993; Diaz et al., 2007; Strelin et al., 2014; Utete and Tsamba, 2017; Utete et al., 2017) are based on assessments done in the lumped littoral zone without realizing the effects of overlapping littoral and drawdown zones on sediment chemistry and shoreline and lake ecology.

3.3.2. Macrophyte ecology

Various research on macrophyte composition in the overlapping drawdown and littoral zones has been done in reservoirs, e.g., Lake Kariba, Malilangwe Dam, and the Wilderness Lake System in South Africa (Machena and Kautsky, 1988; Skarpe, 1997; Dalu et al., 2012; Taljaard, 2018). Most of the studies indicated that emergent (e.g., *Phragmites australis*) and submerged (e.g., *Potamogeton spp)* macrophytes contribute significantly to in-situ processes by taking up dissolved inorganic nutrients and producing large stocks of organic matter, which drives remineralisation, nitrification, and denitrification (Gessner, 2000). This is relevant in the overlap zone of shallow reservoirs, which often support dense beds of emergent and submerged aquatic vegetation (Thomaz et al., 2006; Utete et al., 2017). Studies on macrophytes in the overlap zones in African reservoirs did not show the actual spatial structuring of the plants at different phases of the drawdown cycles. Rather, most researchers are quick to measure diversity indices and vegetation cover with the common mistake of lumping together drawdown, overlap, and littoral zones as the littoral zone (Utete et al., 2017). How significant species co-occurrence patterns over a specified spatial and temporal scale were generated by the drawdown disturbance, and in which zones the effects were prominent, are some missing key results in most studies on macrophytes in African reservoirs (Leira and Cantonati, 2008).

The effects of elevation or bathymetry of the overlap zone on macrophyte composition have been relatively understudied in African reservoirs, with few examples being Dalu et al. (2013), who focused on the bathymetry, stratification, and physicochemical state of Malilangwe Dam in Zimbabwe but did not make a direct inference to the overall influence of elevation on macrophyte composition in the reservoir. In most of the available studies on macrophytes, the key results have been species composition, cover, and diversity indices in the littoral zone, often mislabeled as the shoreline zone. With ambiguity on zonation, i.e., no clarity on drawdown, overlap, and littoral zones at each phase in the drawdown cycle, the results are misleading as altitudinal gradients are not the only determinants of macrophyte biodiversity (Dalu et al., 2012). The drawdown, overlap, and littoral zones are a transient continuum zone conjoined to the next adjacent zone with ephemeral distinct breaks depending on the extent of the drawdown (Utete and Tsamba, 2016). Thus, the biophysical characteristics in each zone may or may not differ significantly at any time (Utete and Tsamba, 2017). This implies that factors such as edaphic characteristics, bedrock geology, and presence/absence of littoral pedestals, other than ephemeral physicochemical parameters, may be key drivers of macrophyte diversity in the overlap zone. However, for macrophytes with a short life cycle, it is imperative to establish the different zones and key drivers for the succession of the macrophytes on a short term, a task missing in all the studies examined in this review.

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3.3.3. Fish ecology

The ecological significance of the littoral shoreline zone to the diversity of fish species has been appreciated in African reservoirs (Dugan, 2003; Kolding and Van Zwieten, 2012, 2014). However, the complexity and heterogeneity of the littoral zone, especially at the overlap point with the drawdown zone, lead to a poor understanding of local fish ecology in African reservoirs (Winfield, 2004; Kolding and Van Zwieten, 2014; Kolding et al., 2015). Fish species may occupy the littoral zone permanently or visit it on diel, seasonal, or ontogenetic timescales in response to a range of intrinsic and extrinsic factors normally caused by changes in drawdowns (Kolding et al., 2015). Currently, literature focuses on fish ecology in the littoral zone without really demarcating the drawdown, overlap, and littoral zones (Kolding et al., 2015). For instance, the predator-prey dynamics of fish on the shorelines are assessed from an impact point of view (Kolding and Van Zwieten, 2014). This focuses on the predator and predation mechanisms, and the resultant effects on the prey, e.g., stock, recruitment, egg incubation, spawning, and escape mechanisms (Marshall, 2011; Kolding and Van Zwieten, 2014). In the studies of shoreline fish ecology in African reservoirs, there is no attempt whatsoever to delineate these relations in the drawdown, overlap, and littoral zones, which tend to shift in drawdowns (Kolding and Van Zwieten, 2012; Marufu et al., 2018). Rather, the majority of limnological studies indicated that the fish ecology assessments were conducted in the littoral zone, a misleading aspect as there should be clarity on the actual zone in the shoreline (Marshall, 2011; Marufu et al., 2018).

Using the example of an invasive alien species, i.e., the redclaw crayfish, *Cherax quadricarinatus,* which has invaded Lake Kariba in Zimbabwe, Marufu et al. (2018) indicated that the species prefers to colonise the littoral zone where it acts as a predator, competitor, and environmental engineer. What this study, among others, did not assess are the activities of the invasive species in the proper littoral zone, and in the overlap and drawdown zones, and for this species, up to the edge of the drawdown zone or the start of the terrestrial zone in different seasons in the whole Sanyati Basin. Because of the shift in drawdowns in the lake and the presence of littoral pedestals in some sections of the lake, there is seasonality and some variations in food availability in the different zones of the shoreline, which have an effect on the upward migration rates of the invasive species and thus, it exerts varying ecological impacts on the shoreline. A combination of factors needs to be investigated in the drawdown, overlap, and littoral zones in relation to the drawdown phases in order to fully understand fish ecology in the overlapping zones of the shoreline. For more advanced studies, it is inadequate to lump the sections of the shoreline as the littoral zone, and this review suggests that a delineation (zonation) may be necessary and results reported in that format rather than simply stating that studies were conducted in the littoral zone.

In the overlap zone, a large spatially continuous habitat (Strayer and Findlay, 2010), there is a high throughput and exchange of nutrients, organic matter, and energy between aquatic and terrestrial ecosystems, which ensures nutrient-rich sediments and resuspension of vital organic matter that supports fish productivity in African reservoirs, e.g., Lakes Kariba, Cahora Bassa, Volta of Ghana, and Lake Nubia in Egypt (Magadza, 2010; Marshall, 2011; Kolding and Van Zwieten, 2014; Kolding et al., 2015). There are few fisheries assessments that have been conducted which indicated the ecological significance of overlapping zones for productivity and conservation of fish through the protection of eggs and fry in African reservoirs (Kolding et al., 2015). The magnitude and rates of drawdowns in African reservoirs determine fisheries productivity and the livelihoods of fishing-dependent communities (Kolding and Van Zwieten, 2012; 2014). Fish catches are driven by drawdowns, which ensure nutrient pulses and stimulate the onset of egg spawning (Kolding and Van Zwieten, 2012). The important point is for ecologists to consider the relative fish productivity of different zones, i.e., drawdown, littoral, and overlapping zones in African reservoirs, which may need different conservation and management strategies. Hitherto, no studies have attempted a spatiotemporal quantitative and qualitative interpretation of the contribution of the various zones to fish productivity and the overall impact on fisheries in African reservoirs. What this highlights is that zonation of the shoreline into clear distinct zones is key to understanding the different physiological, biochemical, and mechanical dynamics driving fish ecology and productivity in African reservoirs, which is not only driven by dynamics in the pelagic and profundal zones (Gownaris et al., 2016).

3.4. Human utilisation of the drawdown zones in African reservoirs

Humans use drawdown zones for multiple purposes, e.g., agriculture, transportation and landing facilities, mineral exploitation, industry, effluent disposal, recreation, religion and worship, and settlement (Strayer and Findlay, 2010; FAO, 2011; Utete et al., 2017). This section reviews some documented uses of drawdown zones in African reservoirs and explores future research areas.

Drawdown zones have many functions in ecology, species and habitat protection, water resource protection, human settlement and welfare, culture and monument preservation, recreation, crocodile ranching, aquaculture enterprises, fishing, and tourism, etc. (Ostendorp et al., 2004). Further, the drawdown zones are used for flood-based farming or drawdown cultivation with adapted crops such as cassava, rice, and sugarcane commonly planted in the zone (FAO, 2011). In the drawdown zones, there is higher soil moisture and improvement in soil quality due to sedimentation, percolation, and nutrient infiltration, which gives higher crop yields and improves and sustains livelihoods (FAO, 2011). Because of alternating drawdowns, there is cyclic production of crops that utilise drawdowns, where farmers plant in wet drawdown zones, such that some grains thrive even in drought or dry seasons (FAO, 2011). Drawdown zone (shoreline) crops tend to reach the market when there is no rainfall elsewhere, thus fetching good prices and filling in an important seasonal time gap in food security (FAO, 2011). Non-seasonal production of crops allows diversification of livelihood strategies; for instance, most fishers alternate between periods of lean fishing and farming in the drawdown zone (FAO, 2011). The downside to farming in drawdown zones has been the recent heavy application of artificial fertilisers and pesticides by farmers, which inevitably leads to the destruction of aquatic organisms, reducing biodiversity, and posing toxicological threats to fish consumers, e.g., humans (FAO, 2011). Moreover, the constant shifts and recessions of the drawdown zones lead to the continuous movement of artisanal fishing camps, especially in developing countries (FAO, 2011; Kolding and Van Zwieten, 2012, Kolding et al., 2015).

3.4.1. Effects of anthropogenic activities on drawdown zone dynamics

Shorelines are among the most productive and threatened habitats in freshwater reservoirs (Wetzel, 2001; Strayer and Findlay, 2010). Throughout history, societies have developed and intensively utilised drawdown zones for various purposes, in the process diminishing their ecosystem services. Increasing human populations will exert more pressure on drawdown zones in the future (IPCC, 2007; Magadza, 2010; Strayer and Findlay, 2010). As economic expansion and growth continue, there will be more demands on the drawdown zones, with increasingly affluent populations and societies demanding more water resources for agriculture, recreation, harbour construction, and settlements (Nicholls et al., 1999, IPCC, 2007, 2014). Changing drawdowns arising from the interactive effects of human activities and climate change will impact heavily on the areal extent, landscape morphometry, and ecosystem services derived from drawdown zones in African reservoirs (IPCC, 2007, 2014). Documented literature indicates that humans have impacted freshwater drawdown zones by laterally disturbing, compressing, and stabilizing the drawdown zones (Wetzel, 2001), altering hydrologic regimes in the catchment (Kolding and Van Zwieten, 2012), and shortening and simplifying shorelines (Abrahams, 2006, 2008). What has been lacking for African reservoirs is research on habitat surveys (LHS) to assess the modification and impacts of natural and human activities on drawdown zones, as well as the extent of human-wildlife interactions and the impact on drawdown zone utilisation, as was done in Lakes Chivero, Malilangwe, and Cleveland Dams by Dalu et al. (2016) and in Lake Kariba by Magadza (2010).

3.5. Current knowledge, gaps, and recommendations for future research

3.5.1. Current knowledge in African reservoirs

Systematic literature reviews on drawdown zones indicate that for most African reservoirs, sediment and nutrient dynamics have been well studied in limnological studies. Nutrient stoichiometry, mainly based on N and P dynamics in the littoral zones, is well documented in African limnological studies (Thornton, 1986; Utete and Tsamba, 2017). The diversity of macrophytes in the littoral and drawdown zones has been relatively well-studied in African reservoirs (McLachlan and McLachlan, 1971; Njiru et al., 2002). Fish species composition and communities along the drawdown and littoral zones have been well-documented in African reservoirs, although most studies still focus on the pelagic zones. Human utilisation of the drawdown zones for agriculture, fisheries, recreation, and other multipurpose activities is well-documented for some reservoirs, e.g., Lake Kariba, Cahora Bassa, and Volta Dam. It suffices to indicate that the age of the available literature indicates a huge knowledge base in some aspects of the ecology and utilisation of the drawdown zones in African reservoirs.

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3.5.2. Knowledge gaps in African reservoirs

The knowledge of the shoreline zone and its ecology, i.e., structure and function, is incomplete for African reservoirs (Utete and Tsamba, 2016). This information gap originates from the failure to demarcate the shoreline zone into drawdown, overlap, and littoral zones (Figure 3). This is an area where only one study (Utete and Tsamba, 2016) has attempted on one reservoir, Manjirenji, such that there is a need for several studies to fully understand the different zones in the shorelines of reservoirs. This review has provided a working definition for the drawdown zone, which helps in the delineation of the shoreline zone, as most researchers still lump the shoreline zone as the littoral zone following conventional limnology (Wetzel, 2001; Monteith et al., 2006). Apart from delineation challenges, the distribution of nutrients in the different zones of the shoreline, particularly the drawdown and overlap zones at different phases of the drawdown cycle, is a particularly complex area in limnological studies of African reservoirs. The focal point is to comprehend the shoreline ecology, especially with regards to primary productivity, where the N: P ratio is regarded as a basis for production in water systems, whereas some studies regard C and S as key drivers for productivity in shorelines under anoxic conditions (Monteith et al., 2006).

Sedimentation, decomposition, de/nitrification, and other key processes are only understood in the context of the littoral zone (Utete and Tsamba, 2017). Yet, the different rates of mineralisation observed in studies examined attest to differences in sediment exposure to oxygen and the wholesome effect of drying in the drawdown zone, and anoxic bacteria in wet sections of the littoral zone on nutrient availability and shoreline productivity (Thornton, 1986). This is an area with glaring knowledge gaps. The varying effects of elevational gradient and other related antecedent factors on macrophytes in the different zones is an area that is understudied in limnological studies of African reservoirs (Thomaz et al., 2006; Brand et al., 2013; Utete et al., 2017). Macrophyte species co-occurrence patterns over a specified spatial and temporal scale, as generated by the drawdown disturbance, and in which zones the effects are prominent, is a research area that is understudied in African reservoirs. There is no clear understanding of the different roles played by the drawdown, overlap, and littoral zones in fish ecology and fisheries productivity in the shorelines of most African reservoirs, with a simple route being to lump them together under the term littoral zone (Scudder, 2005; Kolding et al., 2015). From the examination of the few available papers on the subject, it appears most researchers do not even attempt to delineate the shoreline zone and simply regard it as the littoral zone and proceed with investigations (Utete and Tsamba, 2016). This is simply undercutting the issue, as the paper has revealed a knowledge gap on the need to delineate the shoreline zone into three and more possible zones for a full understanding of the shoreline ecology and its contribution to the overall lake ecology (Utete et al., 2017).

Humans utilise the drawdown zone for various purposes, with agriculture, fisheries, and recreation as key socioeconomic strategies (Strayer and Findlay, 2010; FAO, 2011). At the same time, human activities destroy and diminish the ecosystem services and value of the drawdown zones (FAO, 2011). The missing link in human utility of drawdown zones is research on building resilience and adaptive capacity of humans in drawdown zones in order to ensure sustainable use for future generations in African reservoirs. As human populations grow and their utilisation of the drawdown zone increases, combined with new developmental technologies and the ever-menacing threats of climate change, the ecology of the drawdown zones and its related zones will be key in limnology (Abrahams, 2006, 2008; Strayer and Findlay, 2010; Dube et al., 2016). Table 1 summarises priority areas for future research in drawdown zones. Cited studies provide examples of potential approaches to enhance understanding of the structure and function of drawdown zones.

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Research Theme	Area of Paucity	Reviewed Literature
Freshwater Biota	No complete inventory of the biota of freshwater drawdown zones in African reservoirs	(Machena and Kautsky, 1988)
Climate Change	Actual climatic factors that are important in controlling the abundance and distribution of species in the drawdown zones	(IPCC, 2014)
Atmospheric Physics	The role of water–air exchange dynamics of gases like oxygen, methane, nitrous oxide, and carbon dioxide, which are potent greenhouse gases	(IPCC, 2014)
Microhabitats And Macrophytes	The physical complexity and diversity of microhabitats of the drawdown zones and their effects on biota in African reservoirs. The socio-economic values of macrophytes in drawdown zones	(Skarpe, 1997; Utete and Tsamba, 2016)
Geomorphology	The combined effect of elevational gradient and exposure gradients on the vegetational zonation in the drawdown zones of African reservoirs Methods of assessing the varying physical nature and complexity of drawdown zones	(Dalu et al., 2016; Dube et al., 2016)
Hydrology	Documented integrated water resources management plans interlinking reservoir drawdowns, managed floods, and drawdown zones in African water systems	(IPCC, 2014; Dalu et al., 2016; Dube et al., 2016)
Agriculture	Benefits to be derived from the utilisation of the drawdown zones, in as much as it is a temporary zone, have been one of the most overlooked opportunities by resettlement and urban planners as well as extension officers	(Scudder, 2005; FAO, 2011)
Ecological Modelling	Drawdown zone ecology and dynamics, especially modelling changes in the littoral pedestals, terraces, and contours' width and heights, demarcation of the zone itself, and extensive soil surveys	(Abrahams, 2008)
Tourism	The significance of the drawdown zones in zoning tourism and hospitality areas, wildlife ranching and access sites, water abstraction points, agricultural and livestock grazing, and commercial fisheries including crocodile ranching areas	(Scudder, 2005)
Limnology	Socio-ecological potential and influence of drawdown zones in African tropical reservoirs	(Marshall 1982a, b; 2011)

Table 1. A summary of priority research and understudied areas for drawdown zones in African reservoirs.

4. Conclusion

Most African reservoirs are located in arid or semi-arid areas and are thus prone to natural water level fluctuations and drawdowns (White et al., 2008; Utete and Tsamba, 2017). As much as natural drawdowns are important in regulating nutrient turnover and movement (into and out of) in water bodies, extreme drawdowns are detrimental to the ecology of aquatic systems and hydrobionts living in the systems (Van Oort et al., 2015). The majority of African reservoirs were built for almost exactly the same purposes, i.e., hydroelectricity generation, agricultural irrigation, and potable (domestic) water abstraction, although other ancillary uses such as fisheries, aquaculture, tourism and recreation, religion, shoreline residential developments, etc., have emerged (Marshall, 2011). Thus, a combination of human-induced drawdowns and climate-driven water level fluctuations across time scales creates marked drawdown zones (Utete and Tsamba, 2016). These drawdown zones, besides serving vital ecological functions, have been utilised by humans for various purposes (Strayer and Findlay, 2010). With rapidly growing African economies, increasing demands for close proximity and access to freshwater supply to sustain population growth and the needs of the agriculture and industrial sectors pose significant threats to water resources (FAO, 2011). Anthropogenic-driven environmental alterations such as land use malpractices, groundwater stress, and deforestation, along with complex political and institutional oversight, inadequate infrastructure, and low adaptive capacity, threaten the integrity of drawdown zones in most African reservoirs. The bottom line is that the paucity of literature (as reflected by the outdated and old-aged articles) used for this review exposes a gap in the study of drawdown zones *per se* in limnology and the impacts of human activities in African reservoirs.

5. Future directions and recommendations for research in drawdown zones of African reservoirs

Real-time geographic information systems (GIS) and remote sensing-based modelling of drawdowns, and the potential loss of commercially valuable drawdown zones, have the potential to benefit downstream communities, ecosystems, and drawdown zone communities, wildlife, and livestock affected by dam construction in African reservoirs (Scudder, 2005; Kolding and Van Zwieten, 2012; Dube et al., 2016; Utete et al., 2017). Most research appears to have overlooked the socio-ecological potential and influence of drawdown zones in African reservoirs. Future research may consider the institutional limitations and governance of water quality and quantity in the drawdown zones as a unique habitat (Scudder, 2005; Abrahams, 2008). Physical complexity, including the elevational gradient and areal extent of drawdown zones, must be assessed at regular intervals for a full comprehension of its ecological roles (Dalu et al., 2016; Dube et al., 2016). There need to be concerted efforts to estimate drawdown zone morphometry and elevation using satellite altimetry and unmanned aerial vehicles (UAVs/drones), which lags far behind for African reservoirs (Dube et al., 2016). Integrated approaches combining climate change and anthropogenic activities towards lake productivity in drawdown zones of reservoirs necessitate interminable studies that quantify multiple characteristics of drawdowns such as the duration, frequency, oscillations, and rate, and the socioeconomic benefits. As much as the drawdown zone is ephemeral (and largely viewed as not very important by many researchers), there is a need for discourse to reconsider its existence, delineation, and ecological and socioeconomic roles in African reservoirs, which is still a missing component in limnology.

Appendix

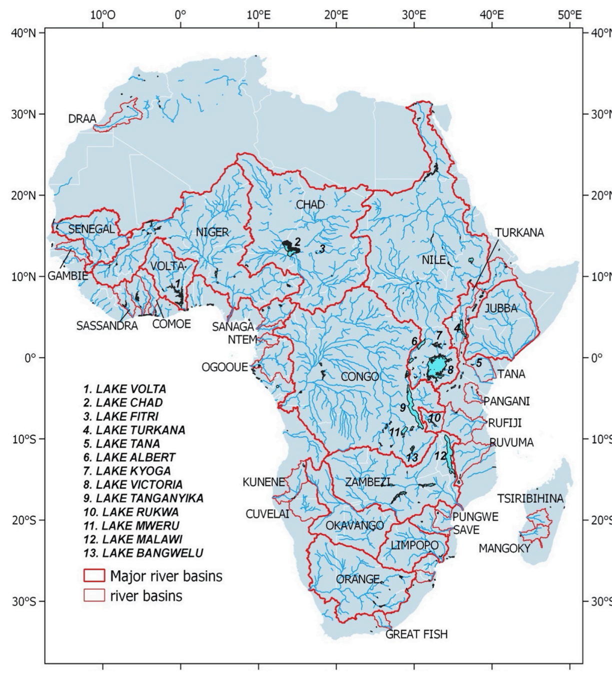

Figure A1. Map showing selected large inland freshwater lakes and reservoirs and rivers in Africa (Source Google, 2022)

Statements and Declarations

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Conflict of Interest

The author declares no conflict of interest for this manuscript.

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