

Influence of waterfalls on patterns of association between trout and Natal cascade frog *Hadromophryne natalensis* tadpoles in two headwater streams in the uKhahlamba Drakensberg Park World Heritage Site, South Africa

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Current literature suggests that little, if any, research has been conducted in South Africa to determine the impact of alien trout on indigenous amphibian biodiversity. The aim of this study was to establish whether waterfalls in the uKhahlamba Drakensberg Park, South Africa, are seasonally important in conserving indigenous Natal cascade frog *Hadromophryne natalensis* tadpole populations from the threat of predation by alien rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* at Injesuthi and Monk's Cowl Nature Reserves, respectively. Relative abundances of trout and tadpoles of Natal cascade frogs were assessed after sampling using electrofishing. Habitat templates were compared for above- versus below-waterfall sites. Trout predation is the most likely causative agent for an observed abrupt decline in *H. natalensis* tadpole abundance occurring below waterfalls. Tadpole abundance in the study was reduced by a factor of 4.69 and 15.71 below the selected waterfalls at Injesuthi and Monk's Cowl in association with *O. mykiss* and *S. trutta* populations, respectively.

Keywords: amphibians, electrofishing, natural barriers, predation

Introduction

Adult amphibians are important carnivores in many systems and are prey species in others (Porter 1972); larval amphibians can be important herbivores (Dickman 1968, Seale 1980, Morin et al. 1990) as well as prey (Duellman and Trueb 1986) in aquatic habitats. Amphibians and reptiles are often considered good indicators of ecological integrity, and therefore knowledge of the status of local amphibian and reptile diversity can be valuable in assessing overall ecosystem integrity (Burton and Likens 1975). Due to their contribution to trophic dynamics in a variety of communities, a global decline in amphibians could have an important impact on other organisms.

Many studies report a negative correlation between the presence of alien predators and the absence of amphibians in natural ecosystems (Kats and Ferrer 2003). Correlative studies typically compare habitats that currently have alien predators to nearby, similar habitats which do not contain alien predators, and provide valuable information into the ecology of invasions and subsequent impacts on amphibians (Diamond and Case 1986, Bradford 1989, Knapp and Matthews 2000, Knapp et al. 2001, Matthews et al. 2001).

In the uKhahlamba Drakensberg Park (UDP), a World Heritage Site, such a dynamic interaction between an indigenous frog species and alien trout has been suspected for some time. The Natal cascade frog *Hadromophryne natalensis* occurs primarily in KwaZulu-Natal, although its distribution range extends into a small portion of the

adjacent Free State province of South Africa, and into Lesotho and Swaziland, over a wide recorded altitudinal range of 580–2 675 m (Boycott 2004). It typically inhabits cool, clear, swift-flowing forested streams. The tadpoles can reach 85–100 mm in length, with metamorphosis taking up to two years (Wager 1965). In the UDP these frogs co-occur in systems where brown and rainbow trout have previously been introduced. Although the frogs are not Red Data listed, they are threatened both by introduced trout and habitat destruction (du Preez and Carruthers 2009).

The history of brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* in the area goes back in excess of 100 years. In 1864 salmon and trout eggs from the United Kingdom were successfully exported across the equator, leading to the establishment of brown trout in Australia, Tasmania and New Zealand (Crass 1986). Following on from these successful introductions, in 1890 John Clarke Parker was the first person successfully to introduce trout into sub-Saharan Africa by stocking brown trout into the Mooi, uMngeni and Bushmans rivers, KwaZulu-Natal (Crass 1986). Rainbow trout were not brought to KwaZulu-Natal until 1899, by which time brown trout were established in several streams (Crass 1964).

The aim of the present study was to establish whether waterfalls in the UDP are seasonally important in conserving indigenous Natal cascade frog *H. natalensis* tadpole populations from the threat of predation by alien rainbow and

brown trout at Injesuthi and Monk's Cowl nature reserves, respectively. Our study followed the approach of previous correlative studies between invasive and indigenous species (Diamond and Case 1986, Bradford 1989, Knapp and Matthews 2000, Knapp et al. 2001, Matthews 2001), and *H. natalensis* tadpole abundance at sampling sites above two selected waterfalls in the UDP, in the absence of trout, was compared to that at sampling sites below these falls, known to be populated by trout.

Materials and methods

While we recognise that the life history of any amphibian is bi-phasic (aquatic and terrestrial stages) and that, ideally, a study should sample adults in their terrestrial habitats and immature stages in their aquatic stages, our study only sampled aquatic habitats. This was in part due to the known difficulty in sampling adult *H. natalensis*, and because the study's focus was on their aquatic stage. The adults are sometimes found quite far from water under vegetation or rocks (du Preez and Carruthers 2009). Males call from under boulders, from deep crevices in rocky ledges or from nearby vegetation in the spray zone of waterfalls and rapids (du Preez and Carruthers 2009). Wager (1965) was unable to find the eggs of this species, despite searching for more than 30 years in all months of the year at different localities. We therefore assumed that the adult stage was not a limiting factor in this study, i.e. that terrestrial habitat was equally suitable in the vicinity of all sites, and that the adult populations were similar at all sites.

Sampling sites

Two headwater streams, the Mobovaneni River at Injesuthi (referred to as Injesuthi or IN) and the Sterkspruit River at Monk's Cowl (referred to as Monk's Cowl or MC), each with waterfall barriers to the upstream migration of fish, were chosen as the study sites within the UDP. Three sampling sites were selected above (sites 1–3) and three below (sites 4–6) each of the selected waterfalls (Figure 1). The six sampling sites located above the two waterfalls, populated by *H. natalensis* tadpoles in the absence of trout, were used as control sites. Conversely, the six sampling sites below the waterfalls, known to be populated by trout, were selected as experimental sites. Sampling sites were further divided into a matrix of 5 m longitudinal \times 0.5 m cross-sectional sampling points by placing knotted ropes marked in 5 m and 0.5 m intervals, respectively. Geophysical features in the form of river biotope type (riffle, run, glide, back eddy, backwater), benthic structure type (bedrock, boulder, stone, cobble, gravel, sand and silt) and depth were recorded at each of these sampling points and used to construct an environmental template in terms of these parameters.

Water quality data collection

Sampling was conducted in September 2007 (spring), February 2008 (summer), May 2008 (autumn) and July 2008 (winter). Spot water quality measurements (pH, electrical conductivity [EC; $\mu\text{S cm}^{-1}$] and dissolved oxygen [DO; mg l^{-1}]) were taken seasonally at each sampling site using a Hanna (HI 991300) pH/EC/TDS/Temperature multimeter and Hanna (HI 9143) DO meter, respectively. Due to

high water levels, pH and EC data were not collected at sampling sites IN2, IN3, IN5, MC2, MC3 and M5 in summer. Monthly average water temperature data were calculated from 1.5-hourly interval temperature time-series collected using Dallas Thermochron® i-Buttons at sampling sites IN1, IN4, IN6, MC1, MC4 and MC6, corresponding broadly to the midpoint axis, upper and lower boundaries of each of the main IN and MC sampling sites. The SASS 5 Rapid Biomonitoring method (Dickens and Graham 2002) was used seasonally at sampling sites IN2, IN5, MC2 and MC5 to assess the biological health of each river section.

Electrofishing

Electrofishing was conducted seasonally at all sampling sites using an AC electrofisher powered by a portable 220 V generator. Electrofishing was done by working upstream for 150 m from each starting point and sampling all available biotope, benthic structure and depth categories. Total fishing time was recorded with a stopwatch, which was intermittently stopped while gathering shocked specimens of either amphibians or fish and subsequently restarted at the resumption of electrofishing. Cork floats attached to lead sinkers were systematically placed in the immediate vicinity where tadpoles or trout had been sampled, and microhabitat data (river biotope type, benthic structure type, depth and water velocity) were noted at these sampling points. Water velocity was estimated using the velocity head rod measurement method (Carufel 1980). The length (mm) of each tadpole was measured and a catch per unit of effort (CPUE) determined based on the number of tadpoles electrofished per minute. No tadpoles were killed or injured during the sampling.

Data analyses

Water quality data were plotted for each respective sampling site. Shapiro-Wilk's test was used to test for normality of the mean monthly water temperature data sets. Water temperature data from sites above the waterfalls were compared to data from sites below the waterfalls using a Student's *t*-test. The mean CPUE of *H. natalensis* tadpoles electrofished seasonally from the combined sampling sites above the waterfalls at IN and MC was compared to that at sites below, using Student's *t*-test for two independent variables. The number of tadpole lengths per 2.5 mm increment was plotted and compared seasonally using line graphs. The preferences of *H. natalensis* tadpoles and trout for specific river biotope types, benthic structure, depths and flow velocity were derived from the field data. Habitat overlaps between trout and *H. natalensis* tadpoles were estimated using a spreadsheet to calculate the proportion of river biotope type, benthic structure type, depth and flow velocity habitat intervals occupied by *H. natalensis* tadpoles and trout, based on species-specific preferences.

Results

Water quality

The pH readings ranged between a minimum of 6.65 at site IN6 in autumn and a maximum of 9.02 at site M3 in autumn. Electrical conductivity ranged between a minimum of 45 $\mu\text{S cm}^{-1}$ at site M4 in summer and a maximum of 105 $\mu\text{S cm}^{-1}$

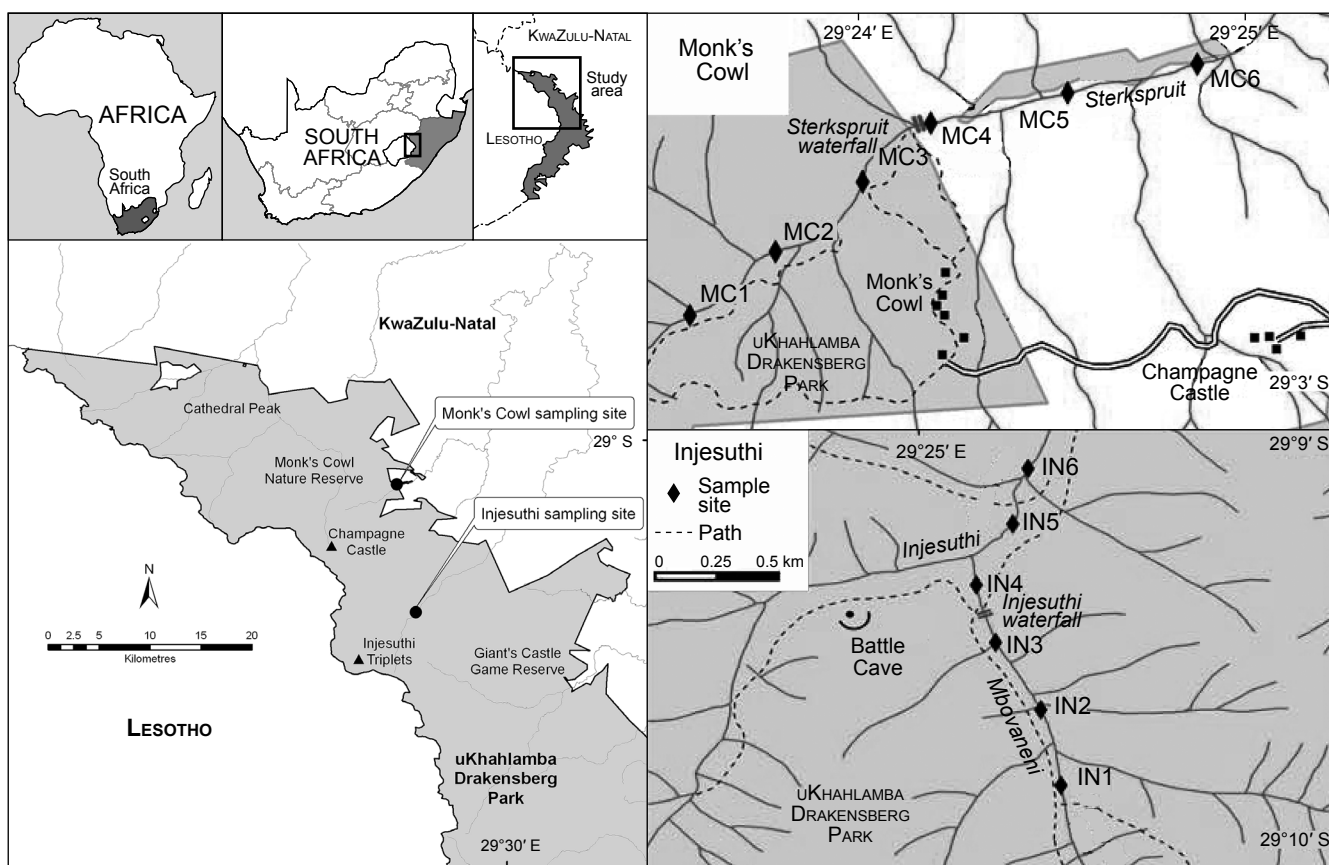


Figure 1: Location of sites that were sampled at Monk's Cowl Nature Reserve (MC) and at Injesuthi (IN) in the Giant's Castle Game Reserve, both in the uKhahlamba Drakensberg Park World Heritage Site, between 1 September 2007 and 31 August 2008

at site IN1 in spring, indicating values commonly associated with oligotrophic ecosystems. DO levels fluctuated between a minimum of 6.40 mg l^{-1} at site IN4 in summer and a maximum of 12.32 mg l^{-1} at site M1 in winter. The SASS average score per taxon (ASPT), determined seasonally at sites IN2, IN5, MC2 and MC5, varied between 6.47 at site M2 and 8.29 at the same site in autumn. All sites showed comparable results and indicated good river health for a mountain stream, i.e. $\text{ASPT} \geq 6$. Mean monthly temperatures were highest in January–February (summer) and lowest in June, July and August (winter) (Figure 2). No temperature records were collected at sites M6 and M4 during February–May 2008 and August–September 2008, respectively, due to the loss of two temperature loggers in the field due to vandalism. No significant differences in the mean monthly water temperature regime occurred between sites IN1 (above the waterfall) and IN6 (below the waterfall) ($t = 0.299$, $\text{df} = 22$, $p = 0.767$). Similarly no significant difference existed between the mean monthly temperature regime at site M1, above the waterfall at MC, and site M6, below it ($t = -0.434$, $\text{df} = 18$, $p = 0.669$).

Electrofishing

The combined mean CPUE of *H. natalensis* tadpoles electrofished above the waterfall at Injesuthi was 0.75 per minute vs 0.16 per minute below it (Table 1). Hence

the mean abundance of *H. natalensis* tadpoles above the waterfall was 4.69 times greater than below it. Similarly, the combined mean CPUE of *H. natalensis* tadpoles electrofished above the waterfall at MC was 1.10 per minute vs 0.07 per minute below it. Hence, the abundance of *H. natalensis* tadpoles at sites above the waterfall at MC was 15.71 times greater than at the sites below it.

The abundance of *H. natalensis* tadpoles was significantly reduced below the waterfall at IN in spring ($t = 3.455$, $\text{df} = 4$, $p = 0.026$) and autumn ($t = 5.509$, $\text{df} = 4$, $p = 0.005$), but not in winter ($t = 4.092$, $\text{df} = 4$, $p = 0.049$). Similarly, the abundance of *H. natalensis* tadpoles was found to be significantly reduced below the selected waterfall at MC during spring ($t = 0.455$, $\text{df} = 4$, $p = 0.026$) and autumn ($t = 5.509$, $\text{df} = 4$, $p = 0.005$), but not in winter ($t = 4.092$, $\text{df} = 4$, $p = 0.049$).

Seasonal size classes of *H. natalensis* tadpoles

The total length of *H. natalensis* tadpoles electrofished in spring was compared with that of those electrofished in summer. A broadly bi-modal tadpole length distribution occurred in both spring and summer (Figure 3). The emergence of a new young tadpole cohort (25–50 mm) in summer suggests that adult frogs had bred between the spring and summer sampling periods. The younger generation of tadpoles (40–60 mm) occurring in spring had

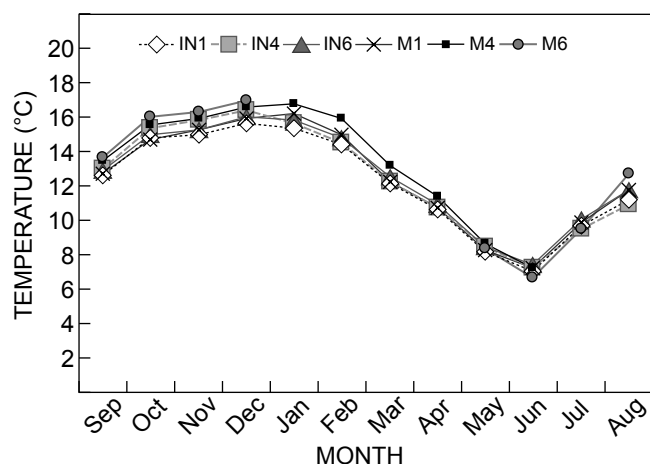


Figure 2: Mean monthly water temperature recorded at sampling sites IN1, IN4, IN6, M1, M4 and M6 between 1 September 2007 and 31 August 2008 (IN1 — Injesuthi 1, IN4 — Injesuthi 4, IN6 — Injesuthi 6, M1 — Monk's Cowl 1, M4 — Monk's Cowl 4 and M6 — Monk's Cowl 6)

Table 1: Percentage change in tadpole catch per unit effort (CPUE) occurring above and below selected waterfalls at Injesuthi and Monk's Cowl, based on spring (September 2007), autumn (May 2008) and winter (July 2008) electrofishing results

Season	CPUE			
	Injesuthi		Monk's Cowl	
	Above waterfall	Below waterfall	Above waterfall	Below waterfall
Spring	0.54	0.02	2.10	0.02
Autumn	1.01	0.30	1.00	0.06
Winter	0.48	0.09	0.83	0.09
Mean	0.75	0.16	1.10	0.07
% Change	-469		-1 571	

probably matured into yearlings (60–80 mm) by summer and the largest tadpoles (70–100 mm) present in spring had developed into adult frogs by summer.

Habitat overlap between *H. natalensis* tadpoles and trout

The greatest degree of habitat overlap between *H. natalensis* tadpoles and trout occurred in run, riffle and glide biotopes associated with gravel, stone and boulder benthic structure. *H. natalensis* tadpoles had a strong positive correlation with river biotope type, subsequently categorised in descending order of associated current velocity ($r = 0.94$) and benthic structure ranked in descending order of particle size ($r = 0.84$). Conversely, trout showed a weak relationship with fast-flowing river biotope types ($r = 0.26$) and a moderate association ($r = 0.66$) with benthic structure ranked in descending order of particle size. *H. natalensis* tadpoles showed a distinct preference (66%) for fast-flowing riffles, but were seldom encountered in pools, whereas trout occurred most commonly (43%) in slow-flowing pools and less frequently (17%) in riffles. Both *H. natalensis* tadpoles and trout displayed tendencies of avoiding benthic structure dominated by silt, sand and bedrock, suggesting that a lack

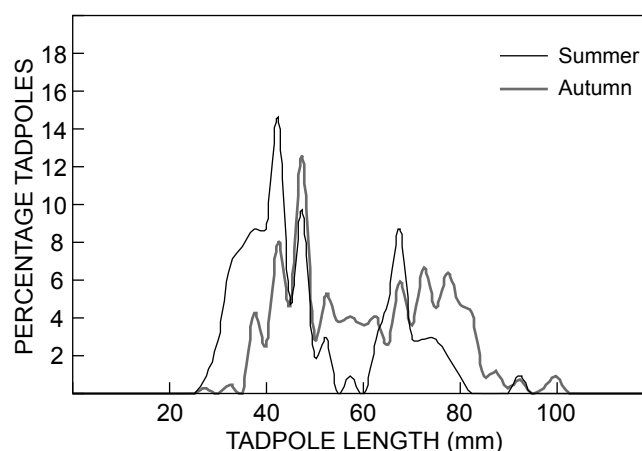


Figure 3: Length distribution of tadpole cohorts measured at all sampling sites during the summer (December 2007) and autumn (May 2008) sampling periods

of associated cover may be an issue. The apportionment of habitat overlap occurring between trout and *H. natalensis* tadpoles, relative to depth and flow velocity preferences, was 27.43% and 42.08%, respectively (Figure 4).

Discussion

Electrofishing results indicated a marked reduction (4.69 and 15.71 times for IN and MC, respectively) in their *H. natalensis* tadpole abundance below the waterfalls at IN and MC, in the presence of *S. trutta* and *O. mykiss* populations, respectively. The greater effect of trout on the tadpoles at MC can be attributed to the greater abundance of trout at MC. The overall mean CPUE (all seasons) of brown trout electrofished at MC was 0.27 per minute vs 0.10 per minute at IN. The abundance of brown trout at MC was therefore 2.7 times higher than that of rainbow trout at IN. The greater abundance of trout at MC vs IN is the result of a combination of more suitable habitat conditions relative to altitude, gradient, cover, biotope and benthic structure. Knapp and Matthews (2000) also found that the abundance of yellow-legged frog *Rana muscosa* tadpoles in the Sierra Nevada was reduced by 6.8 times in water bodies containing trout compared to that in those free of trout. Our results correlate closely with the research findings of Watson et al. (1991) that show that alien trout have played a major role in the decline of the spotted tree frog *Litoria spenceri* in Australia. *Litoria spenceri* was last seen along Buffalo Creek, a near pristine stream in north-eastern Victoria, coinciding with the first reports of trout in this stream (Watson et al. 1991). Similarly, *L. spenceri* was found to occur in high densities along a short reach of the Bogong Creek, Kosciuszko National Park, New South Wales (Gillespie and Hollis 1996, Hunter and Gillespie 1999). This population was restricted to this short reach, only 1.6 km long, which is inaccessible to trout due to the presence of high waterfalls (Hunter and Gillespie 1999).

The geophysical environmental templates occurring at our sites, both above and below the waterfalls, were environmentally similar, suggesting that geophysical habitat conditions

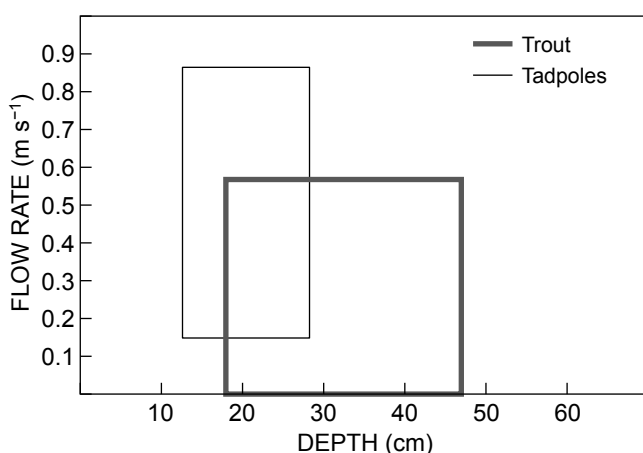


Figure 4: Habitat overlap model between tadpoles ($n = 743$) and trout ($n = 83$) at all sampling sites based on spring (September 2007), summer (December 2007), autumn (May 2008) and winter (July 2008) electrofishing results

alone cannot quite account for the abrupt decline in *H. natalensis* tadpole abundance below the waterfalls. All sites, both above and below the waterfalls, displayed similar pH, EC and DO measurements, and good river health using the SASS 5 biomonitoring technique. Mean monthly water temperatures at sites above the waterfalls vs sites below them were significantly similar in terms of thermal regimes. The importance of water temperature to aquatic biodiversity has been documented by Claska and Gilbert (1998) and Eaton and Scheller (1996). Stuckenberg (1969) also highlighted the links between water temperature, topography and faunal assemblages of snakes and amphibians. Water temperature differences between the sites therefore cannot account for the significant decreases in tadpole abundance below the waterfalls at IN and MC.

Waterfalls have similarly been shown to be of conservation importance in the UDP study by functioning as natural barriers to the upstream migration of predatory *O. mykiss* and *S. trutta*. Trout now occur in all streams in south-eastern Australia where *L. spenceri* has disappeared (Gillespie and Hollis 1996). In south-eastern Australia at least five other riverine frog species have now declined in upland streams (Anstis and Littlejohn 1996, Tyler 1997, Gillespie and Hines 1999) due to trout predation.

Other studies supporting the theory that amphibians either do poorly or are eliminated in the presence of trout due to high mortality rates include *O. mykiss* vs European common brown frog *Rana temporaria* (Nyström et al. 2001), *O. mykiss* vs *L. spenceri* (Gillespie 2001); *O. mykiss* vs leaf green tree frog *Litoria phyllochroa* (Gillespie 2001), *O. mykiss* vs long-toed salamander *Ambystoma macrodactylum* (Tyler et al. 1998) and *O. mykiss* vs northwestern salamander *A. gracile* (Tyler et al. 1998). Feminella and Hawkins (1994) observed a threefold reduction in the activity of tadpoles when exposed to cutthroat trout *O. clarkia* and sixfold when exposed to brook trout *Salvelinus fontinalis*, as compared with unexposed tadpoles.

The bimodal length distribution of *H. natalensis* tadpoles in our study confirms that *H. natalensis* tadpoles in the UDP

have a two-year larval phase, as was previously suggested by Wager (1965). Knapp and Matthews (2000) state that most amphibians utilise shallow water bodies and complete their metamorphosis within weeks or months, whereas in the high elevation habitats of the Sierra Nevada *R. muscova* tadpoles have an extended larval period of two to four years (Zwiefel 1955), prolonging the risk of predation, as in the perceived case of *H. natalensis* tadpoles. Alien predators have almost exclusively affected amphibians with complex life cycles (egg and larval stages) (Stebbins and Cohen 1995). Amphibian eggs and aquatic larvae are particularly vulnerable to alien aquatic predators, with fish being the most common alien predator of amphibians (Stebbins and Cohen 1995). *H. natalensis* tadpoles also have complex life cycles based on a prolonged larval stage and a dependence on cool, clear, swift-flowing water conditions. Both *O. mykiss* and *S. trutta* are listed as some of the world's top 100 worst alien invasive species in terms of the Global Invasive Species Programme (Lowe et al. 2000). Our results clearly show that *H. natalensis* tadpole populations are greatly reduced in the presence of trout, and that waterfalls are ecologically important in respect to the survival and continued persistence of *H. natalensis* populations in the UDP.

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References

- Anstis M, Littlejohn MJ. 1996. The breeding biology of *Litoria subglandulosa* and *L. citropa* (Anura: Hylidae), and a re-evaluation of their geographic distribution. *Transactions of the Royal Society of South Australia* 122: 33–34.
- Boycott RC. 2004. Natal ghost frog *Heleophryne natalensis*. In: Minter LR, Burger M, Harrison JA, Braack HH, Bishop PJ, Kloepfer D (eds), *Atlas and Red Data Book of frogs of South Africa*. Smithsonian Institution/Monitoring and Assessment of Biodiversity Program SIMAB Series #9. Washington: Smithsonian Institute. pp 100–101.
- Bradford DF. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes: implication of the negative effect of fish introductions. *Copeia* 4: 966–976.
- Burton TM, Likens GE. 1975. Salamander populations and biomass in the Hubbard Brook experimental forest, New Hampshire. *Copeia* 3: 541–546.
- Carufel LH. 1980. Construction and use of a velocity head rod for measuring stream velocity and flow. BLM/AK Technical Report 5. Anchorage: US Department of the Interior, Bureau of Land Management, Alaska State Office.
- Claska ME, Gilbert JJ. 1998. The effect of temperature on the response of *Daphnia* to toxic cyanobacteria. *Freshwater Biology* 39: 221–232.
- Crass RS. 1964. *Freshwater fishes of Natal*. Pietermaritzburg: Shuter and Shooter. p 39.
- Crass RS. 1986. *Trout in South Africa*. Johannesburg: McMillan South Africa. pp 135–147.
- Diamond JM, Case TJ. 1986. *Community ecology*. New York: Harper and Row. pp 65–79.
- Dickens C, Graham M. 2002. South African Scoring System (SASS) version 5 rapid bio-assessment method for rivers. *South African Journal of Aquatic Science* 27: 1–10.

- Dickman M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. *Ecology* 49: 1188–1190.
- Duellman WE, Trueb L. 1986. *Biology of amphibians*. New York: McGraw-Hill. p 670.
- du Preez L, Carruthers V. 2009. *A complete guide to the frogs of southern Africa*. Cape Town: Struik Nature. pp 196–199.
- Eaton JG, Scheller RM. 1996. Effects of climate on fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41: 1109–1115.
- Feminella JW, Hawkins CP. 1994. Tailed frog tadpoles differentially alter their feeding behaviour in response to non-visual cues from four predators. *Journal of the North American Benthological Society* 13: 310–320.
- Gillespie GR. 2001. The role of introduced trout in the decline of the spotted tree frog *Litoria spenceri* in south-eastern Australia. *Biological Conservation* 100: 187–198.
- Gillespie GR, Hines HB. 1999. Status of temperate riverine frogs in south-eastern Australia. In: Campbell A (ed.), *Declines and disappearances of Australian frogs*. Canberra: Environment Australia. pp 109–130.
- Gillespie GR, Hollis GJ. 1996. Distribution and habitat of the spotted tree frog *Litoria spenceri* (Anura: Hylidae), and an assessment of potential causes of population declines. *Wildlife Research* 23: 49–75.
- Hunter D, Gillespie GR. 1999. The distribution, abundance and conservation status of riverine frogs in Kosciuszko National park. *Australian Zoologist* 31: 198–209.
- Kats LB, Ferrer RP. 2003. Alien predators and amphibian declines: review of two decades of science and transition to conservation. *Diversity and Distributions* 9: 99–110.
- Knapp RA, Matthews KR. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. *Conservation Biology* 14: 428–438.
- Knapp RA, Matthews KR, Sarnelle O. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs* 71: 401–421.
- Lowe S, Browne M, Boudjelas S, De Poorter M. 2000. 100 of the world's worst invasive alien species: a selection from the Global Invasive Species Database. Auckland: IUCN/SSC invasive species specialist group (ISSG).
- Matthews KR, Pope KL, Preisler HK, Knapp RA. 2001. Effects of non-native trout on Pacific tree frogs *Hyla regilla* in the Sierra Nevada. *Copeia* 4: 1130–1137.
- Morin PJ, Lawler SP, Johnson EA. 1990. Ecology and breeding phenology of larval *Hyla andersonii*: the disadvantage of breeding late. *Ecology* 71: 1590–1598.
- Nyström P, Svensson O, Lardner B, Brönmark, Graneli W. 2001. The influence of multiple introduced predators on a littoral pond community. *Ecology* 82: 1023–1103.
- Porter KR. 1972. *Herpetology*. Philadelphia, Pennsylvania: WB Saunders Company.
- Seale DB. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. *Ecology* 61: 1531–1550.
- Stebbins RC, Cohen NW. 1995. *A natural history of amphibians*. New Jersey: Princeton University Press.
- Stuckenberg BR. 1969. Effective temperature an ecological factor in southern Africa. *Zoological Africana* 4: 145–197.
- Tyler MJ. 1997. *The action plan for Australian frogs*. Canberra: Wildlife Australia: Department of sustainability, environment, water, populations and communities.
- Tyler T, Liss WJ, Ganio LM, Larson GL, Hoffman R, Deimling E, Lomnický G. 1998. Interaction between introduced trout and larval salamanders *Ambystoma macrodactylum* in high elevation lakes. *Conservation Biology* 12: 94–105.
- Wager VA. 1965. *Frogs of South Africa*. Cape Town: Purnell and Sons. pp 99–102.
- Watson GF, Littlejohn MJ, Hero J-M, Robertson P. 1991. *Conservation status, ecology and management of the spotted tree frog Litoria spenceri*. Arthur Rylah Institute Technical Report Series No. 116. Victoria, Australia: Department of Conservation and Environment.
- Zwiefel RG. 1955. Ecology, distribution and systematics of the frogs of the *Rana boylei* group. *University of California Publications in Zoology* 54: 207–292.